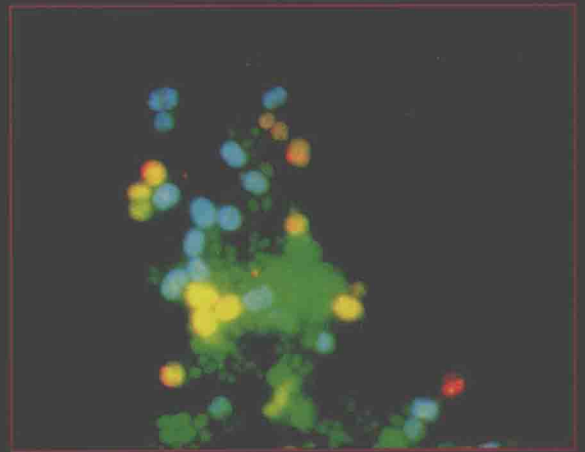
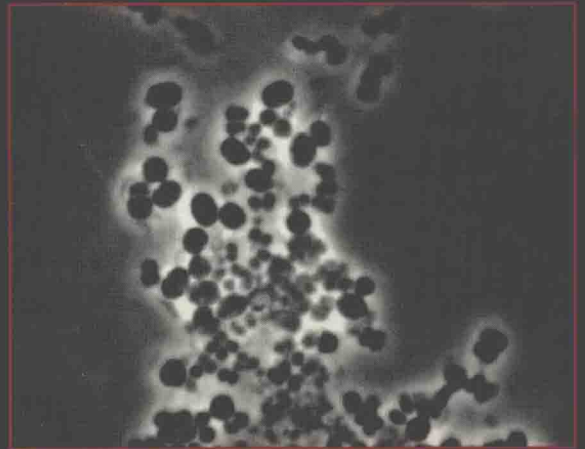


INTERNATIONAL EDITION

BROCK
BIOLOGY
OF
MICROORGANISMS



TENTH EDITION

MICHAEL T. MADIGAN

JOHN M. MARTINKO

JACK PARKER

Tenth Edition

BROCK

**BIOLOGY OF
MICROORGANISMS**

Michael T. Madigan

John M. Martinko

Jack Parker

Southern Illinois University Carbondale

Prentice
Hall

Pearson Education International

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

Executive Editor: Gary Carlson
Editor-in-Chief, Life and Geosciences: Sheri L. Snavelly
Production Editor: Debra A. Wechsler
Vice President of Production and Manufacturing:
David W. Riccardi
Executive Managing Editor: Kathleen Schiaparelli
Senior Marketing Manager for Biology: Martha McDonald
Executive Marketing Manager for Biology:
Jennifer Welchans
Assistant Manufacturing Manager: Michael Bell
Manufacturing Manager: Trudy Piscioti
Director of Creative Services: Paul Belfanti
Creative Director: Carole Anson
Art Director: Kenny Beck
Interior Designer: Susan Anderson
Assistant Managing Editor, Science Media: Nicole Bush

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

Development Editor: Carol Pritchard-Martinez
Editor-in-Chief, Development: Carol Truehart
Assistant Managing Editor, Supplements: Dinah Thong
Media Editor: Andrew Stull
Managing Editor, Audio/Video Assets: Patricia Burns
Art Editor: Adam Velthaus
Copy Editor: Jane Loftus
Editorial Assistants: Susan Zeigler, Lisa Tarabokjia,
Nancy Bauer

Illustrator: Imagineering
Cover Designer: Maureen Eide
Cover Photos: Reproduced by permission of the American
Society for Microbiology from A. T. Nielsen et al. 1999.
Applied Environmental Microbiology 65:1251–58, Fig. 5B.
Image courtesy of Alex T. Nielsen, Technical University
of Denmark, Lyngby, Denmark.

This edition may be sold only in those countries to which it is consigned by Pearson Education International. It is not to be re-exported and it is not for sale in the U.S.A., Mexico, or Canada.



© 2003 Pearson Education, Inc.
Pearson Education, Inc.
Upper Saddle River, NJ 07458

© 1984, 1979 by Thomas D. Brock

First through seventh editions titled *Biology of Microorganisms*

All rights reserved. No part of this book may be reproduced, in any form or by any other means, without permission in writing from the publisher.

Printed in the United States of America

10 9 8 7 6 5 4 3

ISBN 0-13-049147-0

Pearson Education LTD., London
Pearson Education Australia PTY, Limited, Sydney
Pearson Education Singapore, Pte. Ltd.
Pearson Education North Asia Ltd., Hong Kong
Pearson Education Canada Ltd., Toronto
Pearson Education de Mexico, S.A. de C.V.
Pearson Education—Japan, Tokyo
Pearson Education Malaysia, Pte. Ltd.
Pearson Education, Upper Saddle River, New Jersey

BROCK BIOLOGY OF MICROORGANISMS

New Organization

The Tenth Edition is completely reorganized into six units that group chapters together within a major theme, allowing you to easily relate thematic coverage to core materials and to the goals of your course. This edition also features seven new chapters

NEW! Unit I forms the heart of the general microbiology course as envisioned by the Education Division of the ASM.

NEW! Chapter 2 provides an early overview of microbial diversity.

Chapter 9 emphasizes the core concepts of virology. (Chapter 16 explores viral diversity in more detail.)

Chapter 10 was rewritten to better reflect bacterial genetics as it is actually practiced today—a blend of in vivo and in vitro science.

NEW! Chapter 15 covers the essentials of the microbial genomics projects, from bacteria to yeast.

NEW! Chapter 16 allows instructors to easily choose those viral examples they wish to emphasize as a supplement to the essentials material in Chapter 9.

NEW! Chapter 18 emphasizes methods.

I. PRINCIPLES OF MICROBIOLOGY

1. Microorganisms and Microbiology
2. An Overview of Microbial Life
3. Macromolecules
4. Cell Structure/Function
5. Nutrition, Laboratory Culture, and Metabolism of Microorganisms
6. Microbial Growth
7. Principles of Microbial Molecular Biology
8. Regulation of Gene Expression
9. Essentials of Virology
10. Bacterial Genetics

II. EVOLUTIONARY MICROBIOLOGY AND MICROBIAL DIVERSITY

11. Microbial Evolution and Systematics
12. Prokaryotic Diversity: *Bacteria*
13. Prokaryotic Diversity: *The Archaea*
14. Eukaryotic Cell Biology and Eukaryotic Microorganisms
15. Microbial Genomics
16. Bacterial, Plant, and Animal Viruses

III. METABOLIC DIVERSITY AND MICROBIAL ECOLOGY

17. Metabolic Diversity
18. Methods in Microbial Ecology

19. Microbial Habitats, Nutrient Cycles, and Interactions with Plants and Animals

IV. IMMUNOLOGY, PATHOGENICITY, AND HOST RESPONSES

20. Microbial Growth Control
21. Human–Microbe Interactions
22. Essentials of Immunology
23. Molecular Immunology
24. Clinical Microbiology and Immunology

V. MICROBIAL DISEASES

25. Epidemiology
26. Person-to-Person Microbial Diseases
27. Animal-Transmitted, Arthropod-Transmitted, and Soilborne Microbial Diseases
28. Wastewater Treatment, Water Purification, and Waterborne Microbial Diseases
29. Food Preservation and Foodborne Microbial Diseases

VI. MICROORGANISMS AS TOOLS FOR INDUSTRY AND RESEARCH

30. Industrial Microbiology/Biocatalysis
31. Genetic Engineering and Biotechnology

Chapter 19 covers habitats and microbial ecology without including material on methods.

NEW! Two new chapters on immunology: Chapter 22 covers the essentials and Chapter 23 covers the molecular details.

Chapter 24 includes expanded coverage of immunoassays.

Coverage of diseases now spans five chapters instead of two.

NEW! Three new chapters on these important topics in microbiology.

Chapters 30 and 31 have been grouped into their own unit to better reflect their common goals and contrast their industrial production methods.

Section Numbers keyed to page numbers provides easy reference points.

New “Superheads” more effectively organize chapter contents.

The working glossary is the students’ guide to the language of microbiology. Understanding these terms is key to mastery of the concepts in the chapter.



5.1 ■ MICROBIAL NUTRITION ■ 103

WORKING GLOSSARY

Activation energy the energy required to bring substrates to the reactive state

Aerobe a microorganism able to use O₂ in respiration

Anabolism the sum total of all biosynthetic reactions in the cell

Anaerobe a microorganism that either can or must grow in the absence of O₂

Aseptic technique the series of manipulations used to prevent contamination during the handling of sterile objects or microbial cultures

ATP synthase (ATPase) A multiprotein enzyme complex embedded in the membrane that catalyzes the synthesis of ATP coupled to dissipation of the proton motive force

Autotroph an organism capable of biosynthesizing all cell material from CO₂ as the

Coenzyme a small nonprotein molecule that participates in a catalytic reaction as part of an enzyme

Complex medium a culture medium composed of digests of chemically undefined substances such as yeast and meat extracts

Culture medium an aqueous solution of various nutrients suitable for the growth of microorganisms

Defined medium a culture medium whose precise chemical composition is known

Electron acceptor a substance that can accept electrons from some other substance, thereby becoming reduced in the process

Electron donor a substance that can donate electrons to some electron acceptor, thereby becoming oxidized in the process

glucose is fermented yielding energy (ATP) and various fermentation products. Also called the Embden-Meyerhof pathway

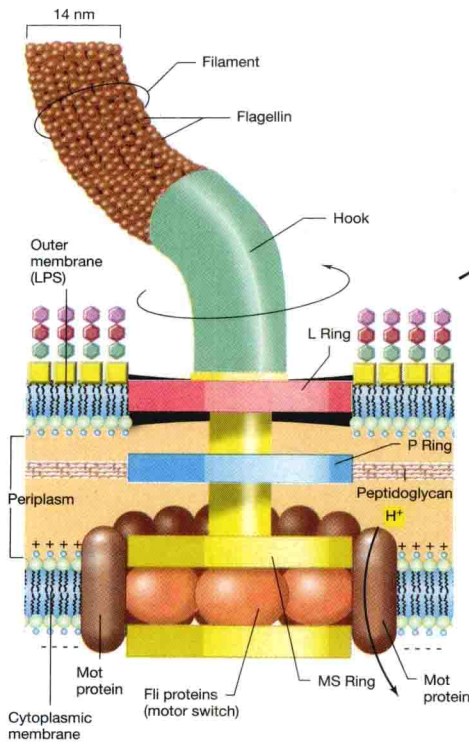
Oxidative phosphorylation the production of ATP at the expense of a proton motive force formed by electron transport

Photophosphorylation the production of ATP from a proton motive force formed from photosynthetic reactions

Proton motive force an energized state of the membrane resulting from the separation of charge and the elements of water (H⁺ versus OH⁻) across the membrane

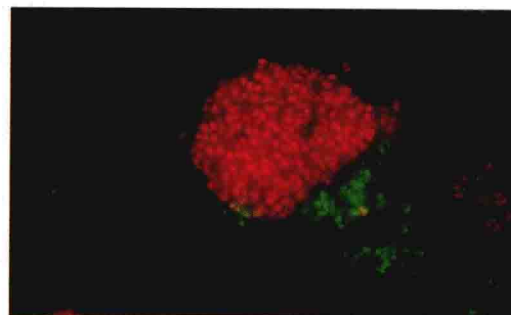
Pure culture a culture that contains a single kind of microorganism

Reduction potential the inherent tendency (measured in volts) of a compound to donate electrons; E₀' is reduction



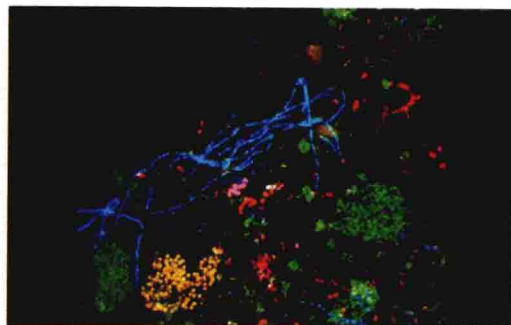
The exceptional art program has been thoroughly reviewed and adjusted to maximize its impact and clarity.

Outstanding micrographs, most obtained from researchers in the field.



(a)

David A. Stahl



(b)

Jiri Svoboda

A Focus On ... The Power of Metabolic Diversity: A Novel Nitrogenase

Tritrogenases have been characterized from a wide variety of prokaryotes, including some Archaea, and all of them show significant sequence homology at both the gene and polypeptide level. All of them, that is, until the nitrogenase from the streptomycete *Streptomyces thermoautotrophicus* was characterized.¹

S. thermoautotrophicus is a thermophilic (optimum temperature 65°C), gram-positive, filamentous prokaryote that occurs naturally in burning compost and charcoal piles (Figure 1). The organism is an aerobic

chemolithotrophic H_2 bacterium that can also use carbon monoxide (CO) as an electron donor. Although *S. thermoautotrophicus* has been known to be a nitrogen fixer for some time, some unusual properties of its nitrogen fixation system (like the fact that ammonia did not repress nitrogenase synthesis and that the enzyme did not reduce acetylene) prompted a more detailed examination of its nitrogenase. What was found represents a totally new paradigm for N_2 fixation.

The *S. thermoautotrophicus* nitrogenase contains Mo, but unlike classic Mo nitrogenase, it is completely insensitive to O_2 . The dinitrogenase component of the *S. thermoautotrophicus* nitrogenase, called Str1, contains three different polypeptides that show some structural similarity to dinitrogenase polypeptides from other nitrogen-fixers, but the dinitrogenase reductase component, called Str2, shows no similarity to other dinitrogenase reductases. However, Str2 shows very high sequence similarity to manganese-containing superoxide dismutases. In fact Str2 is a superoxide dismutase! Recall from Chapter 6 (Section 6.13) that superoxide dismutases function in the cell to consume superoxide HO_2^- , forming O_2 in the process and thus preventing oxidative damage to cell components. But what does superoxide have to do with nitrogen fixation?

It has been shown that Str2 supplies electrons to Str1. The source of the electrons is O_2^- , and the O_2^- is formed from the

reduction of O_2 by a CO dehydrogenase (Figure 2). Thus, in analogy to the pyruvate : flavodoxin : dinitrogenase reductase : dinitrogenase sequence in classical nitrogen-fixation (see Figure 17.70), in *S. thermoautotrophicus* the sequence is CO : O_2^- : Str2 : Str1. And, astonishingly, instead of O_2 -inhibiting nitrogenase (as it does in every nitrogenase that has ever been examined), in *S. thermoautotrophicus* O_2 is actually required in the reaction mechanism of the enzyme!

Clearly, *S. thermoautotrophicus* nitrogenase is a structurally and functionally unique nitrogen-fixing system. How widespread such a system is and whether its primary function in the cell is actually to fix N_2 , is as yet unknown. However, the *S. thermoautotrophicus* nitrogenase system is a good example of the power of metabolic diversity in prokaryotes. Even well-studied systems in which conformity prevails can occasionally yield big surprises and totally new concepts. Discovery of the *S. thermoautotrophicus* nitrogenase system has also renewed hope for the eventual genetic engineering of nitrogenase into agricultural crops such as corn. The fact that this nitrogenase is not oxygen labile and its energy requirements are much lower than those of classical nitrogenases (measurements show the *S. thermoautotrophicus* system to use only 25–50% of the ATP of classic Mo nitrogenases), see Figure 17.70) could make the dream of nitrogen-fixing row crops a reality someday. ■



Figure 1 Two burning charcoal piles in the Bavarian forest, Germany, containing cells of the N_2 -fixing bacterium, *Streptomyces thermoautotrophicus*. The scientist shown is doing temperature measurements at various points in the piles. The piles has gases of CO_2 , CO, CH_4 , and C_2H_2 , and vary in temperature with depth. The surface to about 15 cm into the piles have temperatures of less than 100°C but deeper into the piles, temperatures can be over 300°C.

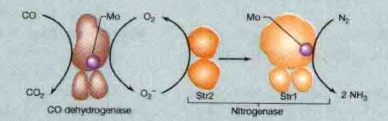


Figure 2 Reactions of nitrogen fixation in *S. thermoautotrophicus*.

¹Hilbe, M., D. Gaskart, and O. Meyer, 1997. *J. Biol. Chem.* 272: 26627–26633.

Interesting scientific asides in boxed inserts—Techniques and Application boxes describe methods in microbiology and their application in the real world; Learning from the Past boxes describe historical developments in microbiology and their implications today; A Focus On boxes address text topics in greater detail.

Completely redesigned graphs facilitate student comprehension.

The maximum growth temperature of a given organism most likely reflects the inactivation of one or more key proteins in the cell. However, the factors controlling an organism's minimum growth temperature are not as clear. As mentioned earlier (Section 4.5), the cytoplasmic membrane must be in a fluid state for proper functioning. Perhaps the minimum temperature of an organism results from "freezing" of the cytoplasmic membrane so it no longer functions properly in nutrient transport or proton gradient formation. This explanation is supported by experiments in which the minimum temperature for an organism is altered to some extent by adjustments in membrane lipid composition (see Section 6.9). It is also observed that the cardinal temperatures of different microorganisms differ widely; some organisms have temperature optima as low as 4°C and some higher than 100°C. The temperature range throughout which growth occurs is even wider than this, from below freezing to greater than boiling. (The archaeon *Pyrolobus fumarii* has a temperature maximum of 113°C!) However, no single organism can grow over this whole temperature range, and the typical range for a given organism is about 30°, although some have a broader temperature range than others.

Temperature Classes of Organisms

Although there is a continuum of organisms, from those with very low temperature optima to those with high temperature optima, it is possible to broadly distinguish four groups of microorganisms in relation to their temperature optima: **psychrophiles**, with low temperature optima, **mesophiles**, with midrange temperature optima, **therm-**

ophiles, with high temperature optima, and **hyperthermophiles**, with very high temperature optima (Figure 6.17). Mesophiles are found in warm-blooded animals and in terrestrial and aquatic environments in temperate and tropical latitudes. Psychrophiles and thermophiles are found in unusually cold and unusually hot environments, respectively. Hyperthermophiles are found in extremely hot habitats such as hot springs, geysers, and deep-sea hydrothermal vents (see Sections 6.10 and 19.8).

In *Escherichia coli*, a typical mesophile, a detailed study of growth as a function of temperature has precisely defined its cardinal temperatures. The optimum temperature of *E. coli* in a complex medium is 39°C, the maximum is 48°C, and the minimum is 8°C. These values are subject to slight strain differences, and in general, the maximum and minimum temperatures supporting growth of an organism are higher and lower, respectively, when tested in complex rather than defined media.

✓ 6.8 Concept Check

Temperature is a major environmental factor controlling microbial growth. The cardinal temperatures describe the minimum, optimum, and maximum temperatures at which each organism grows. Microorganisms can be grouped by the temperature ranges they require.

- ✓ What are the approximate cardinal temperatures for *Escherichia coli*? To what temperature class does it belong?
- ✓ How does a *hyperthermophile* differ from a *psychrophile*?
- ✓ *Escherichia coli* can grow at a higher temperature in complex than in defined medium. Why?

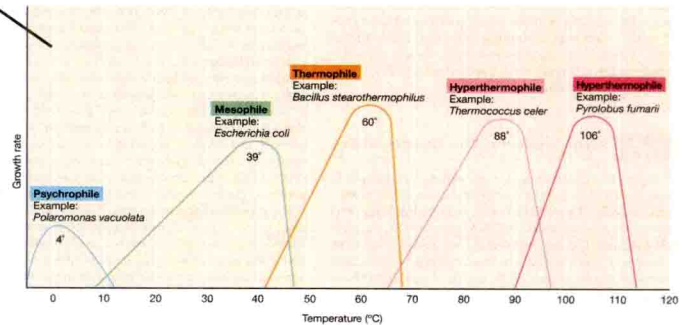


Figure 6.17 Relation of temperature to growth rates of a typical psychrophile, a typical mesophile, a typical thermophile, and two different hyperthermophiles. The temperature optima of the example organisms are shown on the graph.

Concept Checks summarize each section and provide quiz questions so students can evaluate their understanding as they progress through the chapter.

✓ 6.8 Concept Check

Temperature is a major environmental factor controlling microbial growth. The cardinal temperatures describe the minimum, optimum, and maximum temperatures at which each organism grows. Microorganisms can be grouped by the temperature ranges they require.

- ✓ What are the approximate cardinal temperatures for *Escherichia coli*? To what temperature class does it belong?
- ✓ How does a *hyperthermophile* differ from a *psychrophile*?
- ✓ *Escherichia coli* can grow at a higher temperature in complex than in defined medium. Why?

7.2 ■ DNA STRUCTURE: THE DOUBLE HELIX ■ 171

called **exons**, and the intervening noncoding regions, **introns**. Both intron and exon regions are transcribed into the **primary transcript**, or **pre-mRNA**, and the functional mRNA is subsequently formed by removal of noncoding regions. A summary contrasting genetic phenomena in prokaryotes and eukaryotes is given in Figure 7.2.

✓ 7.1 Concept Check

The three key processes of macromolecular synthesis are DNA replication; transcription, the synthesis of RNA from a DNA template; and translation, the synthesis of proteins using messenger RNA as template. Although the basic processes are the same in both prokaryotes and eukaryotes, the organization of genetic information is more complex in eukaryotes. Many eukaryotic genes have both coding regions (exons) and noncoding regions (introns).

- ✓ What three informational macromolecules are involved in genetic information flow?
- ✓ In all cells there are three processes involved in genetic information flow. What are they?

II DNA STRUCTURE

We dealt with the general structure of nucleic acids in Chapter 3. In the next few sections of this chapter we shall discuss the details of DNA structure necessary for an understanding of molecular genetics and the types of genetic elements containing DNA that are found in cells. With this information as a basis, we can then discuss how DNA is replicated, transcribed into RNA, and translated into protein.

7.2 DNA Structure: The Double Helix

The genetic information for all cellular processes is stored in DNA in the *sequence* of bases along the polynucleotide chain. As we have noted, only four different nucleic acid bases are found in DNA: adenine (A), guanine (G), cytosine (C), and thymine (T). As already shown in Figure 3.11, the backbone of the DNA chain consists of alternating units of phosphate and the sugar *deoxyribose*; connected to each sugar is one of the nucleic acid bases. Recall especially the numbering system for the positions of sugar and base; the phosphate connecting two sugars spans from the 3'-carbon of one sugar to the 5'-carbon of the adjacent sugar (see Figure 7.14). At one end of the DNA molecule the sugar has a phosphate on the 5'-hydroxyl, whereas at the other end the sugar has a free hydroxyl at the 3'-position.

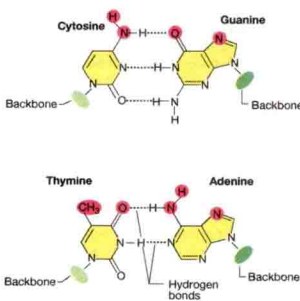


Figure 7.3 Specific pairing between adenine (A) and thymine (T) and between guanine (G) and cytosine (C) via hydrogen bonds. These two base pairs are the base pairs typically found in double-stranded DNA. Atoms that are found in the major groove of the double helix and that interact with proteins are highlighted in red. The deoxyribose phosphate backbones of the two strands of DNA are also indicated.

DNA as a Double Helix

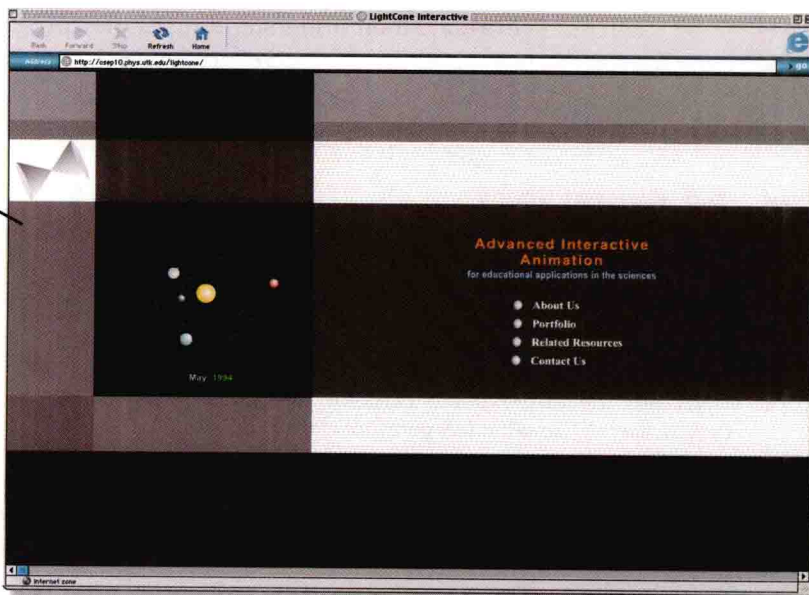
As we will discuss in Chapter 9, the chromosomes of some viruses are single-stranded. In all **cellular organism chromosomes**, however, DNA exists as two polynucleotide strands whose base sequences are **complementary**. The complementarity of DNA arises because of the specific pairing of the purine and pyrimidine bases: Adenine always pairs with thymine, and guanine always pairs with cytosine (Figure 7.3). The two strands in the resulting **double-stranded** molecule are arranged in an *antiparallel* fashion (see Figure 7.4). This means the two strands are in a “head-to-tail” arrangement. In Figure 7.4 the strand on the left is arranged 5' to 3' top to bottom, whereas the other strand is 5' to 3' bottom to top. The two strands are wrapped around each other forming a **double helix** (Figure 7.5). In this double helix, DNA forms two distinct grooves, the *major groove* and the *minor groove*. Of the many proteins that interact specifically with DNA (as we shall see in Chapter 8), most engage predominantly with the major groove, where there is a considerable amount of space. Because of the regularity of the double helix, some atoms of the bases are always exposed in the major groove (and some in the minor groove). Atoms in the major groove that are known to be important in interactions with proteins are shown in Figure 7.3.

The size of a DNA molecule can be expressed in terms of its *molecular weight*, but because a single nucleotide has a molecular weight of about 330, and because DNA molecules are many nucleotides long, the molecular weight mounts up rapidly. (The nucleic acid in



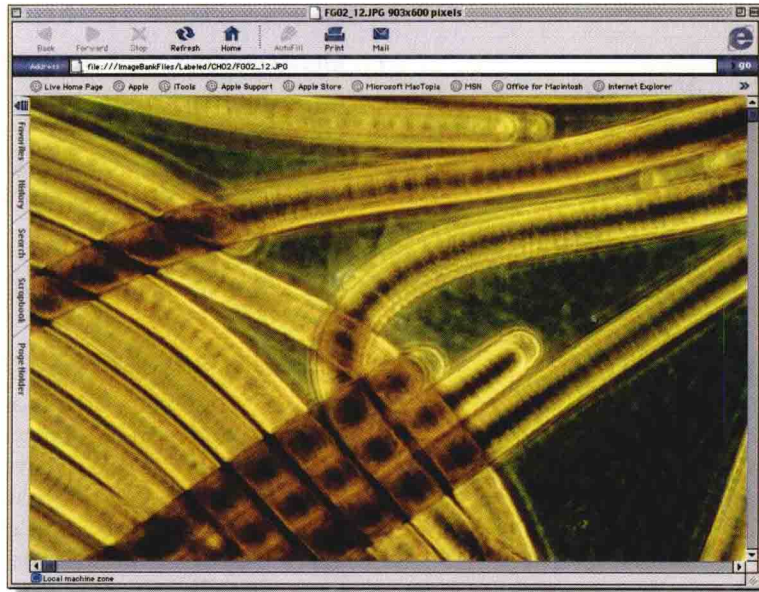
Media Tutorials available on the Companion Web Site are indicated by icons next to key figures.

Media Tutorials consist of animations, interactive exercises, review quizzes, links to important web sites, and much more.



Complete Instructor Package

The Instructor Resource CD will contain PowerPoint presentations as well as an image bank of all illustrations and most of the photographs in the text along with the Instructor's Manual & Test Item File, and reproduction of the student's Companion Web Site.



TRANSPARENCIES

BROCK
BIOLOGY
OF
MICROORGANISMS

TENTH EDITION

MICHAEL T. MADIGAN
JOHN M. MARTINKO
JACK PARKER

INSTRUCTOR'S MANUAL

BROCK
BIOLOGY
OF
MICROORGANISMS

TENTH EDITION

MICHAEL T. MADIGAN
JOHN M. MARTINKO
JACK PARKER

Microbiology is a biological science that has effectively wedded the old and the new. Some of the basic techniques of microbiology discovered over 100 years ago—the isolation of pure cultures, for example—are still practiced with regularity in the laboratory today. But today's microbiologists are also armed with sophisticated tools that facilitate detailed molecular analyses of microbial cells. These tools have fueled new discoveries that are thrusting microbiology into the limelight of disciplines as diverse as medicine, agriculture, and ecology. It is within this exciting period in microbiology that we present the tenth edition of *Brock Biology of Microorganisms (BBOM)*, a textbook of microbiology that blends fundamental principles (the old) with state-of-the-art science (the new) in a format that will appeal to both students and instructors.

What's New?

Organization

This edition of *BBOM* contains many new organizational features that will help students better master the material and help instructors prepare stimulating presentations for the classroom. First, the book has been extensively reorganized into six major units: (1) Principles of Microbiology; (2) Evolutionary Microbiology and Microbial Diversity; (3) Metabolic Diversity and Microbial Ecology; (4) Immunology, Pathogenicity, and Host Responses; (5) Microbial Diseases; and (6) Microorganisms as Tools for Industry and Research. Each unit consists of several chapters whose content define the themes. Unit 1, The Principles, forms the heart of the general microbiology course as currently envisioned by the Education Division of the American Society for Microbiology (ASM); in other words, Unit 1 is the “core” material that every student should know. Included for the first time in this unit is an overview chapter (Chapter 2) on microbial diversity that introduces the major groups of microorganisms and their evolutionary relationships. This chapter will allow instructors who emphasize the medical or molecular aspects of microbiology the opportunity to give their students a taste of microbial diversity without the details. This chapter also covers some of the basic aspects of cell structure/function and is written in such a way that only a minimal background in chemistry and biology is necessary to follow the story.

Other chapters that have been revamped in Unit 1 include Chapters 9 and 10. Compared with previous editions of *BBOM*, Chapter 9 (Essentials of Virology) has been restructured and downsized to place emphasis on the *essential concepts* of virology, instead of viral diversity. The latter material still exists, however, in the

new Chapter 16 (Bacterial, Plant and Animal Viruses), for those instructors who wish to explore viral diversity in more detail. Another substantially reorganized chapter is Chapter 10, Bacterial Genetics. This chapter has been rewritten from two major standpoints, microbial genetics as it occurs in the intact organism (*in vivo*) and microbial genetics as it is practiced *in vitro*. To accomplish the latter, some material from the biotechnology chapter has been reworked and moved to this new chapter on genetics. Thus, Chapter 10 better reflects bacterial genetics as it is actually practiced today—a blend of *in vivo* and *in vitro* science.

As has been a tradition with *BBOM*, the material in each chapter is broken into several *numbered heads* to assist instructors in assigning reading material. But in addition, in parallel to the unit concept that pervades organization at the level of the entire book, the numbered heads within a chapter are themselves grouped into major themes. The latter are signaled by red headings set in all caps, and were introduced in this edition to better group related material within a chapter into logical pieces.

In summary then, the tenth edition of *BBOM* is organized to capture and distill the basics while deploying the full story of the science at those points where it will have maximum impact. The authors and publishers are confident that this new format will make *BBOM 10/e* an even stronger resource for students and instructors alike.

Content

Every three years the authors of this book face one major question: how do we add new material and still keep the book within bounds? Longtime users of *BBOM* will immediately recognize that the tenth edition is essentially no longer than the ninth. This feat was accomplished by balancing the needs of the new material with a careful reevaluation of the old. Nothing essential to a fundamental understanding of microbiology has been deleted from *BBOM*; the tenth edition is still a book built on basic principles and strong science. But streamlining of some chapters along with a first-class art program has given the authors the space necessary to paint an up-to-the-minute picture of the science of microbiology in a volume that does not require weight training to lift off the table.

Several *totally new* chapters will be found in *BBOM 10/e*. The new overview of microbial diversity chapter (Chapter 2) and the viral diversity chapter (Chapter 16) have already been mentioned in this regard. Also new to this edition are Chapter 15

(Microbial Genomics); Chapter 18 (Methods in Microbial Ecology); Chapter 22 (Essentials of Immunology); Chapter 23 (Molecular Immunology); Chapter 27 (Animal-Transmitted, Arthropod-Transmitted, and Soilborne Microbial Diseases); Chapter 28 (Wastewater Treatment, Water Purification, and Waterborne Microbial Diseases); and Chapter 29 (Food Preservation and Foodborne Microbial Diseases). All of these areas are “hot topics” in microbiology today and needed increased visibility and expanded coverage. These new chapters should accomplish just that.

The genomic revolution has transformed microbiology into a new science almost overnight. For the first time, scientists can inspect, almost in a routine fashion now, the entire genetic blueprint of a microorganism, and then compare the blueprint with those of other organisms, from viruses to humans. Genomics has revealed the great genetic unity and diversity of living organisms and has opened the door to new advancements in every discipline of biology. And combined with proteomic analyses, scientists can now ask sophisticated questions about *gene expression* in ways never before possible. Chapter 15 in *BBOM 10/e* tells the genomic story, but goes well beyond just listing organisms whose genomes have been sequenced. The chapter explains what genomics is, how the reams of DNA sequence data that are being generated can be used, and what the genomic revolution has revealed thus far in terms of both the genomic and proteomic capacities of key microorganisms.

The new chapters in immunology were written to provide both the basics and the details of this important science. Chapter 22 (Essentials of Immunology) presents the basic principles of immunology without delving into too much detail. This chapter should therefore be a very student-friendly and readily teachable overview of immunology. We reserve the molecular details of immunology for the rather short Chapter 23. This chapter places the essentials material (Chapter 22) within a molecular context for those students and instructors whose background and interests support the study of immunology at this level. In Chapter 24 (Clinical Microbiology and Immunology) we have expanded our coverage of immunoassays to include more information about the basic mechanisms behind precipitation, agglutination, and antibody production. For those instructors who teach immunology only as a diagnostic or investigative tool, we have also included a very short summary of immune principles here. Thus, with the material on immunology organized as it is, the science of immunology can be integrated into introductory microbiology classes at all levels.


The new chapters in medical microbiology are expansions of this material originally covered in only two

chapters in previous editions. This has given the authors the opportunity to develop this important material in a more thorough way. And in this day and age where foodborne and waterborne illnesses are major public health problems (even in developed countries), and new threats to health and security, such as bioterrorism, are a fact of life, the unit on medical microbiology and immunology will be both a source of basic principles and a reference for keeping up with events in the news.

In summary, long-time users of *BBOM* will find the tenth edition to be the reliable friend they’ve always known. New users will find it to be the most current, accurate, and complete coverage of microbiology available in a textbook today. Coupled with an excellent set of teaching aids (see below) *BBOM 10/e* should set the standard in the field for years to come.

Pedagogical Aids

Art and photos are the mainstay of any textbook in the biological sciences. And frankly speaking, we think *BBOM 10/e* has the best in the business in both regards. The art program has once again been delivered by Imagineering of Toronto, Canada. Virtually every piece of art has seen some modification in order to maximize its impact and clarity. Some stylistic improvements have also been introduced into the art program, including a beautiful new rendering of all graphs in the book. High quality photos and photomicrographs have been a mainstay in *Biology of Microorganisms* since the first edition appeared in 1970, and *BBOM 10/e* proudly carries on this tradition with the inclusion of nearly 50 new B&W and color photos. And, as usual, these photos have been supplied by top researchers in the field.

BBOM 10/e once again employs a variety of student study aids to weave together the concepts and strengthen the learning experience. Instead of placing summary and quiz material only at the *end* of a chapter (as many textbooks like to do), *BBOM 10/e* contains two review tools—concept checks and concept links—*built right into* each chapter. Each **Concept Check** consists of a short summary of the material in the previous numbered head along with a short series of questions that together, reviews the major points in that section. **Concept Links** (signaled by the blue link icon, ) are the ties between the current text and related material found elsewhere in the book. In addition, readers will find the popular **Working Glossary**—a dictionary of essential terms—at the opening of each chapter. The Working Glossary is the student’s lifeline to the *language* of microbiology, an understanding of which is a key to mastering the concepts. Finally, and as in previous editions, the end of each chapter contains a number of review and application questions, many new to

this edition; the questions are designed to probe a student's retention of important concepts and ability to solve problems.

Supplements

A number of supplements accompany this book. Totally new to the tenth edition of *BBOM* are a series of online media tutorials that are found in the *Companion Website* (www.prenhall.com/brock). These cover a number of conceptually challenging topics in microbiology, including basic processes in molecular biology, genetics, medical microbiology and immunology, and microbial metabolism. These unique instructional resources include animations, interactive exercises, and self-quizzes, and will be a major supporting feature for the material in Unit I of *BBOM 10/e*, the heart of the introductory course in microbiology.

These tutorials are designed to guide students' understanding of various fundamental concepts through animations, interactive exercises, and self-assessment. Each concept that is the subject of an Online Media Tutorial is identified by an icon similar to the one in the margin next to this paragraph, placed alongside the relevant figure in the text. Also on the website are additional materials for each chapter along with the popular *Virtual Exam*, first introduced with *BBOM 9/e*. The *Virtual Exam* is a large pool of questions (written in an objective format, multiple choice, true-false, matching, and the like) keyed to individual chapters that students can use as a resource to help prepare for their real exams in the classroom. *Virtual Exam* questions have been assembled from actual examinations given in introductory microbiology courses in the United States that assign *BBOM* as a textbook. With the *Virtual Exam*, students can take an exam online and receive instant feedback on their readiness for exam day.

A variety of supplements are available for instructors. First, a set of over **350 Full Color Transparencies**, far more than is available with any other textbook of microbiology, accompany every adoption of *BBOM 10/e*. Although computer lectures are becoming the norm in many classrooms, the transparency is still the visual aid workhorse for many instructors. To help instructors in this regard, all of the most teachable figures in the book are covered in the transparency set. Second, a first-rate **Instructor's Resource CD-ROM** is available that contains virtually all of the art and photos from *BBOM 10/e* in Microsoft PowerPoint® to assist instructors in tailoring computer presentations to the goals and objectives of their particular course. In addition, all of the animations and exercises that appear on the student website will be on the *Instructor's Resource CD-ROM*. Whether one uses transparencies or CD-ROMs, the *BBOM 10/e* instructor package offers all of the necessary tools for de-

veloping clear, compelling, and stimulating presentations for the classroom.

Acknowledgments

Although the authors have put a strong effort into assembling this classic tenth edition of *BBOM*, the book would never have come together in the way it did without the help of many other individuals. These include all the people at Prentice Hall/Pearson, including in particular our editor, Gary Carlson and his editorial assistant, Susan Zeigler, and our production editor, Debra Wechsler. Gary offered key editorial input into this project, including the commissioning of several very useful reviews. Susan kept the project moving along in the critical reviewing stages, and was extremely helpful in dealing with author requests. Debra, in her usual thorough and professional way, is largely responsible for the beautiful appearance of the final product. Through everyone's gallant efforts in the publishing side of this book, the authors had more freedom than usual to contemplate issues such as organization, content, and pedagogy.

We also wish to acknowledge the excellent input of the developmental editor Carol Pritchard-Martinez (Orinda, CA). Carol saw this project through experienced eyes and gave the authors a critical outside perspective on several editorial and production issues throughout the book. We also thank Jane Loftus (Clackamas, OR) for excellent copy editing input, Steele/Katigbak (Amherst, MA) for composing the index, Toni Huppert, Southern Illinois University, for expert word processing assistance, and Deborah Jung, Southern Illinois University, for her excellent Photoshop® skills and input into the cover design. Finally, we wish to acknowledge those individuals who gave valuable reviewer input on the first draft of *BBOM 10/e* or who supplied color photographs, directly from their research. We are extremely grateful for their efforts and list them below. Special thanks go to Alex T. Nielsen, Technical University of Denmark, whose beautiful photos grace the cover and back cover of this book.

Charles Abella, *University of Girona, Spain*
 Robert E. Andrews, Jr., *Iowa State University*
 Gernot Arp, *Universität Göttingen, Germany*
 Hans-Dietrich Babenzien, *Institut für
 Gewässerökologie und Binnenfischerrei, Berlin,
 Germany*
 Tim Baker, *Purdue University*
 Mary Bateson, *Montana State University*
 Stephen Bentley, *The Sanger Center*
 T. den Blaauwen, *University of Amsterdam*
 Nicholas Blackburn, *Marine Biological Laboratory,
 Helsingør, Denmark*

- Christian Boeker, *Universität Göttingen, Germany*
 Antje Boetius, *Max Planck Institute for Marine Microbiology, Bremen, Germany*
 David R. Boone, *Portland State University*
 Derrick Brazill, *Hunter College*
 John Breznak, *Michigan State University*
 Cheryl Broadie, *Southern Illinois University*
 Michael Cassidy, *University of Waterloo*
 Richard W. Castenholz, *University of Oregon*
 Randall Cohrs, *University of Colorado Health Sciences Center*
 David Crowley, *University of California, Riverside*
 Michael J. Daly, *Uniformed Services University, Maryland*
 Frank B. Dazzo, *Michigan State University*
 Eileen Dimalanta, *University of Wisconsin, Madison*
 Katrina J. Edwards, *Woods Hole Oceanographic Institution*
 Richard Ellis, *Bucknell University*
 Jen Fagg, *Montana State University*
 Michael Ferris, *Montana State University*
 Douglas Fix, *Southern Illinois University*
 Bernard L. Frye, *University of Texas, Arlington*
 John Fuerst, *University of Queensland, Australia*
 Tiffany Full, *Southern Illinois University*
 George M. Garrity, *Michigan State University and Bergey's Manual Trust*
 Eric Grafman, *Centers for Disease Control and Prevention, the Public Health Image Library (PHIL)*
 William D. Grant, *University of Leicester, England*
 Amy Grunden, *North Carolina State University*
 Constance Holden, *Science magazine*
 Johannes F. Imhoff, *Universität Kiel, Germany*
 Michael Jetten, *University of Nijmegen, The Netherlands*
 Deborah Jung, *Southern Illinois University*
 Irena Kaczmarska, *Mount Allison University, Canada*
 Sam Kaplan, *University of Texas, Houston*
 Steve Keating, *Penn State University*
 Joseph E. Kleinman, *North Carolina State University Center for Applied Aquatic Ecology*
 Michael E. Konkel, *Washington State University*
 Robert G. Kranz, *Washington University, St. Louis*
 Alex Lim, *University of Wisconsin, Madison*
 Juergen Marquardt, *Penn State University*
 Mark J. McBride, *University of Wisconsin, Milwaukee*
 William McCleary, *Brigham Young University*
 Joan McCune, *Idaho State University*
 Maura J. Meade, *Allegheny College*
 Susan Merkel, *Cornell University*
 Nanne Ninninga, *University of Amsterdam*
 Alex T. Nielsen, *Technical University of Denmark*
 Bo Normander, *National Environmental Research Institute, Roskilde, Denmark*
 Norm Olson, *Purdue University*
 Aharon Oren, *Hebrew University, Jerusalem*
 Norman R. Pace, *University of Colorado*
 Brian Palenik, *Scripps Institute of Oceanography*
 Ron Parejko, *Northern Michigan University*
 Julian Parkhill, *The Sanger Centre*
 Norbert Pfennig, *Überlingen, Germany*
 Neil Quigley, *University of Tennessee*
 Reinhard Rachel, *Universität Regensburg, Germany*
 Jackie Reynolds, *Richland College*
 Sue Rhee, *Carnegie Institution of Washington, Stanford, CA*
 Timberley Roane, *University of Colorado, Denver*
 Francisco Rodriguez-Valera, *Universidad Miguel Hernandez, Spain*
 Susan Rogers, *Southern Illinois University*
 Wael Sabra, *GBF, Braunschweig, Germany*
 Heinz Schlesner, *Universität Kiel, Germany*
 Steven J. Schmitt, *Southern Illinois University*
 David C. Schwartz, *University of Wisconsin, Madison*
 James P. Shapleigh, *Cornell University*
 Linda Sherwood, *Montana State University*
 Jolynn F. Smith, *Southern Illinois University*
 Kristine M. Snow, *Fox Valley Technical College*
 Gary A. Sojka, *Bucknell University*
 Catherine L. Squires, *Tufts University School of Medicine*
 James T. Staley, *University of Washington*
 Karl O. Stetter, *Universität Regensburg, Germany*
 Richard Stouthamer, *University of California, Riverside*
 Marc Strous, *University of Nijmegen, The Netherlands*
 Michael A. Sulzinski, *University of Scranton*
 James L. Van Etten, *University of Nebraska*
 Lori Van Waasbergen, *University of Texas, Arlington*
 Thomas M. Wahlund, *California State University, San Marcos*
 David M. Ward, *Montana State University*

Frances Westall, *Lunar and Planetary Institute,
Houston*

Carl R. Woese, *University of Illinois*

Alexandra Z. Worden, *Scripps Institute of
Oceanography*

Xiaodong Yan, *Purdue University*

John M. Zamora, *Middle Tennessee State University*

Mark Zelman, *Harper College*

Any errors in this book, either those of commission or omission, are, of course, solely the responsibility of the authors. In this regard, we list author contact information and would greatly appreciate receiving comments, suggestions, and corrections from users. The entire author team has been with the book through a number of editions now and have through the years developed rather “thick skins” to criticism. Thus, we would sincerely enjoy receiving the frank input of users concerning how the book could be made even better in the future.

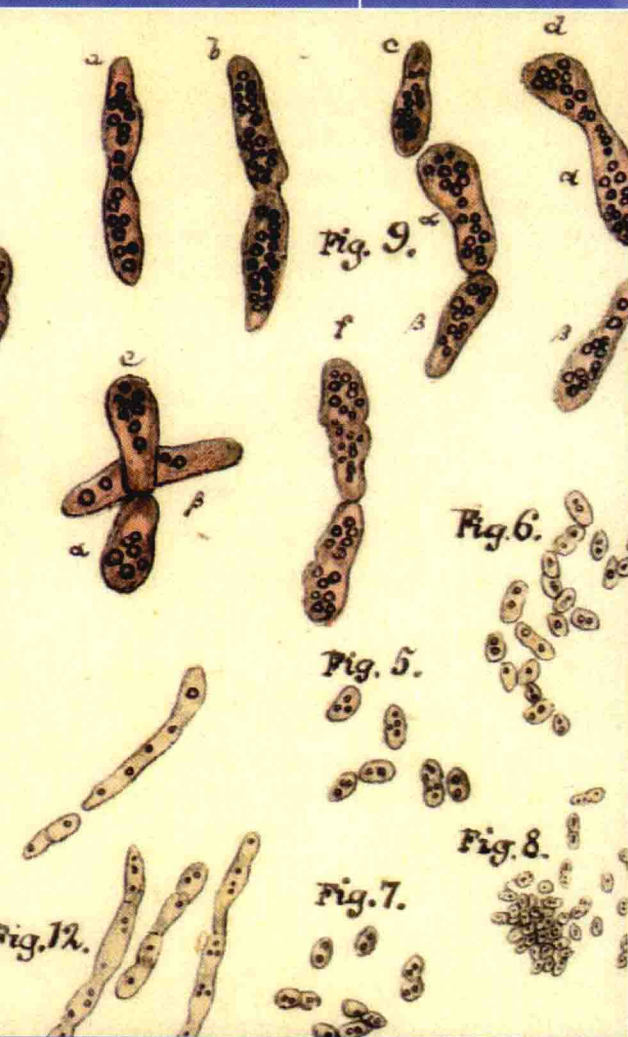
Michael T. Madigan (madigan@micro.siu.edu)

John M. Martinko (martinko@micro.siu.edu)

Jack Parker (parker@cos.siu.edu)

The field of microbiology grew out of the pioneering studies of a handful of early scientists, including the great Russian microbiologist, Sergei Winogradsky. While other giants of the early era focused on the importance of microorganisms as agents of disease, Winogradsky studied bacteria that link key nutrient cycles in nature. His remarkably accurate artistic depictions of microorganisms, such as the phototrophic purple sulfur bacteria shown here, helped other scientists of the day begin to grasp the vast metabolic diversity of microorganisms that we now know exists on Earth.

MICROORGANISMS AND MICROBIOLOGY



I	INTRODUCTION TO MICROBIOLOGY	1
1.1	Microbiology	1
1.2	Microorganisms as Cells	2
1.3	Microorganisms and Their Natural Environments	4
1.4	The Impact of Microorganisms on Humans	7
II	PATHWAYS OF DISCOVERY IN MICROBIOLOGY	9
1.5	The Historical Roots of Microbiology	9
1.6	Microbial Diversity and the Advent of Molecular Microbiology	16

Brief Contents

Unit I	PRINCIPLES OF MICROBIOLOGY	
Chapter 1	Microorganisms and Microbiology	1
Chapter 2	An Overview of Microbial Life	21
Chapter 3	Macromolecules	38
Chapter 4	Cell Structure/Function	55
Chapter 5	Nutrition, Laboratory Culture, and Metabolism of Microorganisms	102
Chapter 6	Microbial Growth	137
Chapter 7	Principles of Microbial Molecular Biology	167
Chapter 8	Regulation of Gene Expression	206
Chapter 9	Essentials of Virology	231
Chapter 10	Bacterial Genetics	264
Unit II	EVOLUTIONARY MICROBIOLOGY AND MICROBIAL DIVERSITY	
Chapter 11	Microbial Evolution and Systematics	321
Chapter 12	Prokaryotic Diversity: <i>Bacteria</i>	351
Chapter 13	Prokaryotic Diversity: The <i>Archaea</i>	445
Chapter 14	Eukaryotic Cell Biology and Eukaryotic Microorganisms	472
Chapter 15	Microbial Genomics	499
Chapter 16	Bacterial, Plant, and Animal Viruses	520
Unit III	METABOLIC DIVERSITY AND MICROBIAL ECOLOGY	
Chapter 17	Metabolic Diversity	547
Chapter 18	Methods in Microbial Ecology	614
Chapter 19	Microbial Habitats, Nutrient Cycles, and Interactions with Plants and Animals	632
Unit IV	IMMUNOLOGY, PATHOGENICITY, AND HOST RESPONSES	
Chapter 20	Microbial Growth Control	695
Chapter 21	Human–Microbe Interactions	727
Chapter 22	Essentials of Immunology	755
Chapter 23	Molecular Immunology	787
Chapter 24	Clinical Microbiology and Immunology	804
Unit V	MICROBIAL DISEASES	
Chapter 25	Epidemiology	846
Chapter 26	Person-to-Person Microbial Diseases	875
Chapter 27	Animal-Transmitted, Arthropod-Transmitted, and Soilborne Microbial Diseases	913
Chapter 28	Wastewater Treatment, Water Purification, and Waterborne Microbial Diseases	934
Chapter 29	Food Preservation and Foodborne Microbial Diseases	950
Unit VI	MICROORGANISMS AS TOOLS FOR INDUSTRY AND RESEARCH	
Chapter 30	Industrial Microbiology/Biocatalysis	965
Chapter 31	Genetic Engineering and Biotechnology	994

Preface	xxi	3.8 Proteins: Higher Order Structure and Denaturation	52
UNIT I PRINCIPLES OF MICROBIOLOGY		✓ CHAPTER 4	55
CHAPTER 1		CELL STRUCTURE/FUNCTION	55
MICROORGANISMS AND MICROBIOLOGY	1	I MICROSCOPY AND CELL MORPHOLOGY	56
I INTRODUCTION TO MICROBIOLOGY	1	4.1 Light Microscopy	56
1.1 Microbiology	1	4.2 Three-Dimensional Imaging: Interference Contrast, Atomic Force, and Confocal Scanning Laser Microscopy	60
1.2 Microorganisms as Cells	2	4.3 Electron Microscopy	62
1.3 Microorganisms and Their Natural Environments	4	4.4 Cell Morphology and the Significance of Being Small	63
1.4 The Impact of Microorganisms on Humans	7	II CELL MEMBRANES AND CELL WALLS	66
II PATHWAYS OF DISCOVERY IN MICROBIOLOGY	9	4.5 Cytoplasmic Membrane: Structure	66
1.5 The Historical Roots of Microbiology	9	4.6 Cytoplasmic Membrane: Function	69
1.6 Microbial Diversity and the Advent of Molecular Microbiology	16	4.7 Membrane Transport Systems	71
		4.8 The Cell Wall of Prokaryotes: Peptidoglycan and Related Molecules	74
		4.9 The Outer Membrane of Gram-Negative Bacteria	79
CHAPTER 2	21	III MICROBIAL LOCOMOTION	82
AN OVERVIEW OF MICROBIAL LIFE	21	4.10 Flagella and Motility	82
I CELL STRUCTURE AND EVOLUTIONARY HISTORY	22	4.11 Gliding Motility	85
2.1 Elements of Cell and Viral Structure	22	4.12 Behavioral Responses: Chemotaxis, Phototaxis, and Other Taxes	87
2.2 Arrangement of DNA in Microbial Cells	24	IV SURFACE STRUCTURES AND INCLUSIONS OF PROKARYOTES	90
2.3 The Tree of Life	26	4.13 Bacterial Cell Surface Structures and Cell Inclusions	90
II MICROBIAL DIVERSITY	27	4.14 Gas Vesicles	94
2.4 Physiological Diversity of Microorganisms	28	4.15 Endospores	95
2.5 Prokaryotic Diversity	29		
2.6 Eukaryotic Microorganisms	34		
		✓ CHAPTER 5	102
CHAPTER 3	38	NUTRITION, LABORATORY CULTURE, AND METABOLISM OF MICROORGANISMS	102
MACROMOLECULES	38	I NUTRITION AND CULTURE OF MICROORGANISMS	103
I CHEMICAL BONDING AND WATER IN LIVING SYSTEMS	39	5.1 Microbial Nutrition	103
3.1 Strong and Weak Chemical Bonds	39	5.2 Culture Media	107
3.2 An Overview of Macromolecules and Water as the Solvent of Life	42	5.3 Laboratory Culture of Microorganisms	108
II MACROMOLECULES	43	II ENERGETICS AND ENZYMES	110
3.3 Polysaccharides	43	5.4 Bioenergetics	110
3.4 Lipids	45	5.5 Catalysis and Enzymes	111
3.5 Nucleic Acids	46	III OXIDATION-REDUCTION AND HIGH-ENERGY COMPOUNDS	113
3.6 Amino Acids and the Peptide Bond	48	5.6 Oxidation-Reduction	114
3.7 Proteins: Primary and Secondary Structure	50		