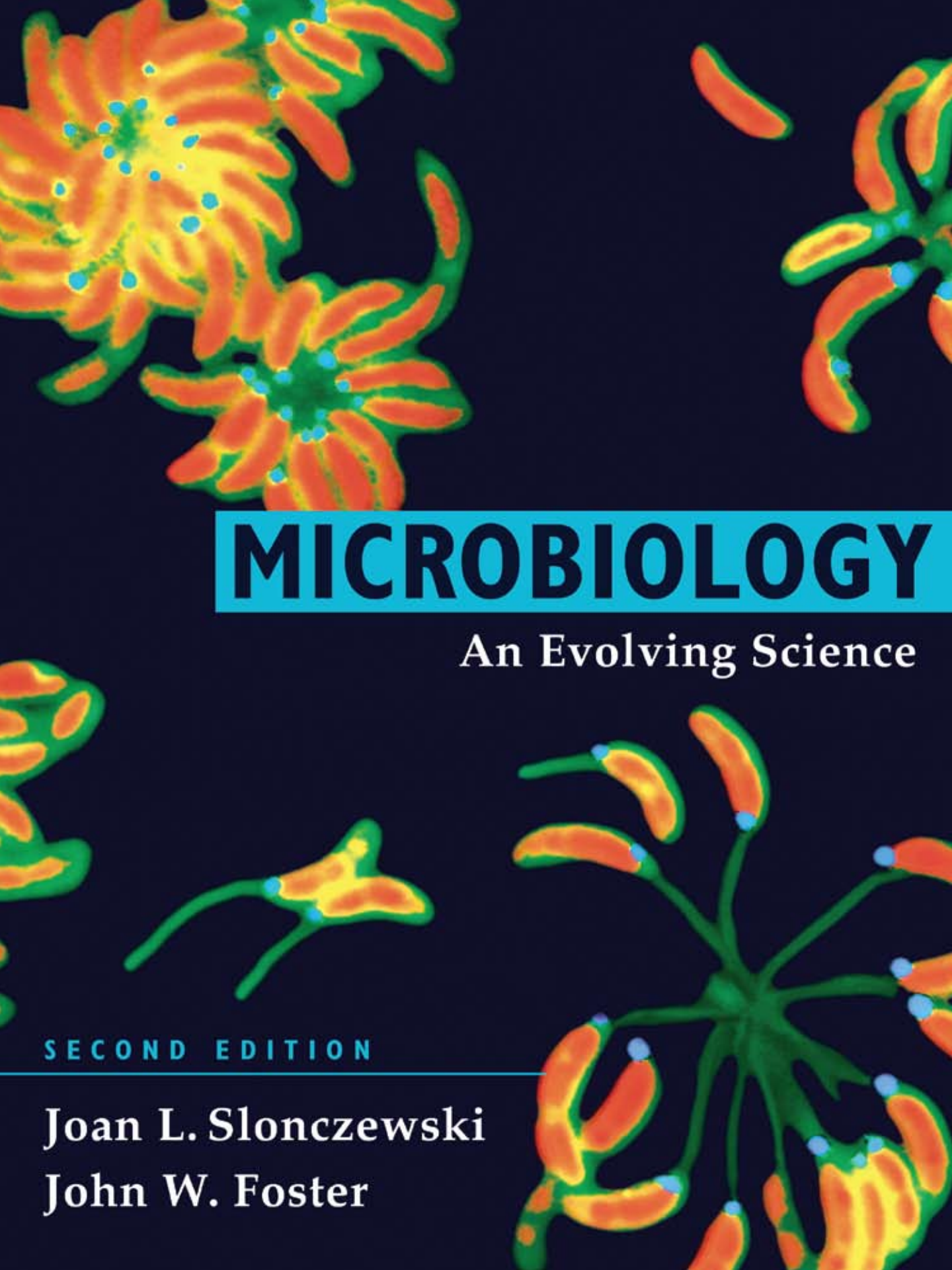

MICROBIOLOGY

An Evolving Science

SECOND EDITION

Joan L. Slonczewski
John W. Foster

The most successful new microbiology text in a generation

"The best microbiology textbook I have used—quasi-perfection!"
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"I liked conveying microbiology as an 'evolving' not evolved science. I think this is more how textbooks should teach science that is in flux, not finished." —SCOTT DAWSON, *UC Davis*

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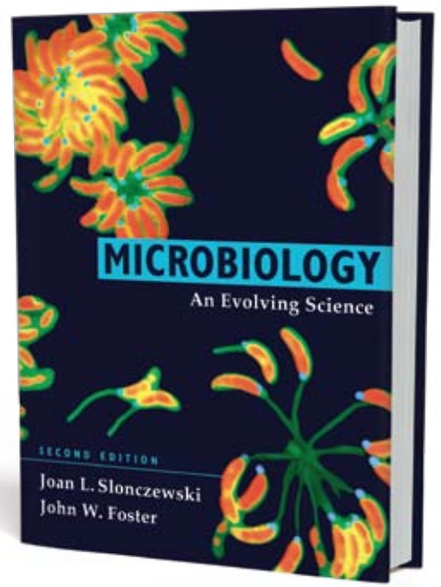
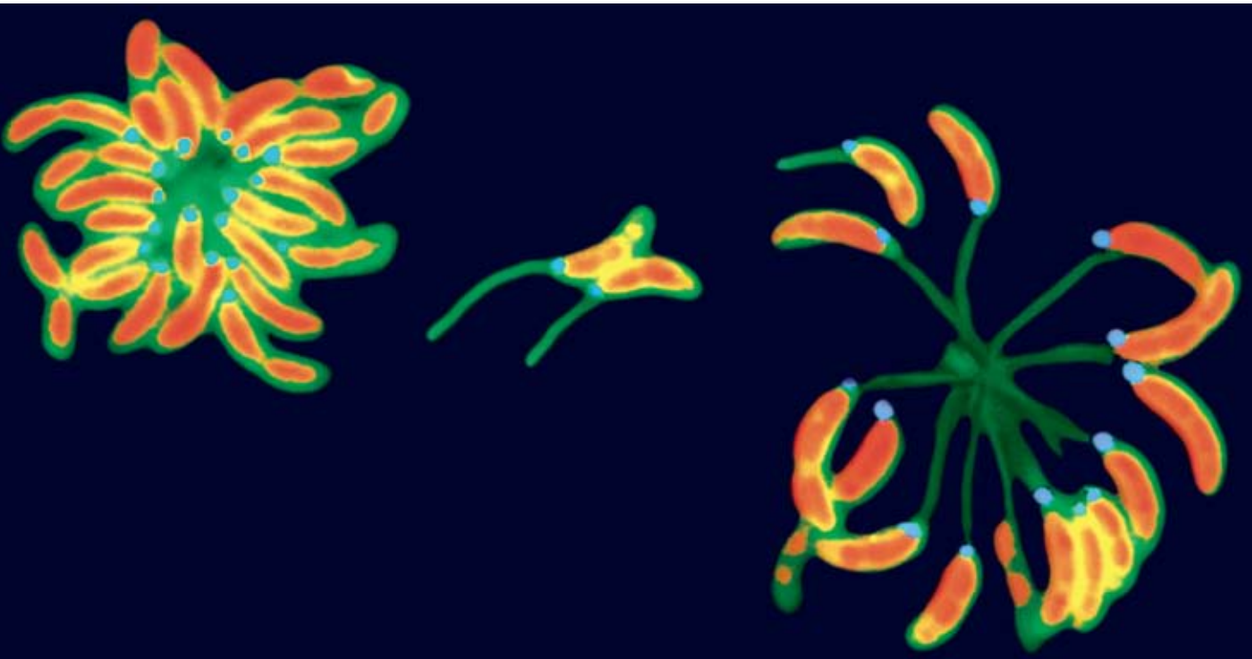




MICROBIOLOGY

An Evolving Science

SECOND EDITION

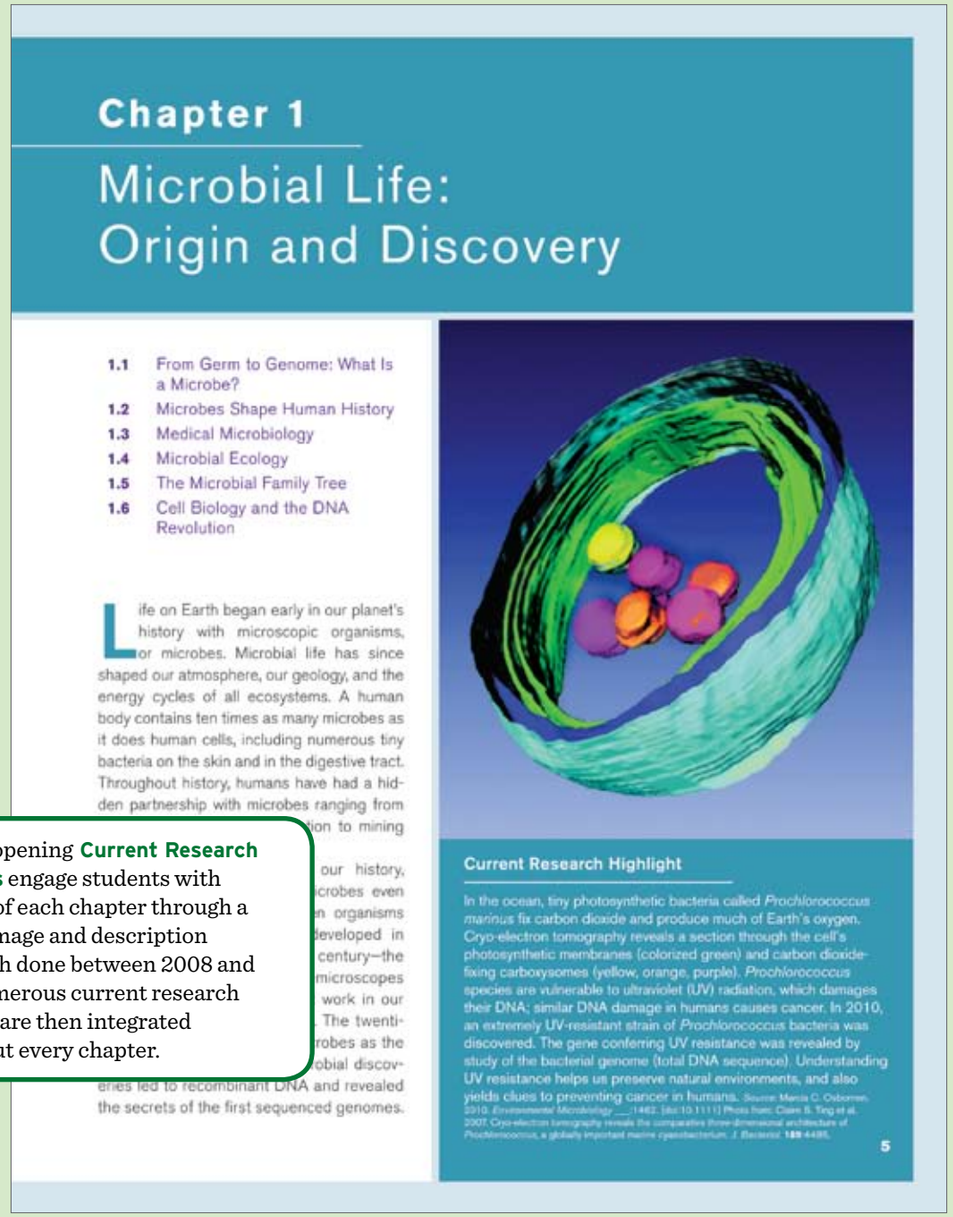
JOAN L. SLONCZEWSKI, Kenyon College
JOHN W. FOSTER, University of South Alabama

Microbiology: An Evolving Science, Second Edition, provides students with the tools they need to understand the rapidly advancing field of microbiology by enriching foundational topics with current research examples. The readable and authoritative text is paired with a stunning and unified art program that helps students visualize key microbial processes and structures.

978-0-393-93447-2 :: 1100 PAGES :: HARDCOVER :: NOVEMBER 2010

An emphasis on current research gives students a contemporary portrait of the dynamic and exciting science of microbiology.

Microbiology: An Evolving Science seamlessly integrates current research within the up-to-date framework of molecular biology, facilitating the incorporation of the latest research into the foundational topics of genetics, physiology, ecology, evolution and immunology.



Chapter 1

Microbial Life: Origin and Discovery

1.1 From Germ to Genome: What Is a Microbe?
1.2 Microbes Shape Human History
1.3 Medical Microbiology
1.4 Microbial Ecology
1.5 The Microbial Family Tree
1.6 Cell Biology and the DNA Revolution

Life on Earth began early in our planet's history with microscopic organisms, or microbes. Microbial life has since shaped our atmosphere, our geology, and the energy cycles of all ecosystems. A human body contains ten times as many microbes as it does human cells, including numerous tiny bacteria on the skin and in the digestive tract. Throughout history, humans have had a hidden partnership with microbes ranging from ion to mining

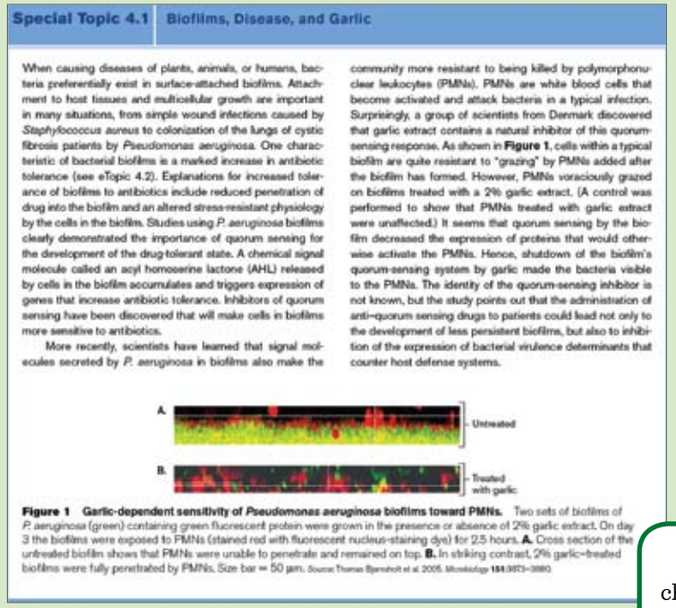
our history, icrobes even n organisms developed in century—the microscopes work in our . The twenti- robes as the obial discov- eries led to recombinant DNA and revealed the secrets of the first sequenced genomes.

Current Research Highlight

In the ocean, tiny photosynthetic bacteria called *Prochlorococcus marinus* fix carbon dioxide and produce much of Earth's oxygen. Cryo-electron tomography reveals a section through the cell's photosynthetic membranes (colorized green) and carbon dioxide-fixing carboxysomes (yellow, orange, purple). *Prochlorococcus* species are vulnerable to ultraviolet (UV) radiation, which damages their DNA; similar DNA damage in humans causes cancer. In 2010, an extremely UV-resistant strain of *Prochlorococcus* bacteria was discovered. The gene conferring UV resistance was revealed by study of the bacterial genome (total DNA sequence). Understanding UV resistance helps us preserve natural environments, and also yields clues to preventing cancer in humans. Source: Marcia C. Osborne, 2010. *Environmental Microbiology* ___:1462. [doi:10.1111] Photo from: Claire S. Ting et al. 2007. Cryo-electron tomography reveals the comparative three-dimensional architecture of *Prochlorococcus*, a globally important marine cyanobacterium. *J. Bacteriol.* **189**:4485.

5

Chapter-opening **Current Research Highlights** engage students with the topic of each chapter through a striking image and description of research done between 2008 and 2010. Numerous current research examples are then integrated throughout every chapter.



Special Topic 4.1 Biofilms, Disease, and Garlic

When causing diseases of plants, animals, or humans, bacteria preferentially exist in surface-attached biofilms. Attachment to host tissues and multicellular growth are important in many situations, from simple wound infections caused by *Staphylococcus aureus* to colonization of the lungs of cystic fibrosis patients by *Pseudomonas aeruginosa*. One characteristic of bacterial biofilms is a marked increase in antibiotic tolerance (see eTopic 4.2). Explanations for increased tolerance of biofilms to antibiotics include reduced penetration of drug into the biofilm and an altered stress-resistant physiology by the cells in the biofilm. Studies using *P. aeruginosa* biofilms clearly demonstrated the importance of quorum sensing for the development of the drug-tolerant state. A chemical signal molecule called an acyl homoserine lactone (AHL) released by cells in the biofilm accumulates and triggers expression of genes that increase antibiotic tolerance. Inhibitors of quorum sensing have been discovered that will make cells in biofilms more sensitive to antibiotics.

More recently, scientists have learned that signal molecules secreted by *P. aeruginosa* in biofilms also make the community more resistant to being killed by polymorphonuclear leukocytes (PMNs). PMNs are white blood cells that become activated and attack bacteria in a typical infection. Surprisingly, a group of scientists from Denmark discovered that garlic extract contains a natural inhibitor of this quorum-sensing response. As shown in **Figure 1**, cells within a typical biofilm are quite resistant to "grazing" by PMNs added after the biofilm has formed. However, PMNs voraciously grazed on biofilms treated with a 2% garlic extract. (A control was performed to show that PMNs treated with garlic extract were unaffected.) It seems that quorum sensing by the biofilm decreased the expression of proteins that would otherwise activate the PMNs. Hence, shutdown of the biofilm's quorum-sensing system by garlic made the bacteria visible to the PMNs. The identity of the quorum-sensing inhibitor is not known, but the study points out that the administration of anti–quorum sensing drugs to patients could lead not only to the development of less persistent biofilms, but also to inhibition of the expression of bacterial virulence determinants that counter host defense systems.

A. Untreated
B. Treated with garlic

Figure 1 Garlic-dependent sensitivity of *Pseudomonas aeruginosa* biofilms toward PMNs. Two sets of biofilms of *P. aeruginosa* (green) containing green fluorescent protein were grown in the presence or absence of 2% garlic extract. On day 3 the biofilms were exposed to PMNs (stained red with fluorescent nucleus-staining dye) for 2.5 hours. **A.** Cross section of the untreated biofilm shows that PMNs were unable to penetrate and remained on top. **B.** In striking contrast, 2% garlic–treated biofilms were fully penetrated by PMNs. Size bar = 50 μm. Source: Thomas Bjarnsholt et al. 2005. *Microbiology* **151**:3873–3880.

Special Topic 5.1 It's Raining Bacteria

How clouds, rain, and snow form has intrigued children and scientists for millennia. Little did anyone know that bacteria are major players in these processes. David Sands at Montana State University first hypothesized a link between rainfall and psychrotolerant bacteria in 1982. Though the scientific community initially scoffed at Sands' idea, he has now been proven right. Without bacteria (or some other tiny particles), clouds would never form because water vapor droplets are too small—about 250 nm (approximately one ten-thousandth of an inch) or less. A powerful surface tension forms the small curved surfaces on each droplet. Water vapor that goes into the liquid state must overcome this surface tension to form the larger droplets that make up clouds. Left alone, water vapor would never form clouds and there would never be rain.

There also would never be snow. Ice formation in clouds is required for snow and even most rainfall. At temperatures above −40°C, however, ice formation is not spontaneous. Tiny catalysts, known as ice nucleators, are required. Scientists knew for years that a protein in the outer membrane of certain bacterial plant pathogens, such as the psychrotolerant *Pseudomonas syringae* and *Erwinia* species, have the capacity to freeze pure water at temperatures as warm as −1°C. The protein binds water molecules in an ordered arrangement, providing a nucleating template that enhances ice crystal formation (**Fig. 1**). The ice crystals that form at this relatively warm temperature break the cell walls of the plants and release nutrients that the bacteria use as food. Ice-nucleating bacteria have been found at altitudes of several kilometers and have been documented in rain and snowfall.

A team led by Brent Christner at Louisiana State University in Baton Rouge has shown the ubiquity of these rainmaking microbes by looking at fresh snow collected at various mid- and high-latitude locations in North America, Europe, and Antarctica. They filtered the snow samples to remove particles, put those particles into containers of pure water, and slowly lowered the temperature, watching closely to see when the water froze. The higher the freezing temperature of any given sample, the greater the number of nuclei and the more likely they were to be biological in nature. To tease apart these two effects, the team treated the water samples with heat or chemicals to kill any bacteria inside, and again checked the freezing temperatures of the samples. In this way they found between 4 and 120 ice nucleators per liter of melted snow. Some 69%–100% of these particles appeared to be biological.

Why is this important? The ability to initiate freezing means that rainmaking bacteria can spur showers as a way of dispersing themselves worldwide. The bacteria facilitate cloud formation, clouds can move large distances in wind currents, and the resulting rain or snow will deposit the bacteria far afield from where they started. So, while climate can affect microbes, microbes can, in turn, affect the weather.

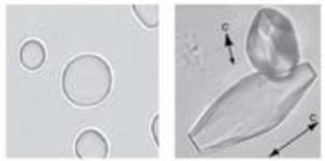


Figure 1 Ice crystallization by a bacterial ice nucleation protein. Photomicrographs of the ice crystal observed for **(A)** solvent buffer alone ([Tris–HCl] = 20 mM (pH 8.0), [EDTA] = 1 mM, [NaCl] = 0.5 M), and **(B)** approximately 400 μM of the ice nucleation protein INP96 from *Pseudomonas syringae* in the buffer. Source: Yoshihiro Kobashigawa et al. 2005. *FEBS Lett.* **579**:1493–1497.

Special Topics boxes in every chapter focus on cutting-edge research with an emphasis on experimental detail and put a human face on the dynamic science of microbiology.

WWW **Weblink icons** throughout the text refer students to current research topics on the Web, including videos, animations, microbial genome databases, and more.

A visually stunning art program teaches students to visualize key concepts.

Successful microbiology students must learn to visualize microbial processes and structures that by nature occur at an unseen level. *Microbiology: An Evolving Science*'s extensive and consistently executed art program helps students visualize key microbial processes and showcases the latest structural discoveries.

Large, engaging figures are accompanied by distinctive bubble captions and numbered labels that help students interpret and analyze microbial processes and structures.

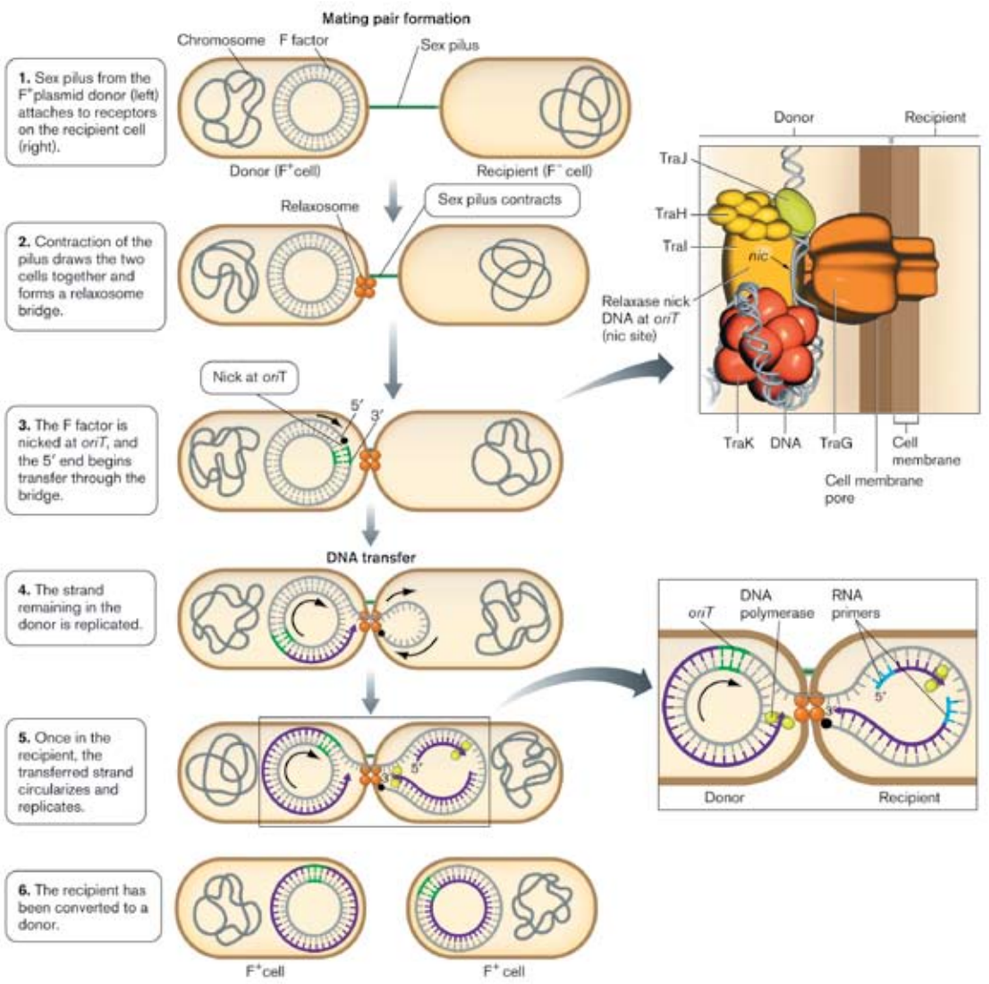


Figure 9.3 The conjugation process. Some plasmids, such as F factor in *E. coli*, can mediate cell-to-cell transfer of DNA. The plasmid is nicked at the *nic* site (step 3), and the 5′ end is transferred to the other cell. Purple arrowheads depict the 3′ end of replicating DNA. The inset at step 3 shows a current model of the DNA secretion apparatus. The relaxosome complex is composed of TraH, TraI (the helicase/endonuclease), TraJ, and TraK. The inset illustrates the step in which the TraI endonuclease is about to nick the donor plasmid. The 5′ end of the nick will move through the pore and remain attached to the membrane while the rest of the single-stranded DNA passes into the recipient. *Source:* Step 3 inset from G. Schröder et al. 2002. *J. Bacteriol.* 184:2767–2779.

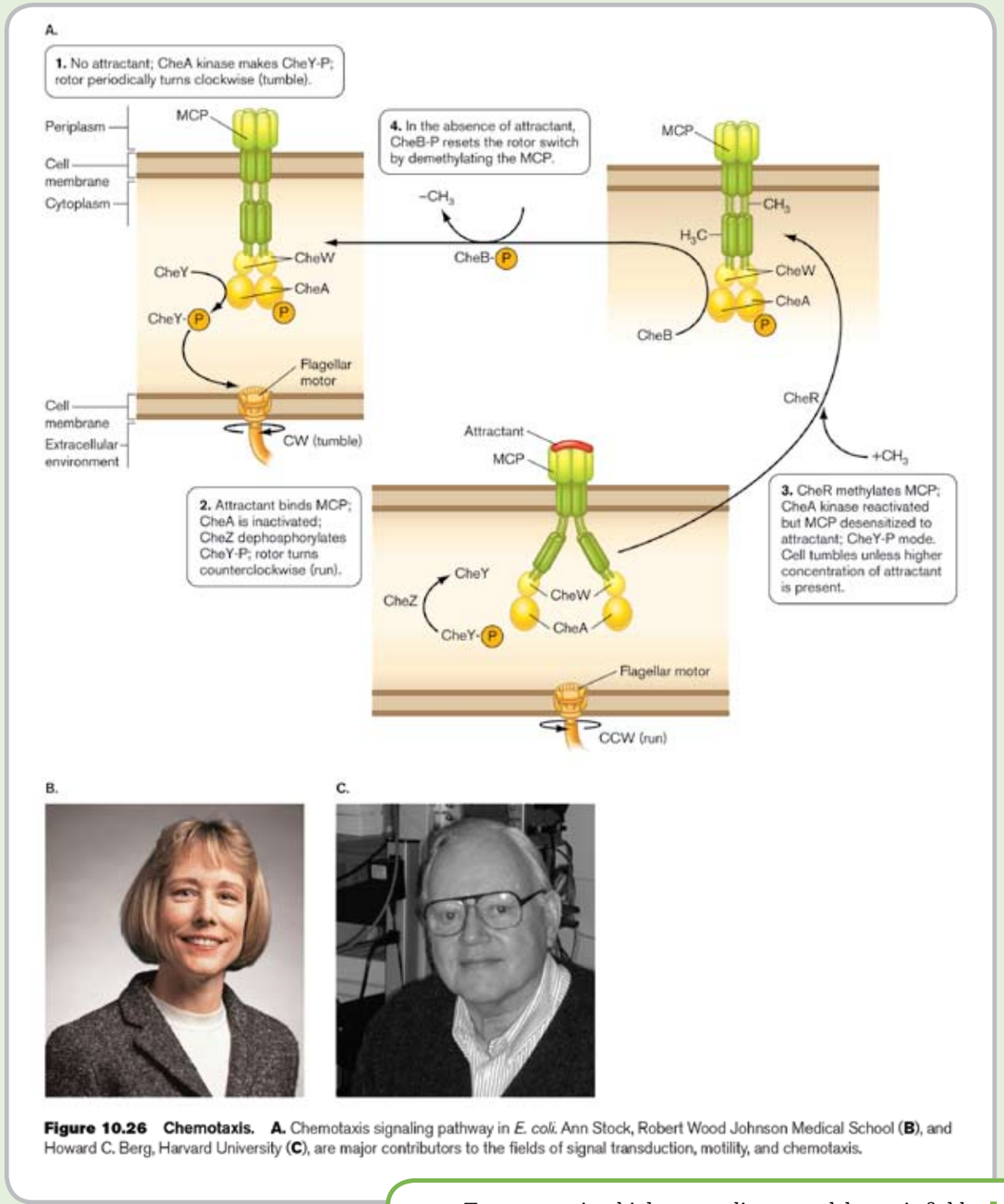


Figure 10.26 Chemotaxis. **A.** Chemotaxis signaling pathway in *E. coli*. Ann Stock, Robert Wood Johnson Medical School (**B**), and Howard C. Berg, Harvard University (**C**), are major contributors to the fields of signal transduction, motility, and chemotaxis.

To convey microbiology as a diverse and dynamic field, **photos** of iconic and contemporary microbiologists are paired with figures of their most important contributions. Many figures are also accompanied by photos of researchers, graduate students and even undergraduates doing research, putting a human face to the science.

Engaging process animations make complex concepts clear.

Each animation topic was chosen by instructors and developed specifically for *Microbiology: An Evolving Science,* in close coordination with the authors. Concepts are presented accurately and with just the right level of detail. Animations are available to students on the free and open StudySpace and are included on the Instructor's Resource Disc for instructors to use in lecture.

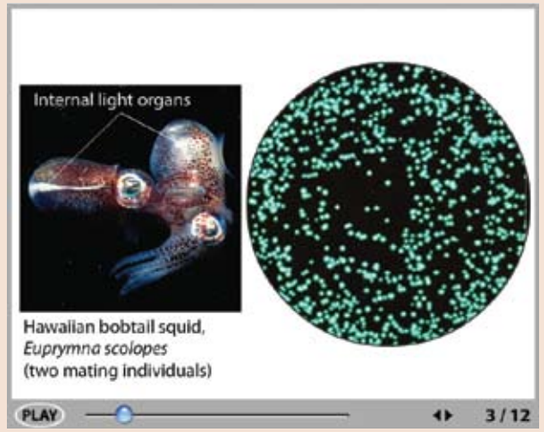
Process Animation Topics

To view these animations, visit microbiology2.com/animations

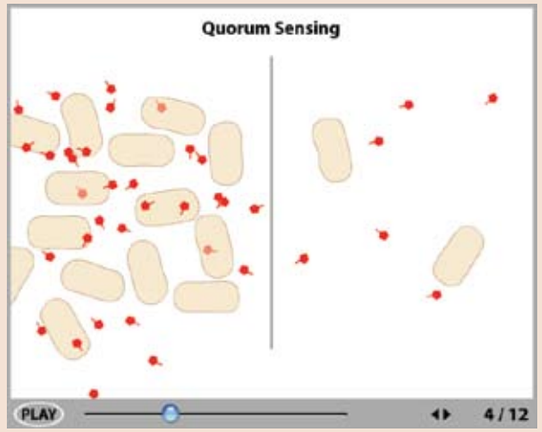
- Microscopy
- Replisome Movement in a Dividing Cell
- Chemotaxis
- Phosphotransferase System (PTS) Transport
- Endospore Formation
- Dilution Streaking Technique
- Biofilm Formation
- Twitching Mobility
- Lysis and Lysogeny
- DNA Replication
- PCR
- Supercoiling and Topoisomerases
- Rolling Circle Mechanism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

Animation: Quorum Sensing

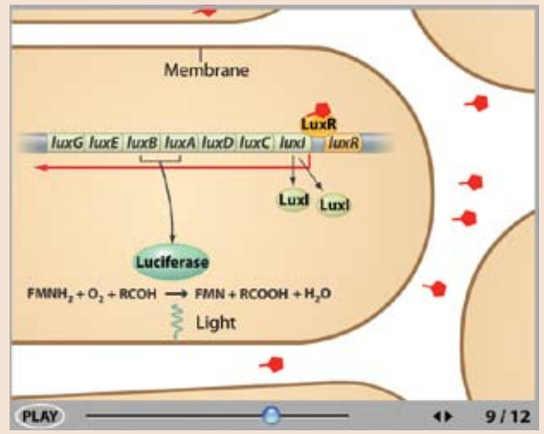
This animation illustrates quorum sensing, the molecular process by which bacteria chemically converse with each other. Quorum sensing in different forms instructs bacteria to form biofilms, activate stress response, and induce virulence genes.



The bacteria glow only under certain conditions. The genes needed to make light are off when bacterial cell densities are low (such as in sea water), but turn on under crowded conditions (such as in the light organ of the squid), when enough cells are together to make a visual impact. How do cells *know* they have achieved an adequate number of nearby individuals—that is, a quorum—before turning on their luminescence genes?



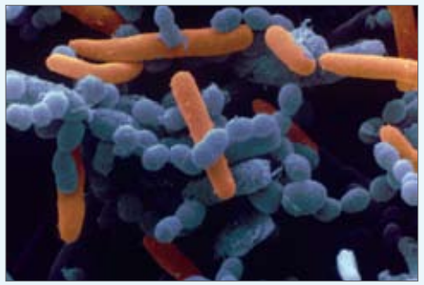
It turns out that this phenomenon, called quorum sensing, is only loosely associated with cell numbers. Induction of a quorum-sensing gene system requires the accumulation of a molecule called an autoinducer. After a cell produces an autoinducer, the molecule rapidly diffuses out of the cell. The more cells in a given space, the faster the autoinducer builds up and the more likely it will reenter cells and trigger the luminescence response.



Luciferase catalyzes a redox reaction that produces oxidized and reduced chemical products as well as blue-green light. Because the Lux proteins, like other proteins, require energy to produce, the cells turn this system on only when appropriate—such as when they are crowded together in the light organ of the squid.

A contemporary organization integrates genomics and molecular genetics and balances medical and ecological microbiology.

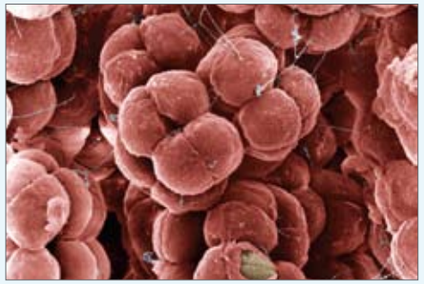
Contents



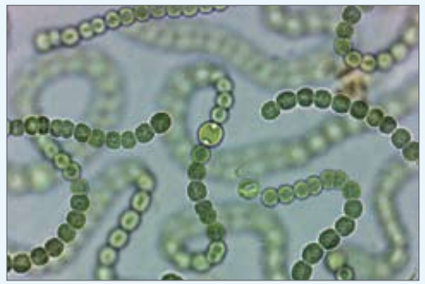
PART I
THE MICROBIAL CELL

PART II: Genetics is covered before metabolism, enabling the authors to show the application of genetic analysis to metabolic questions and microbial diversity. However, since metabolism is introduced earlier in Chapter 4, the chapters of Part III can be covered earlier as desired.

PART II
GENES AND GENOMES



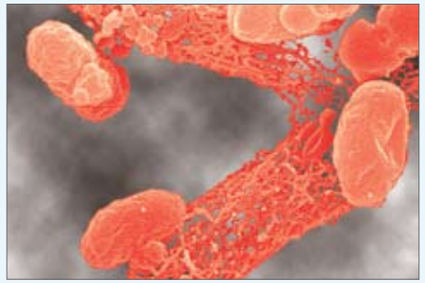
PART III
METABOLISM AND BIOCHEMISTRY



PARTS IV AND V: Microbial ecology and medical microbiology receive equal emphasis, with six chapters devoted to each. Additionally, each time a new principle is introduced, both ecological and medical examples are considered, with an emphasis on the merging of the two fields.

PART IV
MICROBIAL DIVERSITY AND ECOLOGY

PART V
MEDICINE AND IMMUNOLOGY



APPENDICES

In-text tools aid student understanding and stimulate inquiry.

A readable narrative and helpful pedagogical features in every chapter challenge students to review what they've learned, to identify key themes, and to think critically about important questions.

Ample **Thought Questions** throughout each chapter integrate core concepts and get students thinking critically.

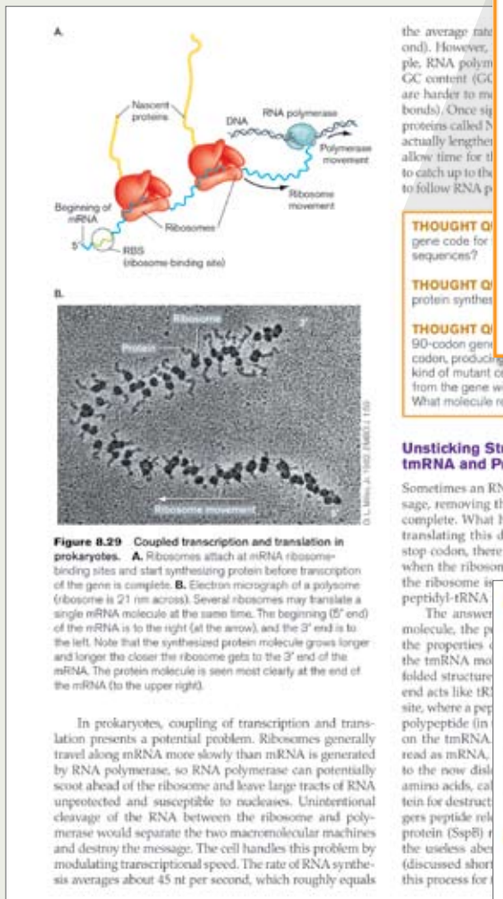


Figure 8.29 Coupled transcription and translation in prokaryotes. A. Ribosomes attach at mRNA ribosome-binding sites and start synthesizing protein before transcription of the gene is complete. **B.** Electron micrograph of a polysome (ribosome is 21 nm across). Several ribosomes may translate a single mRNA molecule at the same time. The beginning (5′ end) of the mRNA is to the right (at the arrow), and the 3′ end is to the left. Note that the synthesized protein molecule grows longer and longer the closer the ribosome gets to the 3′ end of the mRNA. The protein molecule is seen most clearly at the end of the mRNA (to the upper right).

In prokaryotes, coupling of transcription and translation presents a potential problem. Ribosomes generally travel along mRNA more slowly than mRNA is generated by RNA polymerase, so RNA polymerase can potentially scoot ahead of the ribosome and leave large tracts of RNA unprotected and susceptible to nucleases. Unintentional cleavage of the RNA between the ribosome and polymerase would separate the two macromolecular machines and destroy the message. The cell handles this problem by modulating transcriptional speed. The rate of RNA synthesis averages about 45 nt per second, which roughly equals

THOUGHT QUESTION 8.7 How might one gene code for two proteins with different amino acid sequences?

THOUGHT QUESTION 8.8 Why involve RNA in protein synthesis? Why not translate directly from DNA?

THOUGHT QUESTION 8.9 Codon 45 of a 90-codon gene was changed into a translation stop codon, producing a shortened, truncated protein. What kind of mutant cell could produce a full-length protein from the gene *without* removing the stop codon? *Hint*: What molecule recognizes a codon?

Unsticking Stuck Ribosomes: tmRNA and Protein Tagging

Sometimes an RNase will shear off the 3′ end of a message, removing the stop codon before the translation is complete. What happens after a ribosome has finished translating this damaged mRNA molecule? Without a stop codon, there is nothing to trigger ribosome release when the ribosome reaches the end of the message. So the ribosome is

peptidyl-tRNA

The answer

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8.8 Why involve RNA in protein synthesis? Why not translate directly from DNA?

ANSWER: Because transcription enables the cell to amplify the gene sequence information into multiple copies of RNA. Amplification means that more ribosomes can be engaged in translating the same protein, causing the concentration of the protein to rise more quickly than if only a single gene were used. The transcriptional process also presents an opportunity to regulate production of a protein.

8.9 Codon 45 of a 90-codon gene was changed into a translation stop codon. This produced a shortened, truncated protein. What kind of mutant cell could produce a full-length protein from the gene *without* removing the stop codon?

ANSWER: A mutant in which a tRNA gene has been altered by mutation so that the anticondon of the tRNA "sees" the stop codon as an amino acid codon. This mutated tRNA molecule will transfer its amino acid to the peptide chain. The attached amino acid can be used to bridge the gap caused by the stop condon, and a full-length protein is made. These modified tRNAs are called suppressor tRNAs because they suppress the mutant phenotype.

Possible answers are located at the back of the book.

CHAPTER REVIEW

Review Questions

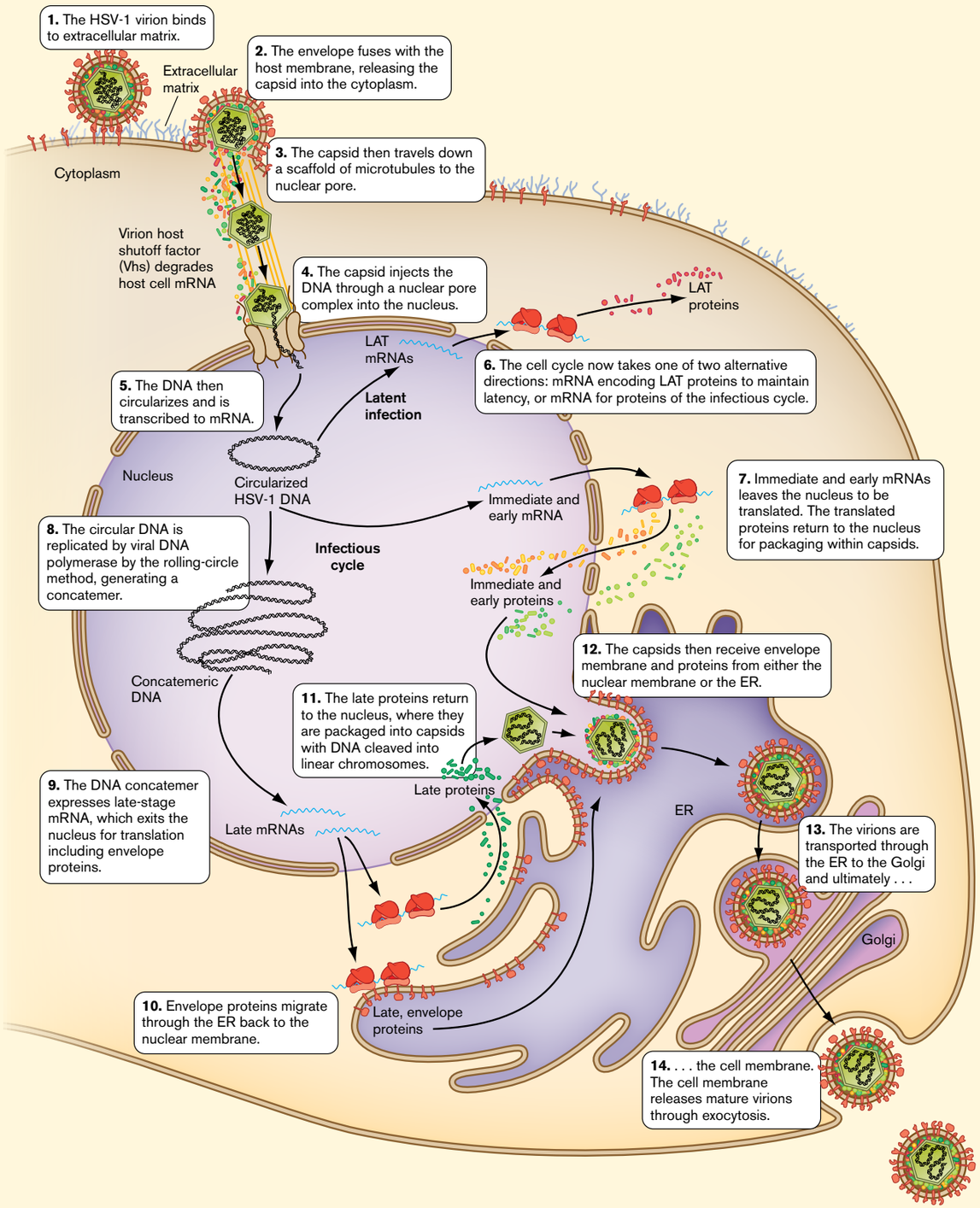
1. What are some characteristics of an ORF?
2. What is a DNA sequence alignment, and what can it tell you?
3. Describe the differences between a pair of orthologous genes and a pair of paralogous genes.
4. How can bioinformatics predict a metabolic pathway for an organism that cannot be grown in the laboratory?
5. What defines a promoter?
6. What are sigma factors, and what role do they play in gene expression?
7. Describe the three stages of transcription.
8. Explain degeneracy of the genetic code. What is the wobble in codon-anticodon recognition?
9. Describe the stages of protein synthesis. Why is the ribosome called a ribozyme?
10. Discuss some antibiotics that affect transcription or translation.
11. What is meant by coupled transcription and translation? Does this occur in eukaryotic cells?
12. How do bacterial cells release ribosomes that are stuck onto damaged mRNA molecules lacking termination codons?
13. What can happen to misfolded proteins?
14. Why are only certain proteins secreted from the bacterial cell? What are some secretion mechanisms?
15. In what major way do proteins transported by the twin arginine translocase (TAT) differ from other exported proteins?
16. Compare protein degradation in eukaryotes and prokaryotes.
17. What is annotation? How does it apply to bioinformatics?

Thought Questions

NEW

1. The process of transcription will generate positive supercoils in front of the polymerase as it moves along a DNA template. Why doesn't the DNA in front of the polymerase become so knotted that the polymerase can no longer separate the DNA strands?
2. Why do cells secrete some proteins into their environments?
3. Type I protein secretion systems transport certain proteins from the cytoplasm of gram-negative bacteria directly to the outside of the cell, across two membranes. How might the system "know" which proteins to transport?

End-of-chapter **Thought Questions** further challenge students to think critically by asking them to consider the big-picture concepts introduced in that chapter. The answers to the questions are included in the instructor's manual only, making them great discussion, quiz, and homework questions.



Replicative cycle of HSV-1. The HSV-1 virion binds to receptors on the host cell membrane and releases its capsid in the cytoplasm. The DNA chromosome is transferred into the host nucleus to conduct the replicative cycle.

Resources for Instructors

The Instructor's Resource Disc includes:

- PowerPoint lecture slides now with additional clicker questions and new summary slides, revised for the Second Edition.
- All of the photographs and drawn figures from the text as jpegs and in PowerPoint format.
- All Process Animations for offline use.

Coursepacks

At no cost to professors or students, Norton coursepacks for online or hybrid courses are available in a variety of formats, including all versions of Blackboard and WebCT. With just a simple download from our instructor's website, an adopter can bring high-quality Norton digital media into a new or existing online course (no extra student passwords required), and it's theirs to keep forever. Content includes chapter-based assignments, test banks and quizzes, interactive learning tools, and all content from the StudySpace website.

Test Bank

Thoroughly revised for the Second Edition and using an evidence-centered approach designed by Valerie Shute (Florida State University) and Diego Zapata-Rivera (Educational Testing Service), each chapter of the Test Bank is structured around a Concept Map and evaluates student knowledge on three distinct levels:

- **Factual** questions test students' basic understanding of facts and concepts.
- **Applied** questions require students to apply knowledge in the solution of a problem.
- **Conceptual** questions require students to engage in qualitative reasoning and to explain why things are as they are.

Questions are further classified by section and difficulty, making it easy to construct tests and quizzes that are meaningful and diagnostic according to instructor need. Questions are multiple-choice and short-answer. The Test Bank is available in *ExamView* Assessment Suite, Word RTF, and PDF formats.

Norton Gradebook

With the free, easy-to-use Norton gradebook, instructors can easily access StudySpace student quiz results and avoid email inbox clutter. No course setup required. For more information and an audio tour of the gradebook, visit WWNORTON.COM/COLLEGE/NRL/GRADEBOOK.

Instructor's Manual

Full of suggestions for enhancing lectures using the Second Edition, the Instructor's Manual includes detailed chapter outlines and summaries, discussion topics to engage students in lecture or recitation, a guide to the electronic media—including animations—that accompanies *Microbiology*, and additional readings to help make your lectures dynamic and interactive. Answers to the end-of-chapter Review Questions and Thought Questions are also included.

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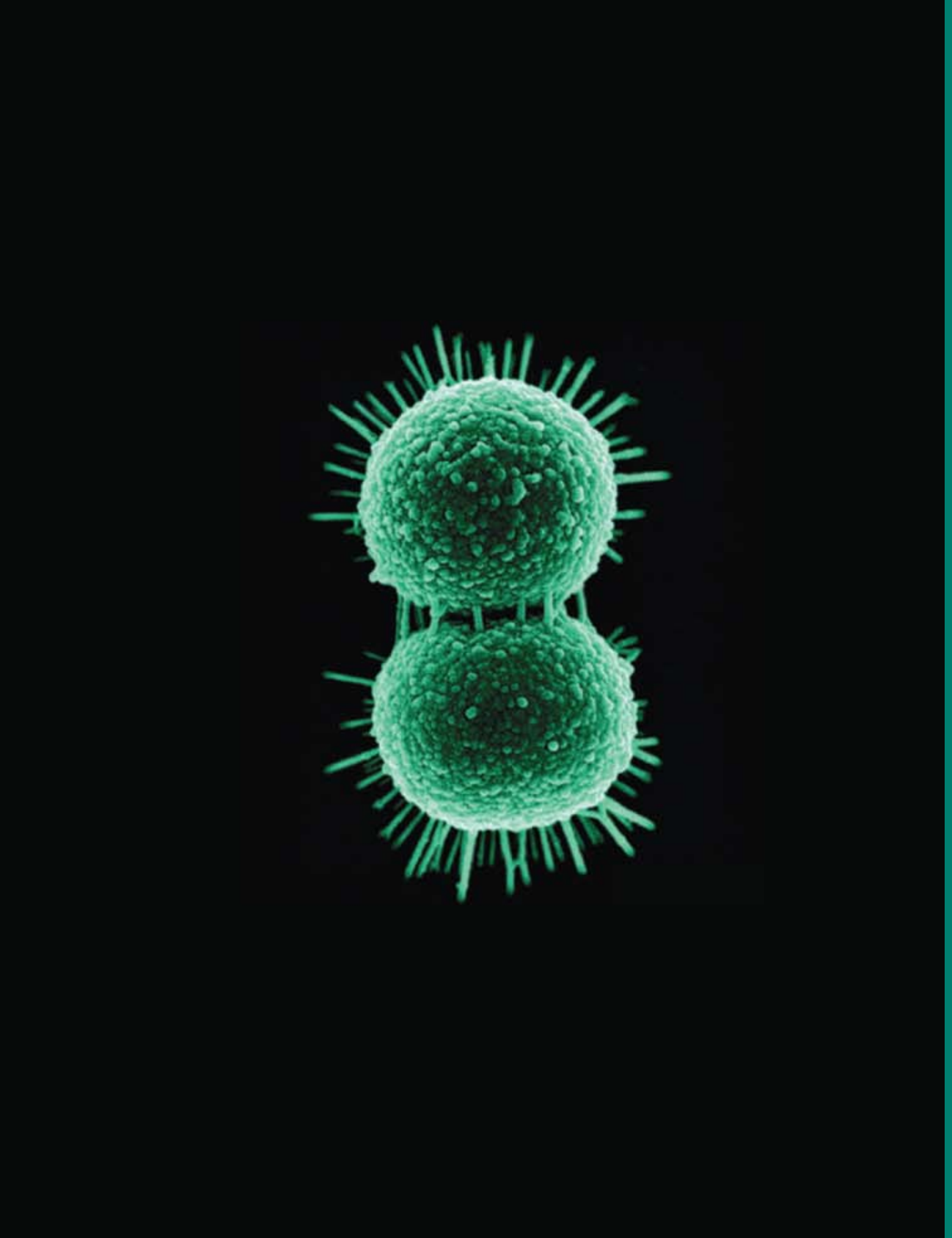

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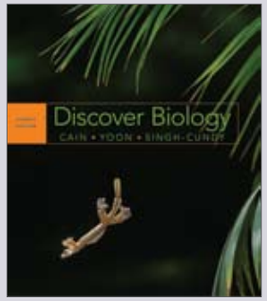

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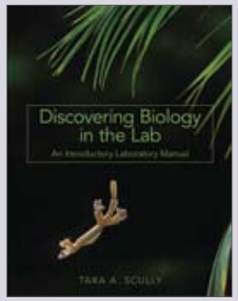

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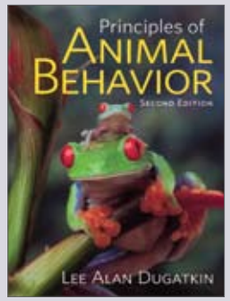

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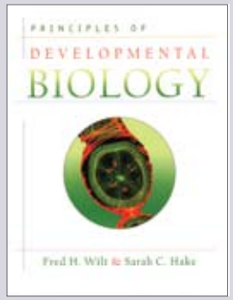

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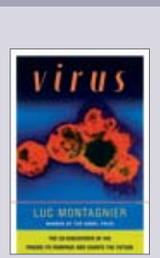

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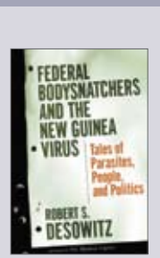

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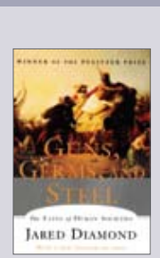

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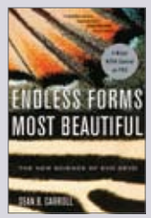

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On the back cover: Mimivirus, a cause of pneumonia, the largest known virus, larger even than some bacteria. Its genome poses intriguing questions for evolution. This cryo-EM model was developed by Michael Rossmann and colleagues. The star-shaped vertex (colorized blue) opens to release viral DNA within the host cell. The coloring is based on radial distance from the center of the virus. Gray is from 0 to 180 nanometers (nm); red, from 180 to 210 nm; and rainbow coloring from red to blue, between 210 and 250 nm. *Source: Chuan Xiao et al. 2009. PLoS Biology 7:e1000092.*

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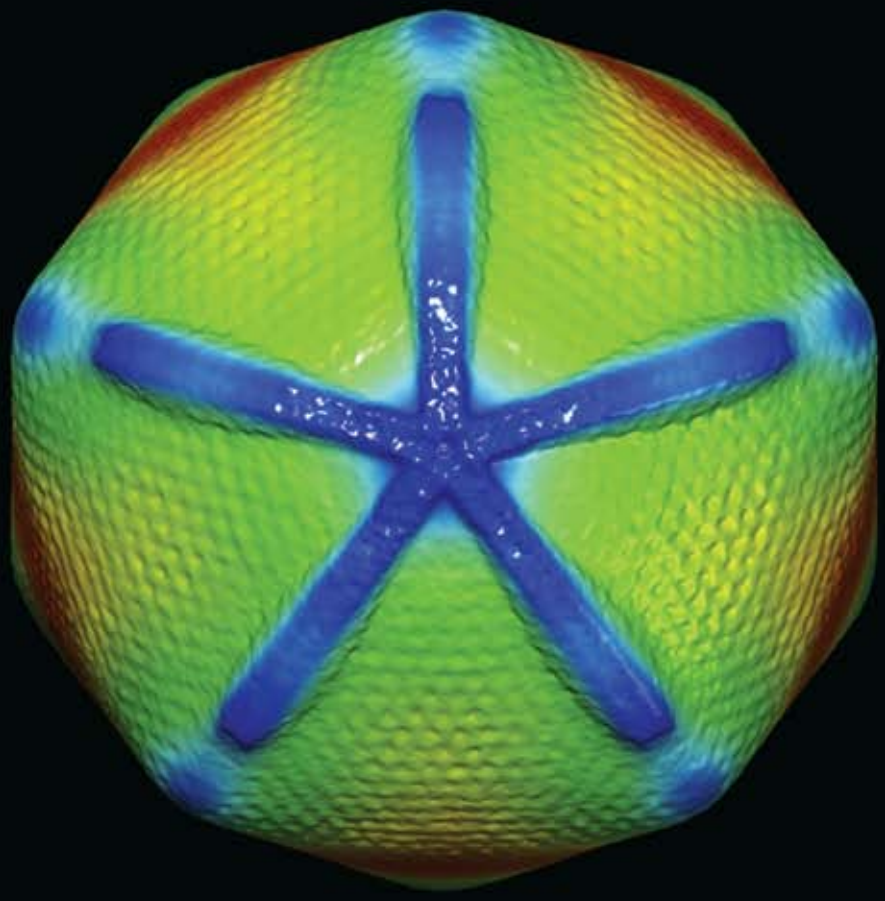

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