

GLOBAL
EDITION



Brock Biology of Microorganisms

FIFTEENTH EDITION

Madigan • Bender • Buckley • Sattley • Stahl



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Microbial Growth and Its Control

microbiology now

Picking Apart a Microbial Consortium

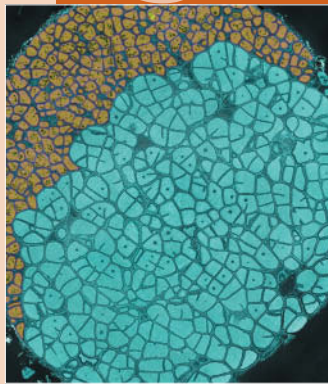
In nature, certain metabolic processes are carried out by microbes that team up to get the job done, a cozy arrangement called a consortium. Such is the case with the oxidation of methane (CH_4) linked to the reduction of sulfate (SO_4^{2-}) in anoxic marine sediments. The overall reaction ($\text{CH}_4 + \text{SO}_4^{2-} \rightarrow \text{HCO}_3^- + \text{HS}^- + \text{H}_2\text{O}$) is exergonic and the small amount of energy released is shared between two distinct microbes. The methane oxidizer in the consortium is a species of Archaea nicknamed ANME (for anaerobic methanotroph, blue in photo), and its sulfate-reducing partner is a species of Bacteria (brown in photo). The consortium is thought to play a key role in the carbon cycle as a major methane sink, and thus a detailed picture of how it works is important to our understanding of the global carbon economy, climate change, and marine biogeochemistry.

Researchers have tried for years to separate the consortium into its components but always found that methane oxidation required both organisms. However, some researchers hypothesized that it might be possible to replace the sulfate reducer with an artificial electron acceptor and that this might unlock the consortium and allow the methanotroph to grow in pure culture. Using an electron acceptor called AQDS, the scientists discovered that they could turn off sulfate reduction in the consortium while maintaining CH_4 oxidation. During this process, the methanotroph used electrons from CH_4 to reduce AQDS rather than passing them on to its sulfate-reducing partner. Several other electron acceptors known to support anaerobic respiration also sustained methane oxidation, giving hope that ANME may eventually be obtained in pure culture.

The ability to grow a microbe in pure culture is the "gold standard" for the study of its physiology, biochemistry, regulation, and several other aspects of its biology. In the case of the ANME-sulfate reducer consortium, several physiologies were active at once, and resolving these many reactions proved to be a major scientific challenge. However, if further work shows that ANME can be removed from the consortium and grown in pure culture, detailed aspects of its biology can be studied that were not possible when the organism was tightly coupled to its partner in the consortium (photo).

Source: Scheller, S., H. Yu, G.L. Chadwick, S.E. McGlynn, and V.J. Orphan. 2016. Artificial electron acceptors decouple archaeal methane oxidation from sulfate reduction. *Science* 351: 703–706.

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Microbial Infection and Pathogenesis

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The Microbial Community That Thrives on Your Teeth

Few people have such superb oral hygiene that they lack dental plaque, the microbial biofilm that forms on and between teeth and along or below the gumline. If not removed regularly, dental plaque invariably leads to dental caries (cavities), the condition in which portions of tooth enamel and dentin break down from the onslaught of bacterial activities. Dental plaque and dental caries develop from the natural tendency of oral bacteria such as *Streptococcus mutans* and its close relative *S. sobrinus* to attach firmly to the teeth and gums and ferment sucrose (table sugar) to lactic acid, which attacks the teeth and slowly rots them away.

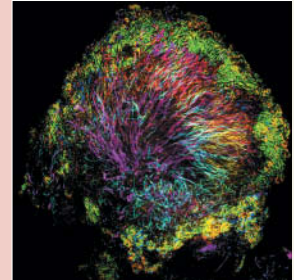
Until recently, dental plaque was thought to consist largely of the aforementioned streptococci. Both species could easily be isolated from dental plaque and both light and electron microscopy typically showed large numbers of cocci in chains, a hallmark of the genus *Streptococcus*. But a recent molecular ecology study of the microbial diversity of dental plaque revealed that this material is composed of more than just streptococci and develops in a precisely structured way.

The photo here is a light micrograph of a section through human dental plaque stained by fluorescence in situ hybridization (FISH). Different oligonucleotides, each specific for a different major phylum of Bacteria and containing a distinct fluorescent dye, were allowed to hybridize to the ribosomal RNA in cells in the plaque and then observed by fluorescence microscopy. Surprisingly, instead of seeing primarily streptococci, the researchers saw a diverse and highly organized microbial community. The micrograph shows streptococci (stained green) located primarily at the periphery of the plaque beyond several other bacteria that combine to form a scaffold emerging from the tooth surface. These include *Corynebacterium* (purple), *Capnocytophaga* (red), *Fusobacterium* (yellow), *Leptotrichia* (blue-green), and *Haemophilus* (orange), among others. A major conclusion that emerged from this study was that the scaffolding microbes likely function to position the streptococci out into the oral cavity where sucrose should be more available.

New views of old problems often reveal surprising results. In the case of dental plaque, FISH technology has revealed a whole new microbial world in a habitat previously thought to be dominated by only two species of well-characterized bacteria.

Source: Mark Welch, J.L., et al. 2016. Biogeography of a human oral microbiome at the micron scale. *Proc. Natl. Acad. Sci. (USA)* 113: doi: 10.1073/pnas.1522149113.

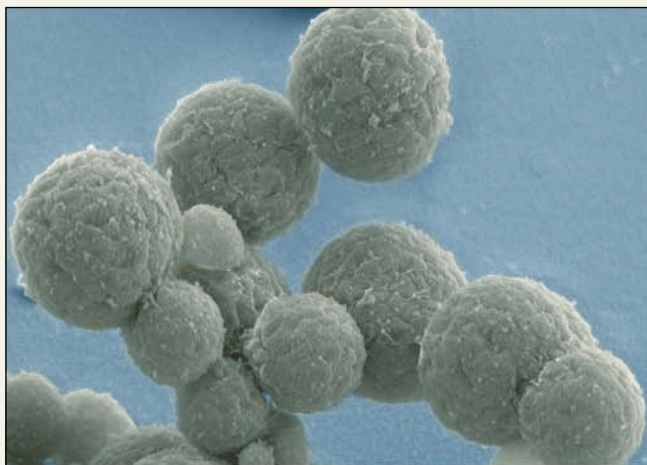
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Microbiology today and tomorrow.

Genomics, and the various “omics” it has spawned, support content throughout the Fifteenth Edition ensuring that today’s students understand the transformation that biology, and specifically microbiology, has undergone – and preparing them for the fast paced nature of the science.



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Creation of a New Life Form: Design of a Minimal Cell

A cell’s genome is its blueprint for life. However, what is the bare minimum number of genes needed to sustain a free-living cell? This is a question that microbiologists at the J. Craig Venter Institute (JCVI) have attempted to answer ever since they sequenced the genomes of several *Mycoplasma* species in the 1990s. Because *Mycoplasma* species are parasitic bacteria, their genomes are already reduced in size and hence provide an excellent foundation for creating a “minimal cell.” However, little did the scientists at JCVI suspect that it would take 20 years to satisfy their scientific curiosity!

Instead of beginning by genetically manipulating a *Mycoplasma* species, microbiologists at JCVI wanted to have more control. To begin unraveling the genetic requirements for life, they first generated a synthetic self-replicating *Mycoplasma* (described in this chapter). The genome of this pioneering synthetic life form was synthesized from scratch based on its known genome sequence. The synthetic cell did not possess a “designer genome,” or even a minimal one; it simply contained its own genome but one completely constructed in the laboratory. This breakthrough in synthetic biology provided the technology needed for microbiologists to create designer genomes.

Using comparative genomics and prior knowledge about specific gene sequences, microbiologists at JCVI continued their work by designing and synthesizing several minimal genomes that they hypothesized would sustain life. To their dismay, none of these resulted in a viable cell. So instead, they generated modules of DNA corresponding to a *Mycoplasma* genome and sewed different combinations together to form synthetic genomes. Once viable cells were obtained from transplanting these genomes, nonessential genes from the smallest genome were identified by transposon mutagenesis. After removing these unnecessary genes, a synthetic minimal cell coined JCVI-syn3.0 was created (see photo). This autonomous life form possesses a 531-kilobase genome encoding 473 genes; JCVI-syn3.0 thus contains a genome smaller than any other free-living cell.

While this work showcases the amazing advancements in synthetic biology and the potential for creating designer cells with novel functions, a surprising mystery surrounds this minimal cell: The roles for almost a third of JCVI-syn3.0’s genes remain unknown, highlighting how much we still need to learn about the genetic foundation of a living cell.

Source: Hutchison, C.A. 3rd, et al. 2016. Design and synthesis of a minimal bacterial genome. *Science* 351(6280): aad6253. Photo provided by Clyde Hutchison and J. Craig Venter, JCVI and Thomas Deerinck and Mark Ellisman, NCMIR.

EXPLORE THE MICROBIAL WORLD

TINY CELLS

Viruses are very small microbes and range in diameter from as small as 20 nm to almost 750 nm. Although no cells exist that are as small as most viruses, the recent discovery of ultra-small bacterial cells,¹ has pushed the lower limits of cell size to what microbiologists feel must be very close to the minimal value.

Microbiologists collected groundwater, which travels through Earth’s deep subsurface, from a Colorado USA aquifer (Figure 1) and ran it through a membrane filter whose pores were only 0.2 µm in diameter. The liquid that passed through the filter was then subjected to microbiological analyses. Surprisingly, since filters with 0.2-µm pores have been used for decades to remove bacterial cells from solutions to generate “sterile solutions,” prokaryotic cells were present in the groundwater filtrate. In fact, a diverse array of bacteria were present in the filtrate, revealing that the groundwater was inhabited by a microbial community of tiny cells that microbiologists have come to call “ultramicrobacteria.”

Cryo-electron microscopy, in which a specimen is examined at extremely cold temperatures without fixation (chemical treatment that can alter a cell’s morphology), showed the groundwater ultramicrobacteria to consist primarily of oval-shaped cells about 0.2 µm in diameter (Figure 2). The volume of these cells was calculated to be about 1/100 that of a cell of the bacterium *Escherichia coli* (see Table 2.1) such that nearly 150 of the small cells could fit into one *E. coli* cell! Each of the tiny cells contained about 50 chromosomes, which is also about 1/100 of the number present in a slowly growing 100-min generation time cell of *E. coli*. The very small size of the



Figure 1 Sampling the anoxic groundwater aquifer that parallels the Colorado River near Rifle, Colorado.

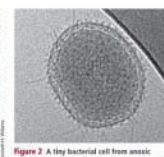


Figure 2 A tiny bacterial cell from anoxic groundwater that passed through a filter with 0.2-µm pores. The cell is oval-shaped 0.2 µm in diameter.

metabolically minimal lifestyle for these tiny cells and a survival strategy of cross-feeding essential nutrients with neighboring species in their microbial community.

Although we do not yet know exactly how small a microbial cell can be, microbiologists are closer to this number than ever.

EXPLORE THE MICROBIAL WORLD

THE GUT-BRAIN AXIS

Interactions between the gut microbes and the host brain and general nervous system called the gut-brain axis have been long appreciated because of possible contributions to behavioral disorders. We know that there is a close relationship between gut microbes and behavior such as inflammation-based stress and obesity (Section 20.8). However, gut microbes also associated with action, a general term for a spectrum of behavioral disorders together called autism spectrum disorders that can emerge in the first 24 months of life, causing substantial impairments in social interaction and communication and later by repetitive behaviors and restricted interests.

Human autism has been attributed to a combination of genetic and environmental factors. An environmental risk factor for a child developing autism after behavioral disorders is maternal immune activation (MIA), which is characterized by inflammatory factors in the blood, placenta, and amniotic fluid during pregnancy and can be caused, for example, by viral infections. Although the role of the gut microbiome in autism remains unclear, some features of autism can be attributed to microbial-mediated defects in the gut microbial community.

The offspring of mice in which MIA has been induced display autism-like behaviors, such as communication deficits and anxiety (Figure 1a). These behavioral changes are associated with a loss of neuronal energy, a shift in the composition of gut microbial and behavioral expression, and altered changes in autism features, and a 40-fold increase in mouse levels of the chemical 4-ethylphenylamine (Figure 1b). This compound is made from the amino acid tyrosine by some gut microbes. When administered alone, it induces anxiety-like behaviors in normal mice. However, a mutation blocking its ability to bind to receptors in cortex, striatum, amygdala, and hippocampus, and its ability to bind to the altered receptors, blocks the anxiety-like behaviors and restores synaptic function in the brain (Figure 1c). This suggests that the gut microbiome may be a target for autism treatment and that the chemical 4-ethylphenylamine is a potential target for autism treatment.

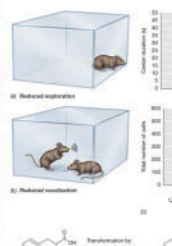


Figure 1 Influence of gut microbes on behavior. (a) Offspring of mother mice induced immune activation (MIA) show autism-like behaviors, related to the loss of neuronal energy in the brain and behavioral expression. (b) Some gut microbes can convert the amino acid tyrosine into 4-ethylphenylamine. The compound is made from the amino acid tyrosine by some gut microbes. When administered alone, it induces anxiety-like behaviors in normal mice. (c) A mutation blocking the ability of 4-ethylphenylamine to bind to receptors in cortex, striatum, amygdala, and hippocampus, and its ability to bind to the altered receptors, blocks the anxiety-like behaviors and restores synaptic function in the brain.

These studies offer an insight of the influence of the gut microbiome on behavior and point to the possibility of using a rational modification of the gut community, such as probiotics with targeted metabolic functions, to improve behavioral disorders such as autism. Furthermore, the production of aberrant behaviors by releasing stress levels of the gut microbiome-derived metabolite 4-ethylphenylamine to normal mice suggests that other neurobiological disorders may also be linked to the abnormal levels of microbial metabolites in certain brain regions. However, the use of probiotics to improve behavioral disorders is still in the early stages of assessing the gut microbiome’s role in autism.

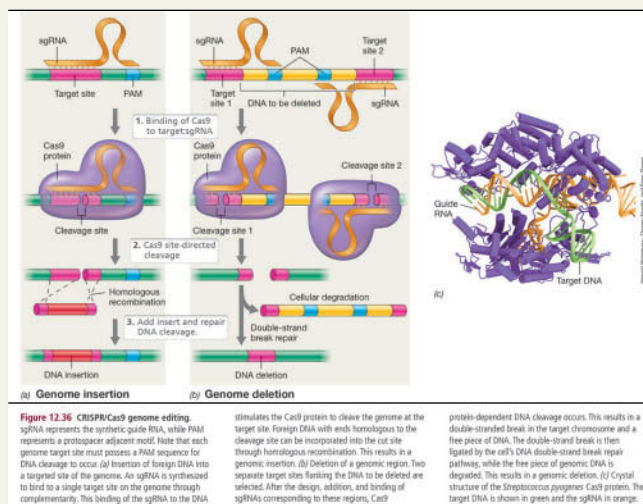
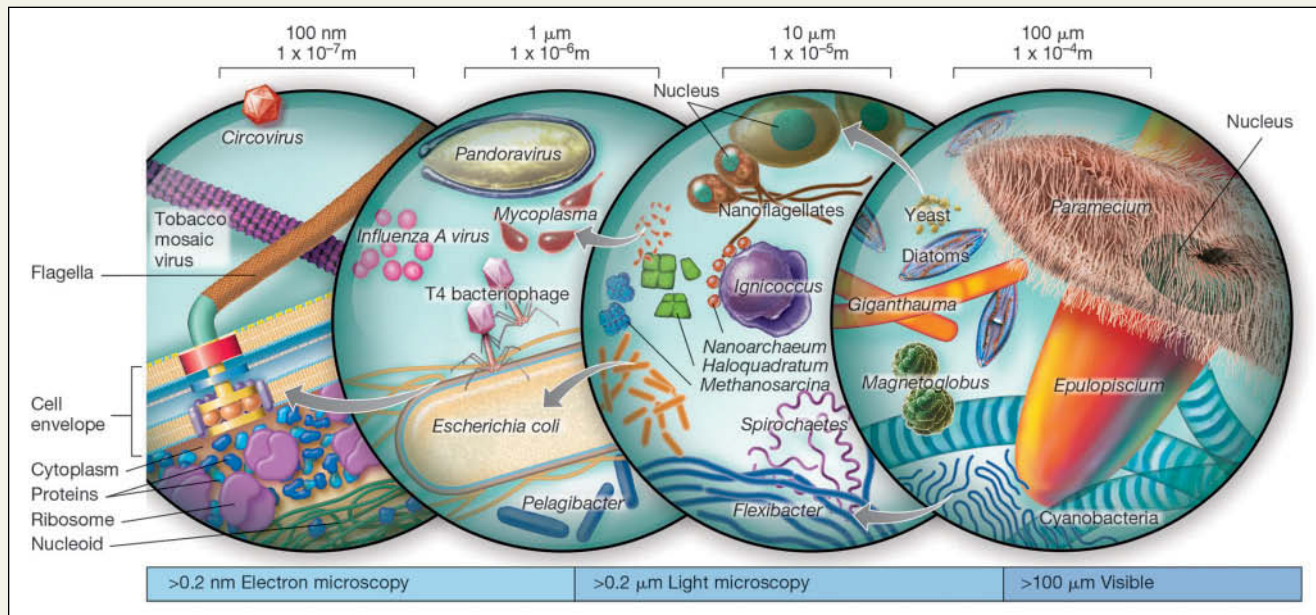


Figure 12.36 CRISPR/Cas9 genome editing. sgRNA represents the synthetic guide RNA, while PAM represents a protospacer adjacent motif. Note that each genome target site must possess a PAM sequence for DNA cleavage to occur. (a) Insertion of foreign DNA into a targeted site of the genome. An sgRNA is synthesized to bind to a single target site on the genome through complementarity. This binding of the sgRNA to the DNA stimulates the Cas9 protein to cleave the genome at the target site. Foreign DNA with ends homologous to the cleavage site can be incorporated into the cut site through homologous recombination. This results in a genomic insertion. (b) Deletion of a genomic region. Two separate target sites flanking the DNA to be deleted are selected. After the design, addition, and binding of sgRNAs corresponding to these regions, Cas9 protein-dependent DNA cleavage occurs. This results in a double-strand break in the target chromosome and a free piece of DNA. The double-strand break is then repaired by the cell’s DNA double-strand break repair pathway, while the free piece of genomic DNA is degraded. This results in a genomic deletion. (c) Crystal structure of the Streptococcus pyogenes Cas9 protein. The target DNA is shown in green and the sgRNA in orange.

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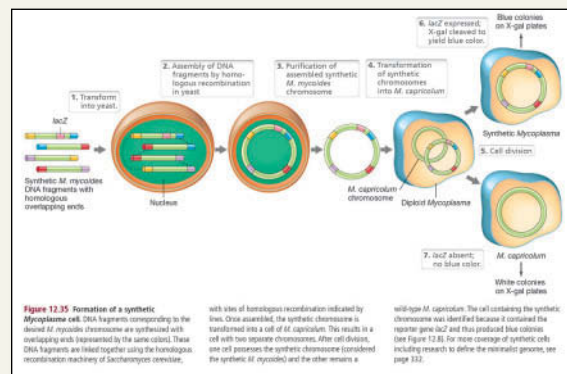
The Fifteenth Edition continues its legacy of authoritative, accessible writing; beautiful and clear art; and student-focused pedagogy, engaging learners in the science.



Student focused pedagogy informs the organization and design of each chapter feature

TABLE 9.6 Some omics terminology

| | |
|--------------------|---|
| DNA | <p>Genome the total complement of genetic information of a cell or a virus</p> <p>Metagenome the total genetic complement of all the cells present in a particular environment</p> <p>Epigenome the total number of possible epigenetic changes</p> <p>Methylome the total number of methylated sites on the DNA (whether epigenetic or not)</p> <p>Mobilome the total number of mobile genetic elements in a cell</p> |
| RNA | <p>Transcriptome the total RNA produced in an organism under a specific set of conditions</p> |
| Protein | <p>Proteome the total set of proteins encoded by a genome; sometimes also used in place of <i>translatome</i></p> <p>Translatome the total set of proteins present under specified conditions</p> <p>Interactome the total set of interactions between proteins (or other macromolecules)</p> <p>Secretome the total set of proteins secreted by a cell</p> |
| Metabolites | <p>Metabolome the total complement of small molecules and metabolic intermediates</p> <p>Glycome the total complement of sugars and other carbohydrates</p> |
| Organisms | <p>Microbiome the total complement of microorganisms in an environment (including those associated with a higher organism)</p> <p>Virome the total complement of viruses in an environment</p> <p>Mycobiome the total complement of fungi in a natural environment</p> |



Chapter Review

I - Fundamentals of Host Defense

- 26.1 Innate immunity is an inborn protective response to infection characterized in part by recognition and elimination of common pathogens, primarily through the activity of phagocytes. Adaptive immunity is the acquired ability of the immune system to eliminate specific pathogens from the body via lymphocyte-mediated responses, including the production of antibodies that bind foreign antigens on pathogens or their products.
- 26.2 The human body possesses numerous protective defenses against infectious agents. Natural host resistance to infection includes physical barriers to infection posed by the skin and mucosa, as well as chemical barriers to infection including acidic secretions, detritus, and lysozyme. The specificity of pathogens for particular tissues limits which hosts and tissues might be susceptible to infection.

II - Cells and Organs of the Immune System

- 26.3 Cells involved in innate and adaptive immunity originate from hematopoietic stem cells in bone marrow. The blood and lymph systems circulate cells and proteins that are important components of the immune response. Diverse leukocytes participate in immune responses in all parts of the body.

- 26.4 What is the origin of the phagocytes and lymphocytes active in the immune response? Track the maturation of B cells and T cells.

III - Phagocyte Response Mechanisms

- 26.5 Pathogens may colonize host tissues when appropriate nutrients and growth conditions are present, such as on mucosal surfaces, especially where the composition of the normal microbiota has been altered. Innate responses to microbial invasion and tissue damage are initiated by the release of chemokines, which recruit phagocytes and other immune cells to sites of infection.
- 26.6 Innate recognition of common pathogens occurs through pathogen-associated molecular patterns (PAMPs). Phagocytes recognize PAMPs through preformed pattern recognition receptors (PRRs). The recognition and interaction process stimulates phagocytes to destroy the pathogens through a signal transduction mechanism that induces phagocytosis of the infectious agent.
- 26.7 Phagocytosis is the engulfing of infectious particles by phagocytes. Engulfed pathogens are bathed in toxic oxygen compounds inside the phagosome, killing and degrading them. However, some pathogens have developed various defense mechanisms to avoid or inhibit phagocytes, including secretion of leukostathins, the presence of a capsule, and biosynthesis of carotenoid pigments, which combat oxidative stress.

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BEFORE CLASS

Reading Questions, art-based activities and MCAT Prep, along with Quantitative Questions, prepare students for in-depth class discussion.

Alphaproteobacteria can be distinguished by which of the following characteristics?

- They are the smallest class of *Proteobacteria*.
- All the organisms are anaerobic.
- All the organisms are gram-negative.
- All the organisms are copiotrophs.

Submit Hints My Answers Give Up Review Part

Identify the steps that lead to a mutation, and also correctly identify which type of mutation is indicated after these steps have occurred. Drag the appropriate labels to their respective targets.

Labels to be dragged:

- Translation
- Misense mutation
- Silent mutation
- Normal DNA replication
- Nonsense mutation
- Transcription of light green strand

Submit My Answers Give Up

Microbial Symbioses with Humans

24

microbiologynow

Frozen in Time: The Iceman Microbiome

Humans and their microbial associates—collectively called the human microbiome—have coevolved for millennia. As we will see in this chapter, the human microbiome influences a person's health, disease, and predisposition to disease. Among our intimate microbial associates, the pathogenic bacterium *Helicobacter pylori* is known to have developed a close relationship with humans in the distant past and to have coevolved with humans. *H. pylori* colonizes the stomachs of about half the human race. Although this bacterium generally does not cause overt disease, it is a major risk factor for the development of ulcers and stomach cancer. Moreover, because *H. pylori* is transmitted primarily by contact within families, the distribution of genetic variants of this bacterium may yield clues to past human migrations.

Unraveling the details of the *H. pylori* ancestry is complicated by the ability of different strains of this bacterium to recombine their genetic information. Because the DNA of various strains has mixed over long periods, the reconstruction of population movement inferred from genome sequences of modern *H. pylori* strains is incomplete. One of the biggest unanswered questions was the origin of strains now common among modern Europeans, which appear to be hybrids of strains originating in Asia and Africa. Unfortunately, the sequence data did not point to a reliable time interval in which that mingling of human populations occurred—an important period of human migration that was estimated to have occurred 10,000–50,000 years ago.

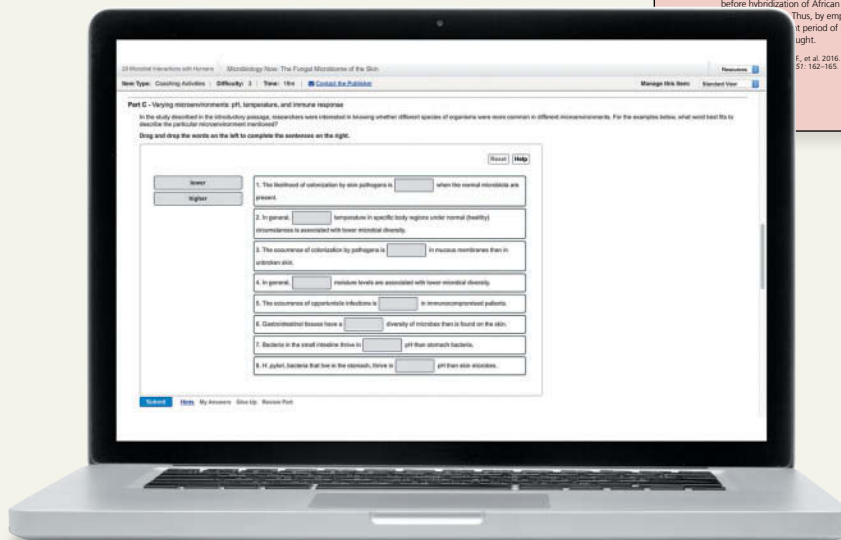
This estimate has now been greatly refined following the remarkable discovery of a well-preserved 5300-year-old European Copper Age mummy frozen in the Italian Alps. Using the newest methods for DNA sequencing, it was possible to reconstruct the genome of *H. pylori* preserved in the stomach of the “Iceman” (see photo), the corpse discovered when melting ice revealed the human remains on the side of a mountain. The Iceman *H. pylori* genome sequence turned out to be an almost pure representative of the Asian population, which means this *H. pylori* strain was present in Europe before hybridization of African and Asian strains produced the modern European population. Thus, by employing historical biogeography, we now know that the period of human migration was much more recent than previously thought.

F. et al. 2016. The 5300-year-old *Helicobacter pylori* genome of the Iceman. *PLoS ONE* 11(2): e0162165.

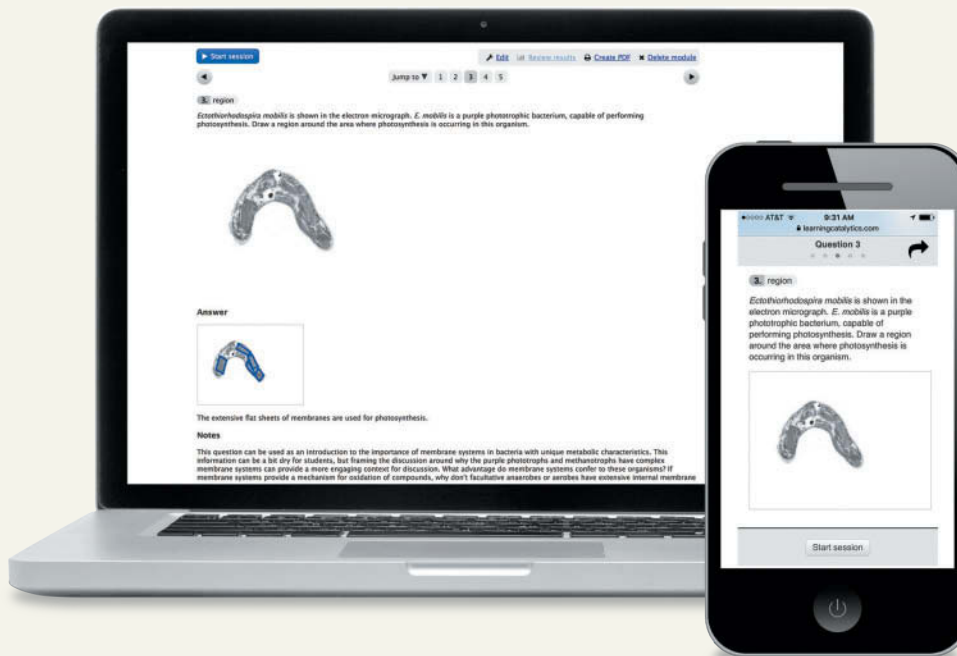


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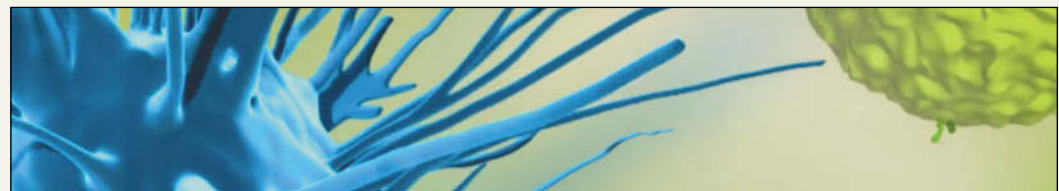
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MicroFlix Activity: Immunology -- Cell-Mediated Immunity

Can you put the steps of cell-mediated immunity in order and label the cells and molecules involved? To review cell-mediated immunity, watch this MicroFlix animation: [T Cells and Cellular Immunity](#).

Part A - Correctly sort the steps involved in cell-mediated immunity

Put the steps involved in cell-mediated immunity in order.

In the lymph nodes, cytotoxic T cells encounter dendritic cells displaying epitope on MHC-I. The Tc cell is activated.

The active cytotoxic T cell (CTL) leaves the lymph node “looking” for infected host cells displaying the same epitope on their MHC-I. The CTL uses its surface receptors to recognize the infected cell.

The CTL secretes specialized molecules to penetrate the infected host cell causing programmed cell death.

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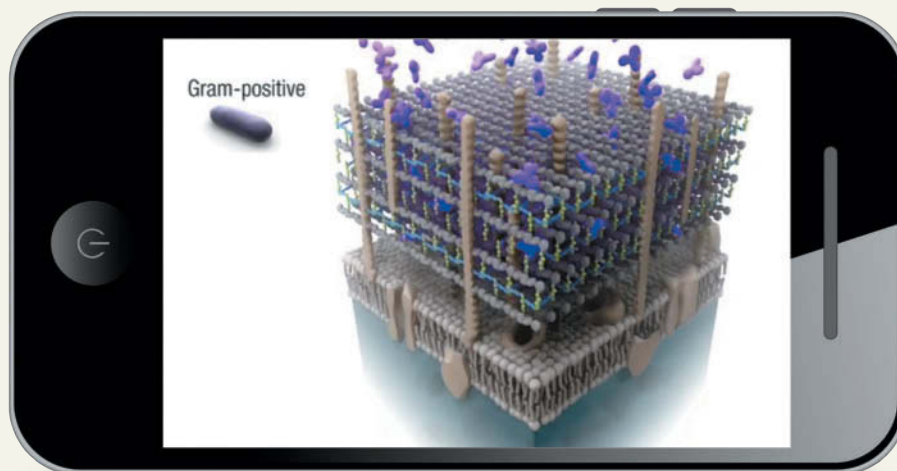
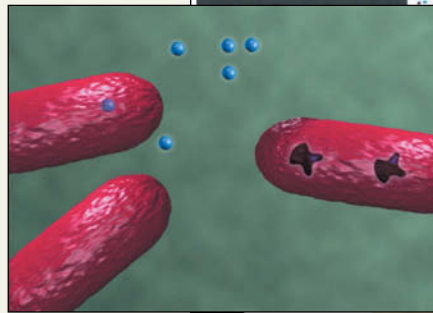
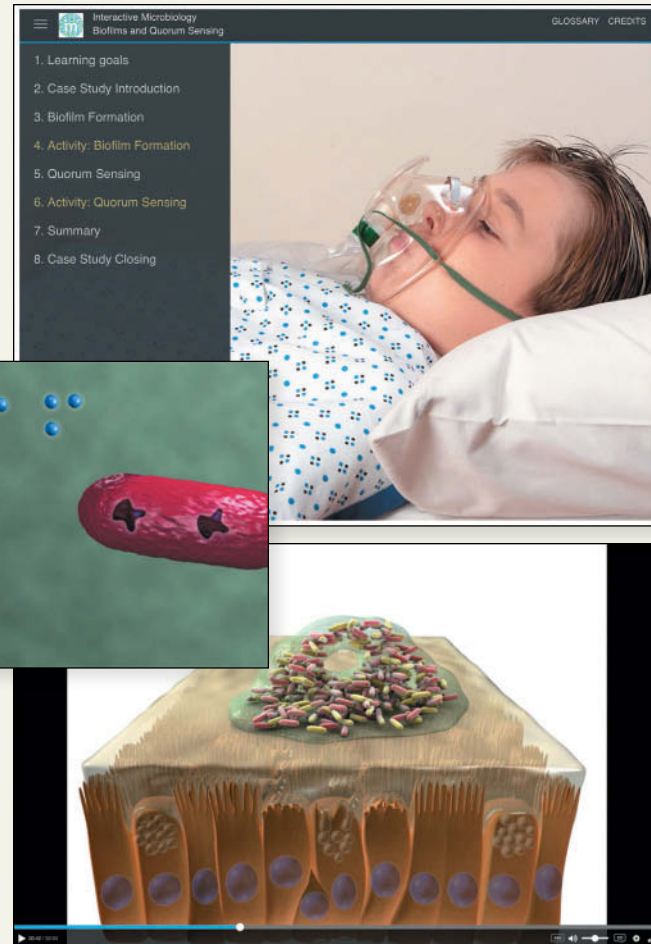
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Submit Hints My Answers Give Up Review Part

Visualize Microbiology

AFTER CLASS

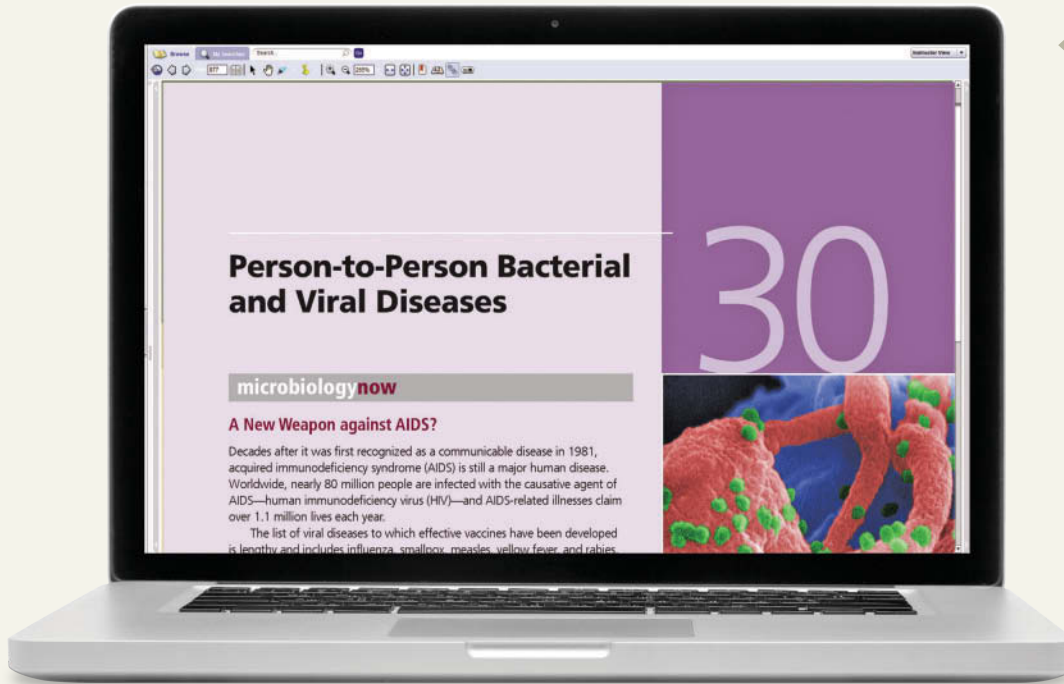
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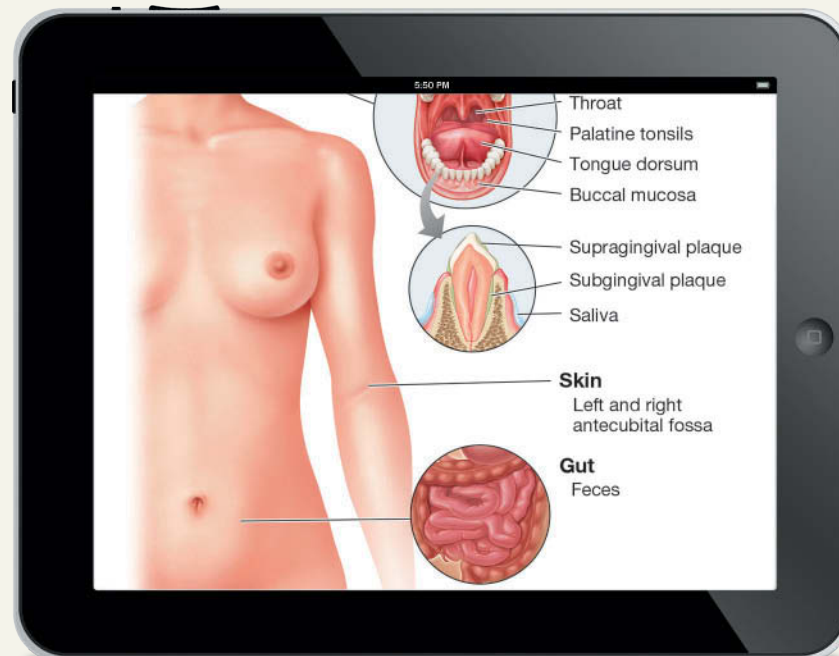
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KELLY S. BENDER

Southern Illinois University Carbondale

DANIEL H. BUCKLEY

Cornell University

W. MATTHEW SATTLEY

Indiana Wesleyan University

DAVID A. STAHL

University of Washington Seattle



330 Hudson Street, NY NY 10030

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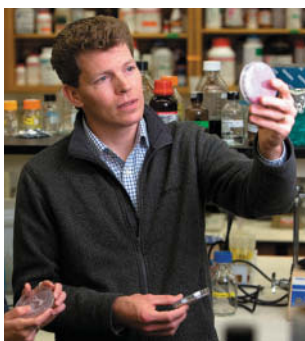
About the Authors



Michael T. Madigan received his B.S. in Biology and Education from Wisconsin State University–Stevens Point (1971) and his M.S. (1974) and Ph.D. (1976) in Bacteriology from the University of Wisconsin–Madison in the laboratory of Thomas Brock. Following a postdoc at Indiana University with Howard Gest, Mike moved to Southern Illinois University Carbondale, where he taught courses in introductory microbiology and bacterial diversity as a professor of microbiology for 33 years. In 1988 Mike was selected as the Outstanding Teacher in the College of Science and in 1993, the Outstanding Researcher. In 2001 he received the SIUC Outstanding Scholar Award. In 2003 he received the Carski Award for Distinguished Undergraduate Teaching from the American Society for Microbiology, and he is an elected Fellow of the American Academy of Microbiology. Mike’s research is focused on bacteria that inhabit extreme environments, and for the past 20 years his emphasis has been Antarctic microbiology. Mike has co-edited a major treatise on phototrophic bacteria and served for 10 years as chief editor of the journal *Archives of Microbiology*. He currently serves on the editorial board of the journals *Environmental Microbiology* and *Antonie van Leeuwenhoek*. Mike’s other interests include forestry, swimming, reading, and caring for his dogs and horses. He lives on a quiet lake with his wife, Nancy, three dogs (Kato, Nut, and Merry), and three horses (Eddie, Gwen, and Georgie).



Kelly S. Bender received her B.S. in Biology from Southeast Missouri State University (1999) and her Ph.D. (2003) in Molecular Biology, Microbiology, and Biochemistry from Southern Illinois University Carbondale. Her dissertation research focused on the genetics of perchlorate-reducing bacteria. During her postdoctoral fellowship, Kelly worked on the genetic regulation of sulfate-reducing bacteria in the laboratory of Judy Wall at the University of Missouri–Columbia. She also completed a transatlantic biotechnology fellowship at Uppsala University in Sweden researching regulatory small RNAs in bacteria. In 2006, Kelly returned to her alma mater, Southern Illinois University Carbondale, as an Assistant Professor in the Department of Microbiology and in 2012 was tenured and promoted to Associate Professor. Her lab studies a range of topics including regulation in sulfate-reducing bacteria and the microbial community dynamics of sites impacted by acid mine drainage. Kelly teaches courses in introductory microbiology and microbial diversity, has served on numerous federal grant review panels, and is an active member of the American Society for Microbiology (ASM). Her other interests include spending time with her daughter, Violet, and husband, Dick.



Daniel H. Buckley is a Professor at Cornell University in the School of Integrative Plant Science. He earned his B.S. in Microbiology (1994) at the University of Rochester and his Ph.D. in Microbiology (2000) at Michigan State University. His graduate research focused on the ecology of soil microbial communities and was conducted in the laboratory of Thomas M. Schmidt in affiliation with the Center for Microbial Ecology. Dan’s postdoctoral research examined linkages between microbial diversity and biogeochemistry in marine microbial mats and stromatolites and was conducted in the laboratory of Pieter T. Visscher at the University of Connecticut. Dan joined the Cornell faculty in 2003. His research program investigates the ecology and evolution of microbial communities in soils with a focus on the causes and consequences of microbial diversity. He has taught both introductory and advanced courses in microbiology, microbial diversity, and microbial genomics. He received a National Science Foundation Faculty Early Career Development (CAREER) award in 2005 for excellence in integrating research and education. He has served as Director of the Graduate Field of Soil and Crop Sciences at Cornell and Co-Director of the Microbial Diversity summer course of the Marine Biological Laboratory in Woods Hole, Massachusetts. He currently serves on the editorial boards of *Applied and Environmental Microbiology* and *Environmental Microbiology*. Dan lives in Ithaca, New York, with his wife, Merry, and sons, Finn and Colin.



W. Matthew Sattley received his B.A. in Biology in 1998 from Blackburn College (Illinois) and his Ph.D. (2006) in Molecular Biology, Microbiology, and Biochemistry from Southern Illinois University Carbondale. His graduate studies focused on the microbiology of sulfur cycling and other biogeochemical processes in permanently ice-covered lakes of Antarctica. In his postdoctoral research at Washington University in Saint Louis, he studied the physiology and genomics of anoxygenic phototrophic bacteria in Robert Blankenship's laboratory. Matt then accepted a faculty appointment to the Department of Biology at MidAmerica Nazarene University (Kansas), where he supervised undergraduate research and taught courses in microbiology, environmental science, and cell biology. In 2010, Matt transitioned to the Division of Natural Sciences at Indiana Wesleyan University, where he is a Professor of Biology and Director of the Hodson Summer Research Institute, a faculty-led summer research program for undergraduate students in the Natural Sciences. His research group investigates the ecology, diversity, and genomics of bacteria that inhabit extreme environments. Matt is a member of the American Society for Microbiology (including its Indiana Branch) and the Indiana Academy of Science, and he currently serves as an expert reviewer for the undergraduate microbiology research journal *Fine Focus*. Matt lives in Marion, Indiana, with his wife, Ann, and sons, Josiah and Samuel. Outside of teaching and research, Matt enjoys playing drums, reading, motorcycling, and talking baseball and cars with his boys.



David A. Stahl received his B.S. degree in Microbiology from the University of Washington, Seattle, and completed graduate studies in microbial phylogeny and evolution with Carl Woese in the Department of Microbiology at the University of Illinois at Urbana-Champaign. Subsequent work as a postdoctoral fellow with Norman Pace, then at the National Jewish Hospital in Colorado, involved early applications of 16S rRNA-based sequence analysis to the study of natural microbial communities. In 1984 Dave joined the faculty at the University of Illinois with appointments in Veterinary Medicine, Microbiology, and Civil Engineering. In 1994 he moved to the Department of Civil Engineering at Northwestern University, and in 2000 returned to the University of Washington as professor in the Departments of Civil and Environmental Engineering and Microbiology. Dave is known for his work in microbial evolution, ecology, and systematics, and received the 1999 Bergey Award and the 2006 ASM Procter & Gamble Award in Applied and Environmental Microbiology. Dave is an elected fellow of the American Academy of Microbiology and a member of the National Academy of Engineering. His main research interests surround the biogeochemistry of nitrogen and sulfur and the microbial communities that sustain the associated nutrient cycles. His laboratory was first to culture ammonia-oxidizing *Archaea*, a group believed to be the key mediators of this process in the nitrogen cycle. Dave has taught several courses in environmental microbiology, was one of the founding editors of the journal *Environmental Microbiology*, and has served on many advisory committees. Outside the lab, Dave enjoys hiking, bicycling, spending time with family, reading a good science fiction book, and—with his wife, Lin—renovating an old farmhouse on Bainbridge Island.

Dedications

Michael T. Madigan

dedicates this edition to students who have drawn inspiration from his textbook to make some aspect of microbiology their life's work.

Kelly S. Bender

dedicates this book to the memory of her grandmother, Alberta, whose biggest regret in life was not being able to attend school past the fifth grade.

Daniel H. Buckley

dedicates this book to the memory of his mother, Judy, who taught me to see joy and wonder, even in the smallest of things.

W. Matthew Sattley

dedicates this book to his amazing wife, Ann, for her endless support and understanding.

David A. Stahl

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

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Preface

Welcome to an exciting new edition of *Brock Biology of Microorganisms* (BBOM). This Fifteenth Edition is the strongest yet and presents microbiology in the context of the excitement this science generates today. For three generations, students and instructors have relied on the accuracy, authority, consistency, and up-to-date presentation of BBOM to learn or teach the principles of modern microbiology. Both students and instructors will benefit from the Fifteenth Edition in at least four major ways: (1) from the use of cutting-edge research to illustrate basic concepts; (2) from the seamless integration of molecular and ecological microbiology with evolution, diversity, the immune system, and infectious diseases; (3) from the visually stunning art program and spectacular photos; and (4) from the wide assortment of teaching and learning tools that accompany the book itself.

Veteran authors Madigan, Bender, Buckley, and Stahl welcome new coauthor Matt Sattley to the Fifteenth Edition. Matt, a professor at Indiana Wesleyan University, teaches both general microbiology and health professions microbiology and did a great job of reorganizing and refreshing our coverage of immunology and related areas. With an extremely strong author team that employs experts in each of our major areas of emphasis, we sincerely feel that BBOM 15e is the best learning resource available in microbiology today.

What's New in the 15th Edition?

The Fifteenth Edition guides students through the six major themes of microbiology as outlined by the American Society for Microbiology Conference on Undergraduate Education (ASMCUE): Evolution, Cell Structure and Function, Metabolic Pathways, Information Flow and Genetics, Microbial Systems, and the Impact of Microorganisms. With enhanced and revised artwork complemented with over 90 new color photos, BBOM 15e presents microbiology as the visual science it is. Thirty-three new MicrobiologyNow chapter-opening vignettes were composed for this edition, each designed to introduce a chapter's theme through a recent discovery published in the microbiology literature. Several new Explore the Microbial World features were also developed for this edition, each designed to give students a feel for exciting special topics in microbiology and to fuel their scientific curiosity.

Genomics, and all of the various “omics” it has spawned, support content in every chapter of BBOM 15e, reflecting how the omics revolution has transformed all of biology, especially microbiology. Mastering the principles of the dynamic field of microbiology today requires an understanding of the supportive molecular biology. Hence, we have constructed BBOM 15e in a way that provides both the foundation for the science and the science itself. The result is a robust and modern treatment of microbiology that now includes exciting new chapters devoted to microbial systems

biology, synthetic biology, the human microbiome, and the molecular biology of microbial growth.

To strengthen the learning experience, each section summary in the chapter review is followed immediately by a review question to better link concept review with concept mastery. BBOM 15e is supported by MasteringMicrobiology™, Pearson's online homework, tutorial, and assessment system that assists students in pacing their learning and keeps instructors current on class performance. MasteringMicrobiology includes chapter-specific reading quizzes, MicrobiologyNow, Clinical Case and MicroCareer coaching activities, animation quizzes, MCAT Prep questions, and many additional study and assessment tools, including tutorials and assessments for the microbiology lab. Collectively, the content and presentation of BBOM 15e, coupled with the powerful learning tools of MasteringMicrobiology, create an unparalleled educational experience in microbiology.

Revision Highlights

Chapter 1

- The book begins with a revised and reorganized kickoff chapter that weaves introductory concepts in microbiology within an historical narrative. Foundational aspects of microbiology are now presented in the context of the major discoveries that have expanded our knowledge of the microbial world.
- Some highlights: introducing the principles of microscopy in a historical context; a new section on molecular biology and the importance of microbes in understanding the unity of life; the contributions of Carl Woese and the use of rRNA sequences to develop the universal tree of life; an introduction to the viral world; spectacular new summary art that explores the diversity of microbial life across a wide range of spatial scales.

Chapter 2

- Microbial cell structure and function are key pillars of microbiology, and this newly reworked and streamlined chapter offers a thorough introduction to comparative cell structure and provides the instructor with all of the tools necessary for effective classroom presentations. Coverage of nutrient transport systems has been moved to Chapter 3 to better present this topic in its proper context.
- Some highlights: a new Explore the Microbial World entitled “Tiny Cells”; unique attachment structures of *Archaea*; new coverage of archaeella.

Chapter 3

- The essential features of microbial metabolism necessary for understanding how microbes transform energy are laid out in a

logical sequence and at just the right level for introductory students. With the material on membrane transport now located here, the uptake of nutrients is highlighted as the initial step of any metabolic process.

- Some highlights: new coverage of the macromolecular composition of a cell; a more complete picture of energy transformation and the importance of free energy change; coverage of the citric acid cycle prior to (rather than following) discussion of the proton motive force.

Chapter 4

- Chapter 4 has been reorganized to provide the streamlined view of molecular biology necessary for both supporting and understanding virtually all aspects of microbiology today.
- Some highlights: new coverage of coupled transcription and translation in *Bacteria* and *Archaea*; new material on the assembly of cofactor-containing enzymes; stronger coverage of types I–VI secretion systems in gram-negative bacteria; updated art throughout.

Chapter 5

- Unit 2 is all about growth and begins with the Chapter 5 presentation of the essential principles of microbial growth and cultivation. Coverage of microbial growth control balances this chapter with a practical view of how microbial growth can be suppressed for both health and aesthetic reasons.
- Some highlights: new material on budding cell division and on biofilms; reworked chemostat coverage better explains continuous culture and its connection to basic growth principles; new coverage on how the environment affects growth previews the extensive coverage of microbial ecology and environmental microbiology later in the book.

Chapter 6

- This chapter on microbial regulation includes broad coverage of the classic forms of regulation but has been streamlined by moving the regulation of cell differentiation and biofilm formation to Chapter 7; this allowed for enhanced coverage of hot new areas in metabolic regulation such as regulation by anti-sigma factors and transcriptional regulation in *Archaea*.
- Some highlights: new coverage of the global phosphate regulon; new coverage of dual-acting transcriptional regulators in *Archaea* and how the stringent response affects the ecology of bacteria as diverse as *Escherichia coli*, *Caulobacter crescentus*, and *Mycobacterium tuberculosis*; updated art throughout.

Chapter 7

- A new chapter focused on the molecular biology of microbial growth showcases the orchestrated events leading to cell division and surveys the molecular processes targeted by antibiotics. Coverage of peptidoglycan synthesis, developmental stages in various *Bacteria*, and biofilm formation—previously scattered through the book—has been consolidated here to unite their common underlying themes.

- Some highlights: An introduction to the powerful tool of super-resolution microscopy includes several spectacular examples of how this breakthrough in resolution has remolded our view of molecular events in microbial growth; expanded coverage of biofilm formation; new coverage of bacterial persistence, a growing problem in medical microbiology; updated art throughout.

Chapter 8

- The introductory virology chapter is now included in the microbial growth unit and provides an introduction to the structure, replication, and lifestyles of viruses without overshadowing these important principles with the extensive diversity of the viral world, now covered in Chapter 10.
- Some highlights: discussion of the parallels between bacterial growth and viral replication; expanded coverage of how host cell growth is impacted by viral infection; high-resolution viral images; updated art throughout.

Chapter 9

- This revolutionary chapter on microbial systems biology kicks off our unit on genomics and genetics by underscoring the importance of microbial genome sequences and the field of functional “omics” to modern microbiology today. The chapter also includes examples of how systems biology can be used to model an organism’s response to its environment.
- Some highlights: how functional and metabolic predictions are gleaned from genomic analyses; expanded coverage of RNA-Seq and metabolomic analyses; coverage of all of the common “omics” and how they relate to one another; new coverage of the systems biology of the important pathogen *Mycobacterium tuberculosis* and other systems biology studies related to human health; metagenomics and metabolomics of human skin; updated and spectacular new art and photos throughout.

Chapter 10

- Chapter 10, entitled “Viral Genomics, Diversity, and Ecology,” now includes coverage of viral ecology and diversity that was previously in Chapter 8. The many diverse genomes and replication schemes of viruses form the foundation for coverage of the diversity and ecological activities of viruses.
- Some highlights: the viral “immune system” of *Bacteria* and *Archaea*—CRISPR; large viruses and viral evolution; the human virome; beneficial prions; viral host preferences; updated and new art throughout.

Chapter 11

- Chapter 11, “Genetics of *Bacteria* and *Archaea*,” has been streamlined to focus on the essential concepts of mutation and gene transfer in prokaryotic cells. New high-resolution images have been included to illustrate gene transfer processes.
- Some highlights: new coverage on the utility of transposon mutagenesis; a spectacular photo series illustrating the concept of competence; new coverage on defective bacteriophages as “gene transfer agents”; updated art throughout.

Chapter 12

- This highly reorganized chapter entitled “Biotechnology and Synthetic Biology” covers the essential tools of biotechnology and discusses commercial products produced by genetically engineered microbes. New coverage presents the remarkable advances in synthetic biology and CRISPR genome editing.
- Some highlights: engineering microbes to produce biofuels; expanded coverage of synthetic pathways and synthetic cells; new coverage of the biocontainment of genetically modified organisms; updated art throughout.

Chapter 13

- Chapter 13 sets the stage for our unit on evolution and diversity by revealing how nucleic acid sequences have revealed the true diversity of the microbial world. The chapter has also been revised and reorganized to increase the emphasis on the origin and diversification of life and microbial systematics.
- Some highlights: revised text places phylogeny into firm context with microbial systematics; how the tree of life and molecular sequences form the foundation of our understanding of the origin and diversification of the three domains; revised coverage of phylogenetic tree construction and what such trees can tell us about microbial evolution.

Chapter 14

- Our discussion of microbial metabolism has been revised and reorganized to highlight the modularity of microbial metabolism and to include coverage of newly discovered microbial metabolisms.
- Some highlights: a new section on assimilatory processes of autotrophy and nitrogen fixation; grouping respiratory processes by electron donor, electron acceptor, or one-carbon metabolisms; new art depicting electron flow in oxygenic photosynthesis, sulfur chemolithotrophy, and acetogenesis; discussion of the role of flavin-based electron bifurcation in energy conservation; coverage of the exciting discoveries of intra-aerobic methanotrophy and interspecies electron transfer in anaerobic methane oxidation.

Chapters 15 and 16

- These chapters, covering functional and phylogenetic diversity of *Bacteria*, respectively, have been updated and streamlined in spots to provide the highly organized view of bacterial diversity that offers instructors the freedom to present this subject in the way that best suits their course needs.
- Some highlights: functional diversity organized by metabolism, unique morphologies, and other special properties shows how functional diversity is often unlinked to phylogenetic diversity; phylogenetic diversity organized around the major phyla of *Bacteria* shows how phylogenetic diversity is often unlinked to metabolic properties.

Chapter 17

- Chapter 17, entitled “Diversity of *Archaea*,” has been updated to include new coverage of recent discoveries in archaeal diversity

including the fact that *Archaea* are widespread in nature and not just restricted to extreme environments.

- Some highlights: updated coverage of methanogenic *Archaea* to include the extensive diversity characteristic of this group; new coverage of the evolutionary origins and distribution of methanogens within the archaeal domain; the latest story on *Archaea* and the upper temperature limit for life.

Chapter 18

- Coverage of the microbial eukaryotes has been revised to include significant new advances in our understanding of the phylogeny of *Eukarya*.
- Some highlights: a new phylogenetic tree of *Eukarya*; updated terminology throughout; the “SAR” lineages; the new understanding of fungal diversity that incorporates the *Microsporidia* as a deeply divergent fungal group.

Chapter 19

- This chapter begins a new unit on ecology and environmental microbiology. The modern tools of the microbial ecologist are described with examples of how each has helped sculpt the science.
- Some highlights: complete coverage of the omics revolution and how it is being exploited to solve complex problems in microbial ecology; Raman microspectroscopy and its use for nondestructive molecular and isotopic analyses of single cells; high-throughput cultivation methods and how they can be used to bring novel microbes into laboratory culture.

Chapter 20

- The properties and microbial diversity of major microbial ecosystems including soils and both freshwater and marine systems are compared and contrasted in an exciting new way.
- Some highlights: new environmental census data for deep marine sediments reveal the novel *Archaea* and *Bacteria* living thousands of meters below the seafloor; expanded coverage of the links between terrestrial and marine microorganisms and climate change.

Chapter 21

- Extensive coverage of the major nutrient cycles in nature and the microbes that catalyze them presented in a fashion that allows the cycles to be taught as individual entities or as interrelated metabolic loops.
- Some highlights: new coverage of how humans are affecting the nitrogen and carbon cycles; microbial respiration of solid metal oxides in the iron and manganese cycles including the concept of “microbial wires” that can carry electrons over great distances; how microbes contribute to mercury contamination of aquatic life.

Chapter 22

- A newly revised chapter on the “built environment” shows how humans create new microbial habitats through construction of buildings, supporting infrastructure, and habitat modification.

- Some highlights: coverage of the effects microbes have on wastewater treatment, mining and acid mine drainage, the corrosion of metals, and the degradation of stone and concrete; the pathogens of most concern in drinking water and how we eliminate them; the major microbes that inhabit our household and work environments.

Chapter 23

- A chapter devoted to nonhuman microbial symbioses describes the major microbial partners that live in symbiotic or other types of close associations with plants and animals.
- Some highlights: using our knowledge of plant and animal symbioses to develop microbially centered insect pest controls; revealing the common symbiotic mechanism used by certain bacteria and fungi to provide plants with key nutrients.

Chapter 24

- A new chapter devoted exclusively to the human microbiome kicks off our unit on microbe–human interactions and the immune system by introducing the dramatic advances in our understanding of the microbes that inhabit the human body and their relationship to health and disease.
- Some highlights: extensive coverage of “who lives where (and why)” in and on the human body; how the new understanding of our intimate microbial partners was used to develop novel microbial-based disease therapies; mapping the biogeography of our skin microbiota using new molecular techniques; how gut microbes likely influence both our health and behavior; a new Explore the Microbial World entitled “The Gut–Brain Axis.”

Chapter 25

- This heavily reworked and more visually appealing chapter is devoted exclusively to microbial infection and pathogenesis. Major topics in the first part include microbial adherence, colonization, invasion and pathogenicity, and virulence and attenuation. The second part is focused on the destructive enzymes and toxins produced by pathogenic bacteria. Microbial and host factors are compared as to how each can tip the balance toward health or disease.
- Some highlights: eight new color photos bring host–microbe relationships into better focus; new coverage of dental caries is supported by a spectacular fluorescent micrograph that reveals the previously hidden diversity of this disease; increased coverage of microbial infection and the compromised host.

Chapter 26

- Coverage of the immune response has been completely reorganized to provide a fresh take on immune mechanisms. Concepts of innate and adaptive immunity are now organized into separate chapters (26 and 27, respectively) that provide a more teachable format and enhance the student experience. The new organization provides a natural progression to the updated topics in clinical microbiology and immunology presented in Chapter 28.

- Some highlights: extensively revised and reorganized text and vibrant new artwork clearly illustrate the roles of inflammation, fever, and interferons in the innate immune response; stronger, clearer coverage of the complement system, including extensive new artwork, helps clarify its important role in innate immunity.

Chapter 27

- Fundamental concepts of the adaptive immune response are now reorganized into a dedicated chapter and presented in a thoroughly revised and more streamlined format.
- Some highlights: beautifully enhanced art and new photos more clearly orient students to key concepts including clonal selection and deletion of B cells and T cells, antibody structure, and antigen binding and presentation.

Chapter 28

- Clear and concise new text now includes automated culture systems, antibody precipitation, and monoclonal antibody production, as well as a reorganized treatment of antimicrobial drugs. Both reimagined and totally new art supported by 20 new color photos brightly illustrate complex topics and enhance the visual experience.
- Some highlights: how a clinical microbiology laboratory actually functions; an exciting new Explore the Microbial World feature on MRSA describes how emerging resistance to antibiotics in *Staphylococcus aureus* has led to high global incidence of what is now a virtually untreatable bacterial pathogen.

Chapter 29

- A significantly reworked and streamlined discussion of epidemiology kicks off our unit on infectious diseases with a visual presentation of the everyday language of epidemiology and then closely integrates this terminology throughout the chapter. Fewer lengthy tables are presented and visual appeal is greater, while the essential concepts of disease spread and control remain the major themes of the chapter.
- Some highlights: updated and new coverage of emerging infectious diseases and current pandemics, including HIV/AIDS, cholera, and influenza; the key role of the epidemiologist in tracking disease outbreaks and maintaining public health.

Chapter 30

- This is the first of four chapters on microbial diseases grouped by their modes of transmission; this approach emphasizes the common ecology of these diseases despite differences in etiology. Classical as well as emerging and reemerging bacterial and viral diseases transmitted person to person are the focus of this highly visual chapter.
- Some highlights: several new photos add to the already extensive visual showcase of infectious diseases; new coverage of Ebola describes why this pathogen is so dangerous and the extraordinary precautions healthcare workers must take to prevent infection; new coverage of hepatitis, a widespread disease with serious implications.

Chapter 31

- Vectorborne microbial diseases are becoming more and more common worldwide and are covered in detail in this visually appealing chapter. From diseases with high mortality, such as rabies and hantavirus syndromes, to those with high incidence and low mortality but significant side effects, such as Lyme and West Nile diseases, all of the major vectorborne infectious diseases found today are consolidated in one place.
- Some highlights: new coverage of Zika and Chikungunya diseases and their relationship to dengue and yellow fevers; updated coverage of Lyme, West Nile, and *Coxiella* (Q fever) infections supported by new color photos.

Chapter 32

- Food- and waterborne illnesses are still common, even in developed countries. This chapter consolidates these topics to emphasize their “common source” modes of transmission while differentiating the major pathogens seen in each vehicle.

- Some highlights: a clearer distinction between food infections and food poisonings; new coverage of the potentially fatal food-borne infection caused by the intracellular pathogenic bacterium *Listeria*.

Chapter 33

- Major infectious diseases caused by eukaryotic microbes—fungi, parasites, and pathogenic helminths—are organized into one highly visual chapter. With climate change affecting infectious disease ecology, many of these diseases previously found only in tropical or subtropical countries are now creeping northward.
- Some highlights: new emphasis on the different modes of transmission (food, water, vector) of major eukaryotic pathogens; new coverage of river blindness and trichinosis as common filariases.

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Hubert Bahl, *Universität Rostock (Germany)*
Jenn Baker, *Indiana Wesleyan University*
Jill Banfield, *University of California, Berkeley*
Jeremy Barr, *San Diego State University*
J. Thomas Beatty, *University of British Columbia (Canada)*
R. Howard Berg, *Danforth Plant Science Center, St. Louis*
James Berger, *Johns Hopkins School of Medicine*
Robert Blankenship, *Washington University in St. Louis*
Melanie Blokesch, *Swiss Federal Institute of Technology Lausanne (Switzerland)*
Antje Boetius, *Max Planck Institute for Marine Microbiology (Germany)*
F. C. Boogerd, *Vrije Universiteit (The Netherlands)*
Emily Booms, *(Northeastern Illinois University)*
Timothy Booth, *Public Health Agency of Canada*
Gary Borisy, *The Forsyth Institute*
Amina Bouslimani, *University of California, San Diego*
Laurie Bradley, *(Hudson Valley CC)*
Samir Brahmachari, *Institute of Genomics and Integrative Biology (India)*
Yves Brun, *Indiana University*
Linda Bruslind, *(Oregon State University)*
Heiki Bücking, *South Dakota State University*
Gustavo Caetano-Anollés, *University of Illinois*
Elisabeth Carniel, *Institut Pasteur (France)*
Luis R. Comolli, *Lawrence Berkeley National Laboratory*
Wei Dai, *Baylor College of Medicine*

- Holger Daims, *University of Vienna (Austria)*
 Christina Davis, *Davis Photography, Logan, Ohio*
 Thomas Deerinck, *National Center for Microscopy and Imaging Research, University of California, San Diego*
 Cees Dekker, *Delft University of Technology (The Netherlands)*
 Pieter Dorrestein, *University of California, San Diego*
 Paul Dunlap, *University of Michigan*
 Michelle Dunstone, *Monash University (Australia)*
 Harald Engelhardt, *Max Planck Institute of Biochemistry (Germany)*
 Thijs Ettema, *Uppsala University (Sweden)*
 Babu Fathepure, *Oklahoma State University*
 Jingyi Fei, *University of Illinois*
 Derek J. Fisher, *Southern Illinois University*
 Patrick Forterre, *Institut Pasteur (France)*
 Patricia Foster, *Indiana University*
 Melitta Franceschini, *South Tyrol Museum of Archaeology (Italy)*
 James Frederickson, *Pacific Northwest National Laboratory*
 Jed Fuhrman, *University of Southern California*
 Eric Gillock, *Fort Hays State University*
 Heidi Goodrich-Blair, *University of Wisconsin*
 James Golden, *University of California, San Diego*
 Cynthia Goldsmith, *Centers for Disease Control, Atlanta*
 Eric Grafman, *Centers for Disease Control Public Health Image Library*
 Peter Graumann, *Universität Marburg (Germany)*
 Claudia Gravekamp, *Albert Einstein College of Medicine*
 A.D. Grossman, *Massachusetts Institute of Technology*
 Ricardo Guerrero, *University of Barcelona (Spain)*
 Maria J. Harrison, *Cornell University*
 Stephen Harrison, *Harvard Medical School*
 Ryan Hartmaier, *University of Pittsburgh*
 Zhili He, *University of Oklahoma*
 Monique Heijmans, *Wageningen University (The Netherlands)*
 Bart Hoogenboom, *London Centre for Nanotechnology (England)*
 Matthias Horn, *University of Vienna (Austria)*
 M.D. Shakhawat Hossain, *University of Missouri*
 Ji-Fan Hu, *Stanford University*
 Jenni Hultman, *University of Helsinki (Finland)*
 Rustem Ismagilov, *California Institute of Technology*
 Christian Jogler, *Leibniz-Institut DSMZ (Germany)*
 Robert Kelly, *North Carolina State University*
 Takehiko Kenzaka, *Osaka Ohtani University (Japan)*
 Jan-Ulrich Kreft, *University of Birmingham (England)*
 Misha Kudryashev, *University of Basel (Switzerland)*
 Alberto Lerner, *CHROMagar (France)*
 Jennifer Li-Pook-Than, *Stanford University*
 Jun Liu, *University of Texas Health Science Center*
 Martin Loose, *Institute of Science and Technology (Austria)*
 Brigit Luef, *Norwegian University of Science and Technology (Norway)*
 Marina Lusic, *University Hospital Heidelberg (Germany)*
 Liang Ma, *California Institute of Technology*
 Terry Machen, *University of California, Berkeley*
 Sergei Markov, *Austin Peay State University*
 Stephen Mayfield, *University of California, San Diego*
 John McCutcheon, *University of Montana*
 Michael Minnick, *University of Montana*
 William E. Moerner, *Stanford University*
 Robert Moir, *Massachusetts General Hospital and Harvard Medical School*
 Christine Moissl-Eichinger, *Medical University Graz (Austria)*
 Nancy Moran, *University of Texas*
 Katsuhiko Murakami, *The Pennsylvania State University*
 Dieter Oesterhelt, *Max Planck Institute of Biochemistry (Germany)*
 George O'Toole, *Dartmouth University*
 Joshua Quick, *University of Birmingham (England)*
 Nicolás Pinel, *Universidad de Antioquia (Colombia)*
 Rodrigo Reyes-Lamothe, *McGill University (Canada)*
 Charisse Sallade, *Indiana Wesleyan University*
 Bernhard Schink, *University of Konstanz (Germany)*
 Christa Schleper, *University of Vienna (Austria)*
 Matthew Schrenk, *Michigan State University*
 Hubert Schriebl, *Schriebl Photography, Londonderry, Vermont*
 Howard Shuman, *University of Chicago*
 Gary Siuzdak, *Scripps Center for Metabolomics*
 Justin L. Sonnenburg, *Stanford University School of Medicine*
 Rochelle Soo, *University of Queensland (Australia)*
 John Stark, *Utah State University*
 Andrzej Stasiak, *University of Lausanne (Switzerland)*
 S. Patricia Stock, *University of Arizona*
 María Suárez Diez, *Wageningen University (The Netherlands)*
 Lei Sun, *Purdue University*
 Andreas Teske, *University of North Carolina*
 Tammy Tobin, *Susquehanna University*
 Stephan Uphoff, *Oxford University (England)*
 Joyce Van Eck, *Cornell University*
 Gunter Wegener, *Max Planck Institute of Marine Microbiology (Germany)*
 Jessica Mark Welch, *Marine Biological Laboratory, Woods Hole*
 Mari Winkler, *University of Washington*
 Cynthia Whitchurch, *University of Technology Sydney (Australia)*
 Conrad Woldringh, *University of Amsterdam (The Netherlands)*
 Steven Yannone, *Cinder Biological*
 Shige Yoshimura, *Kyoto University (Japan)*
 Feng Zhang, *Massachusetts Institute of Technology*
 Joseph Zhou, *University of Oklahoma*
 Steve Zinder, *Cornell University*

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Michael T. Madigan (madigan@siu.edu)

Kelly S. Bender (bender@siu.edu)

Daniel H. Buckley (dbuckley@cornell.edu)

W. Matthew Sattley (matthew.sattley@indwes.edu)

David A. Stahl (dastahl@uw.edu)

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Contributors

Aurélien Carlier, *Universiteit Gent (Belgium)*

HE Jianzhong, *National University of Singapore (Singapore)*

Joy Pang, *Singapore Institute of Technology (Singapore)*

Wei-Qin Zhuang, *University of Auckland (New Zealand)*

Reviewers

Qaiser I Sheikh, *University of Sheffield (England)*

Quek Choon LAU, *Ngee Ann Polytechnic (Singapore)*

Aurélien Carlier, *Universiteit Gent (Belgium)*

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