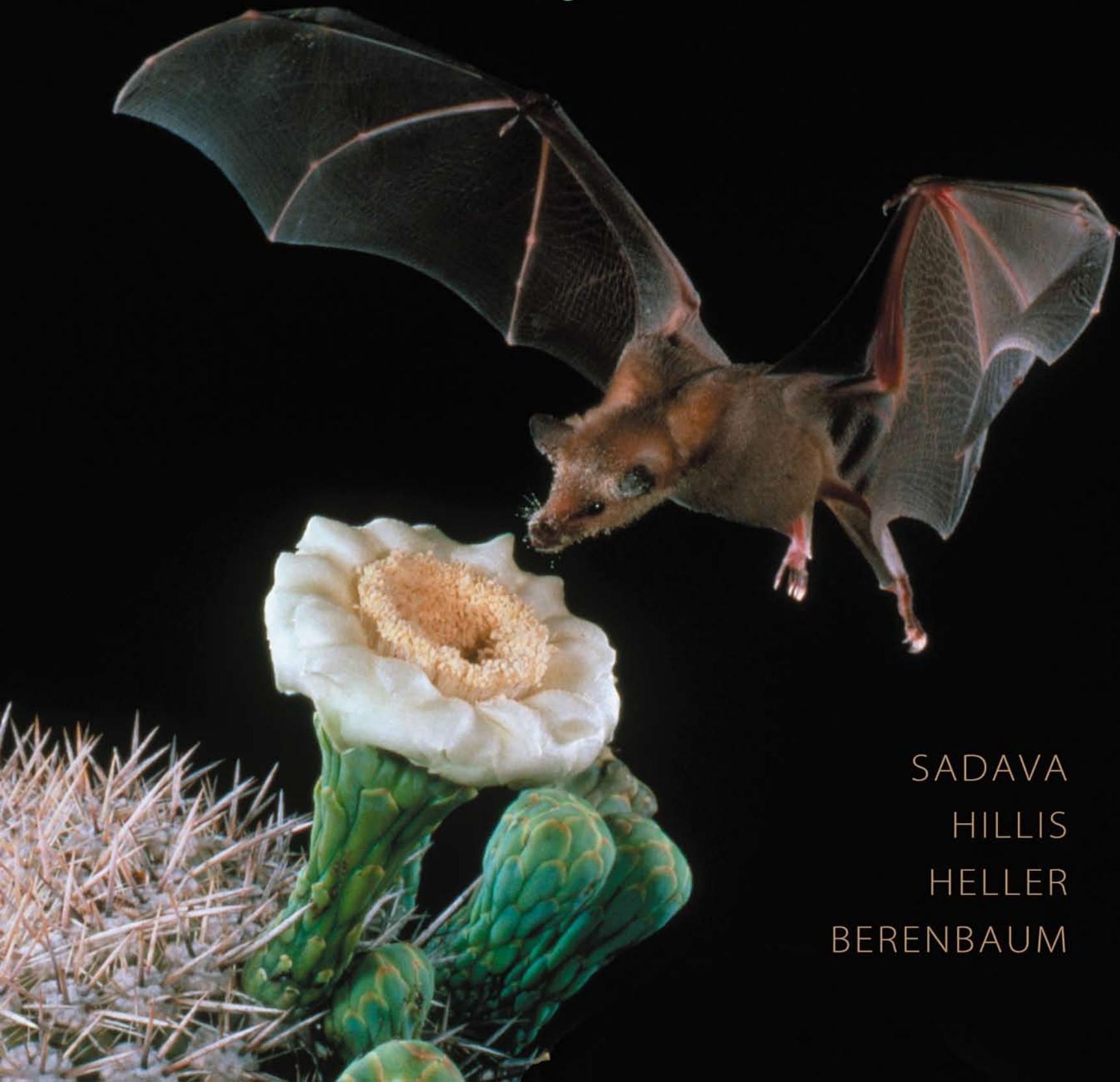


# *Life*

The Science  
of Biology  
NINTH EDITION



SADAVA  
HILLIS  
HELLER  
BERENBAUM



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The Science of Biology

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NINTH  
EDITION

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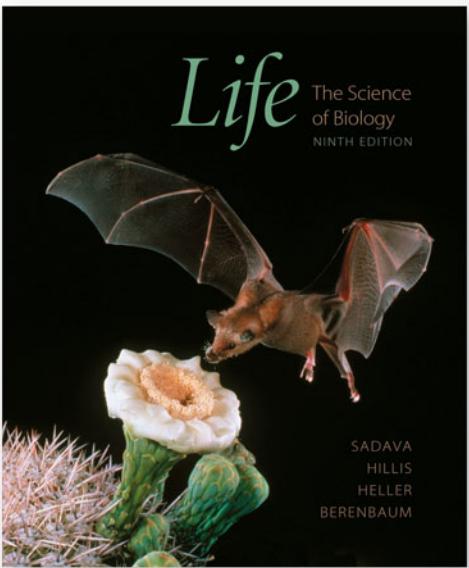


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## About the Cover

The cover of *Life* captures many themes that echo throughout the book. The photograph shows a lesser long-nosed bat pollinating a saguaro cactus. This cactus has evolved large flowers that produce copious quantities of nectar. The nectar attracts many species that pollinate the cactus, including bats. The ability of bats to hover as they feed on the nectar of the cactus is an excellent example of adaptation of body form and physiology. These themes of adaptation, evolution, nutrition, reproduction, species interactions, and integrated form and function are ideas that are repeated throughout the chapters of *Life*. Photograph copyright © Dr. Merlin D. Tuttle/Photo Researchers, Inc.

## The Frontispiece

Blue wildebeest and Burchell's zebra migrate together through Serengeti National Park, Tanzania. Copyright © Art Wolfe, [www.artwolfe.com](http://www.artwolfe.com).

## LIFE: The Science of Biology, Ninth Edition

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Address orders to:

MPS / W. H. Freeman & Co., Order Dept., 16365 James Madison Highway,  
U.S. Route 15, Gordonsville, VA 22942 U.S.A.

Examination copy information: 1-800-446-8923

Orders: 1-888-330-8477



## Library of Congress Cataloging-in-Publication Data

Life, the science of biology / David Sadava .. [et al.]. — 9th ed.

p. cm.

Includes index.

ISBN 978-1-4292-1962-4 (hardcover) — 978-1-4292-4645-3 (pbk. : v. 1) —

ISBN 978-1-4292-4644-6 (pbk. : v. 2) — ISBN 978-1-4292-4647-7 (pbk. : v. 3)

1. Biology. I. Sadava, David E.

QH308.2.L565 2011

570—dc22

2009036693

Printed in U.S.A.

First Printing October 2009

The Courier Companies, Inc.

*To Bill Purves and Gordon Orians,  
extraordinary colleagues, biologists, and teachers,  
and the original authors of LIFE*

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**MAY BERENBAUM** is the Swanlund Professor and Head of the Department of Entomology at the University of Illinois at Urbana-Champaign. She has taught courses in introductory animal biology, entomology, insect ecology, and chemical ecology, and has received awards at the regional and national level for distinguished teaching from the Entomological Society of America. A fellow of the National Academy of Sciences, the American Academy of Arts and Sciences, and the American Philosophical Society, she served as President of the American Institute for Biological Sciences in 2009. Her research addresses insect–plant coevolution, from molecular mechanisms of detoxification to impacts of herbivory on community structure. Concerned with the practical application of ecological and evolutionary principles, she has examined impacts of genetic engineering, global climate change, and invasive species on natural and agricultural ecosystems. Devoted to fostering science literacy, she has published numerous articles and five books on insects for the general public.

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# Preface

Biology is a dynamic, exciting, and important subject. It is dynamic because it is constantly changing, with new discoveries about the living world being made every day. (Although it is impossible to pinpoint an exact number, approximately 1 million new research articles in biology are published each year.) The subject is exciting because life in all of its forms has always fascinated people. As active scientists who have spent our careers teaching and doing research in a wide variety of fields, we know this first hand.

Biology has always been important in peoples' daily lives, if only through the effects of achievements in medicine and agriculture. Today more than ever the science of biology is at the forefront of human concerns as we face challenges raised both by recent advances in genome science and by the rapidly changing environment.

*Life's* new edition brings a fresh approach to the study of biology while retaining the features that have made the book successful in the past. A new coauthor, the distinguished entomologist May R. Berenbaum (University of Illinois at Urbana-Champaign) has joined our team, and the role of evolutionary biologist David Hillis (University of Texas at Austin) is greatly expanded in this edition. The authors hail from large, medium-sized, and small institutions. Our multiple perspectives and areas of expertise, as well as input from many colleagues and students who used previous editions, have informed our approach to this new edition.

## Enduring Features

We remain committed to blending the presentation of core ideas with an emphasis on introducing students to the *process of scientific inquiry*. Having pioneered the idea of depicting seminal experiments in specially designed figures, we continue to develop this here, with 79 **INVESTIGATING LIFE** figures. Each of these figures sets the experiment in perspective and relates it to the accompanying text. As in previous editions, these figures employ a structure: Hypothesis, Method, Results, and Conclusion. They often include questions for further research that ask students to conceive an experiment that would explore a related question. Each *Investigating Life* figure has a reference to BioPortal ([yourBioPortal.com](http://yourBioPortal.com)), where citations to the original work as well as additional discussion and references to follow-up research can be found.

A related feature is the **TOOLS FOR INVESTIGATING LIFE** figures, which depict laboratory and field methods used in biology. These, too, have been expanded to provide more useful context for their importance.

Over a decade ago—in *Life's* Fifth Edition—the authors and publishers pioneered the much-praised use of **BALLOON CAPTIONS** in our figures. We recognized then, and it is even truer today, that many students are visual learners. The balloon cap-

tions bring explanations of intricate, complex processes directly into the illustration, allowing students to integrate information without repeatedly going back and forth between the figure, its legend, and the text.

*Life* is the only introductory textbook for biology majors to begin each chapter with a story. These **OPENING STORIES** provide historical, medical, or social context and are intended to intrigue students while helping them see how the chapter's biological subject relates to the world around them. In the new edition, all of the opening stories (some 70 percent of which are new) are revisited in the body of the chapter to drive home their relevance.

We continue to refine our well-received *chapter organization*. The chapter-opening story ends with a brief **IN THIS CHAPTER** preview of the major subjects to follow. A **CHAPTER OUTLINE** asks questions to emphasize scientific inquiry, each of which is answered in a major section of the chapter. A **RECAP** at the end of each section asks the student to pause and answer questions to review and test their mastery of the previous material. The end-of-chapter summary continues this inquiry framework and highlights key figures, bolded terms, and activities and animated tutorials available in BioPortal.

## New Features

Probably the most important new feature of this edition is *new authorship*. Like the biological world, the authorship team of *Life* continues to evolve. While two of us (Craig Heller and David Sadava) continue as coauthors, David Hillis has a greatly expanded role, with full responsibility for the units on evolution and diversity. New coauthor May Berenbaum has rewritten the chapters on ecology. The perspectives of these two acclaimed experts have invigorated the entire book (as well as their coauthors).

Even with the enduring features (see above), this edition has a different look and feel from its predecessor. A fresh *new design* is more open and, we hope, more accessible to students. The extensively *revised art program* has a contemporary style and color palette. The information flow of the figures is easier to follow, with numbered balloons as a guide for students. There are new conceptual figures, including a striking visual timeline for the evolution of life on Earth (Figure 25.12) and a single overview figure that summarizes the information in the genome (Figure 17.4).

In response to instructors who asked for more real-world data, we have incorporated a feature introduced online in the Eighth Edition, **WORKING WITH DATA**. There are now 36 of these exercises, most of which relate to an *Investigating Life* figure. Each is referenced at the end of the relevant chapter and is available online via BioPortal ([yourBioPortal.com](http://yourBioPortal.com)). In these exercises, we describe in detail the context and approach of the

research paper that forms the basis of the figure. We then ask the student to examine the data, to make calculations, and to draw conclusions.

We are proud that this edition is a *greener Life*, with the goal of reducing our environmental impact. This is the first introductory biology text to be printed on paper earning the Forest Stewardship Council label, the “gold standard” in green paper products, and it is manufactured from wood harvested from sustainable forests. And, of course, we also offer *Life* as an eBook.

## The Ten Parts

We have reorganized the book into ten parts. **Part One, The Science of Life and Its Chemical Basis**, sets the stage for the book: the opening chapter focuses on biology as an exciting science. We begin with a startling observation: the recent, dramatic decline of amphibian species throughout the world. We then show how biologists have formed hypotheses for the causes of this environmental problem and are testing them by carefully designed experiments, with a view not only to understanding the decline, but reversing it. This leads to an outline of the basic principles of biology that are the foundation for the rest of the book: the unity of life at the cellular level and how evolution unites the living world. This is followed by chapters on the basic chemical building blocks that underlie life. We have added a new chapter on nucleic acids and the origin of life, introducing the concepts of genes and gene expression early and expanding our coverage of the major ideas on how life began and evolved at its earliest stages.

In **Part Two, Cells**, we describe the view of life as seen through cells, its structural units. In response to comments by users of our previous edition, we have moved the chapter on cell signaling and communication from the genetics section to this part of the book, with a change in emphasis from genes to cells. There is an updated discussion of ideas on the origin of cells and organelles, as well as expanded treatment of water transport across membranes.

**Part Three, Cells and Energy**, presents an integrated view of biochemistry. For this edition, we have worked to clarify such challenging concepts as energy transfer, allosteric enzymes, and biochemical pathways. There is extensive revision of the discussions of alternate pathways of photosynthetic carbon fixation, as well as a greater emphasis on applications throughout these chapters.

**Part Four, Genes and Heredity**, is extensively revised and reorganized to improve clarity, link related concepts, and provide updates from recent research results. Separate chapters on prokaryotic genetics and molecular medicine have been removed and their material woven into relevant chapters. For example, our chapter on cell reproduction now includes a discussion of how the basic mechanisms of cell division are altered in cancer cells. The chapter on transmission genetics now includes coverage of this phenomenon in prokaryotes. New chapters on gene expression and gene regulation compare prokaryotic and eukaryotic mechanisms and include a discussion of

epigenetics. A new chapter on mutation describes updated applications of medical genetics.

In **Part Five, Genomes**, we reinforce the concepts of the previous part, beginning with a new chapter on genomes—how they are analyzed and what they tell us about the biology of prokaryotes and eukaryotes, including humans. This leads to a chapter describing how our knowledge of molecular biology and genetics underpins biotechnology (the application of this knowledge to practical problems). We discuss some of the latest uses of biotechnology, including environmental cleanup. Part Five finishes with two chapters on development that explore the themes of molecular biology and evolution, linking these two parts of the book.

**Part Six, The Patterns and Processes of Evolution**, emphasizes the importance of evolutionary biology as a basis for comparing and understanding all aspects of biology. These chapters have been extensively reorganized and revised, as well as updated with the latest thinking of biologists in this rapidly changing field. This part now begins with the evidence and mechanisms of evolution, moves into a discussion of phylogenetic trees, then covers speciation and molecular evolution, and concludes with the evolutionary history of life on Earth. An integrated timeline of evolutionary history shows the timing of major events of biological evolution, the movements of the continents, floral and faunal reconstructions of major time periods, and depicts some of the fossils that form the basis of the reconstructions.

In **Part Seven, The Evolution of Diversity**, we describe the latest views on biodiversity and evolutionary relationships. Each chapter has been revised to make it easier for the reader to appreciate the major changes that have evolved within the various groups of organisms. We emphasize understanding the big picture of organismal diversity, as opposed to memorizing a taxonomic hierarchy and names (although these are certainly important). Throughout the book, the tree of life is emphasized as a way of understanding and organizing biological information. A *Tree of Life Appendix* allows students to place any group of organisms mentioned in the text of our book into the context of the rest of life. The web-based version of this appendix provides links to photos, keys, species lists, distribution maps, and other information to help students explore biodiversity of specific groups in greater detail.

After modest revisions in the past two editions, **Part Eight, Flowering Plants: Form and Function**, has been extensively reorganized and updated with the help of Sue Wessler, to include both classical and more recent approaches to plant physiology. Our emphasis is not only on the basic findings that led to the elucidation of mechanisms for plant growth and reproduction, but also on the use of genetics of model organisms. There is expanded coverage of the cell signaling events that regulate gene expression in plants, integrating concepts introduced earlier in the book. New material on how plants respond to their environment is included, along with links to both the book’s earlier descriptions of plant diversity and later discussions of ecology.

**Part Nine, Animals: Form and Function**, continues to provide a solid foundation in physiology through comprehensive coverage of basic principles of function of each organ system and then emphasis on mechanisms of control and integration. An important reorganization has been moving the chapter on immunology from earlier in the book, where its emphasis was on molecular genetics, to this part, where it is more closely allied to the information systems of the body. In addition, we have added a number of new experiments and made considerable effort to clarify the sometimes complex phenomena shown in the illustrations.

**Part Ten, Ecology**, has been significantly revised by our new coauthor, May Berenbaum. A new chapter of biological interactions has been added (a topic formerly covered in the community ecology chapter). Full of interesting anecdotes and discussions of field studies not previously described in biology texts, this new ecology unit offers practical insights into how ecologists acquire, interpret, and apply real data. This brings the book full circle, drawing upon and reinforcing prior topics of energy, evolution, phylogenetics, Earth history, and animal and plant physiology.

### Exceptional Value Formats

We again provide *Life* both as the full book and as a cluster of paperbacks. Thus, instructors who want to use less than the whole book can choose from these split volumes, each with the book's front matter, appendices, glossary, and index.

Volume I, The Cell and Heredity, includes: Part One, The Science of Life and Its Chemical Basis (Chapters 1–4); Part Two, Cells (Chapters 5–7); Part Three, Cells and Energy (Chapters 8–10); Part Four, Genes and Heredity (Chapters 11–16); and Part Five, Genomes (Chapters 17–20).

Volume II, Evolution, Diversity, and Ecology, includes: Chapter 1, Studying Life; Part Six, The Patterns and Processes of Evolution (Chapters 21–25); Part Seven, The Evolution of Diversity (Chapters 26–33); and Part Ten, Ecology (Chapters 54–59).

Volume III, Plants and Animals, includes: Chapter 1, Studying Life; Part Eight, Flowering Plants: Form and Function (Chapters 34–39); and Part Nine, Animals: Form and Function (Chapters 40–53).

Responding to student concerns, we offer two options of the entire book at a *significantly reduced cost*. After it was so well received in the previous edition, we again provide *Life* as a *loose-leaf version*. This shrink-wrapped, unbound, 3-hole punched version fits into a 3-ring binder. Students take only what they need to class and can easily integrate any instructor handouts or other resources.

*Life* was the first comprehensive biology text to offer the entire book as a truly robust *eBook*. For this edition, we continue to offer a flexible, interactive ebook that gives students a new way to read the text and learn the material. The ebook integrates the student media resources (animations, quizzes, activities, etc.) and offers instructors a powerful way to customize the textbook with their own text, images, Web links, documents, and more.

### Media and Supplements for the Ninth Edition

The wide range of media and supplements that accompany *Life*, Ninth Edition have all been created with the dual goal of helping students learn the material presented in the textbook more efficiently and helping instructors teach their courses more effectively. Students in majors introductory biology are faced with learning a tremendous number of new concepts, facts, and terms, and the more different ways they can study this material, the more efficiently they can master it.

All of the *Life* media and supplemental resources have been developed specifically for this textbook. This provides strong consistency between text and media, which in turn helps students learn more efficiently. For example, the animated tutorials and activities found in BioPortal were built using textbook art, so that the manner in which structures are illustrated, the colors used to identify objects, and the terms and abbreviations used are all consistent.

For the Ninth Edition, a new set of Interactive Tutorials gives students a new way to explore many key topics across the textbook. These new modules allow the student to learn by doing, including solving problem scenarios, working with experimental techniques, and exploring model systems. All new copies of the Ninth Edition include access to the robust new version of BioPortal, which brings together all of *Life*'s student and instructor resources, powerful assessment tools, and new integration with Prep-U adaptive quizzing.

The rich collection of visual resources in the Instructor's Media Library provides instructors with a wide range of options for enhancing lectures, course websites, and assignments. Highlights include: layered art PowerPoint® presentations that break down complex figures into detailed, step-by-step presentations; a collection of approximately 200 video segments that can help capture the attention and imagination of students; and PowerPoint slides of textbook art with editable labels and leaders that allow easy customization of the figures.

For a detailed description of all the media and supplements available for the Ninth Edition, please turn to "Life's Media and Supplements," on page xvii.

## Many People to Thank

"If I have seen farther, it is by standing on the shoulders of giants." The great scientist Isaac Newton wrote these words over 330 years ago and, while we certainly don't put ourselves in his lofty place in science, the words apply to us as coauthors of this text. This is the first edition that does not bear the names of Bill Purves and Gordon Orians. As they enjoy their "retirements," we are humbled by their examples as biologists, educators, and writers.

One of the wisest pieces of advice ever given to a textbook author is to "be passionate about your subject, but don't put your ego on the page." Considering all the people who looked over our shoulders throughout the process of creating this book, this advice could not be more apt. We are indebted to many people who gave invaluable help to make this book what it is. First and foremost are our colleagues, biologists from over 100 institutions. Some were users of the previous edition, who suggested many improvements. Others reviewed our chapter drafts in detail, including advice on how to improve the illustrations. Still others acted as accuracy reviewers when the book was almost completed. All of these biologists are listed in the Reviewer credits.

Of special note is Sue Wessler, a distinguished plant biologist and textbook author from the University of Georgia. Sue looked critically at Part Eight, Flowering Plants: Form and Function, wrote three of the chapters (34–36), and was important in the revision of the other three (37–39). The new approach to plant biology in this edition owes a lot to her.

The pace of change in biology and the complexities of preparing a book as broad as this one necessitated having two developmental editors. James Funston coordinated Parts 1–5, and Carol Pritchard-Martinez coordinated Parts 6–10. We benefitted from the wide experience, knowledge, and wisdom of both of them. As the chapter drafts progressed, we were fortunate to have experienced biologist Laura Green lending her critical eye as in-house editor. Elizabeth Morales, our artist, was on her third edition with us. As we have noted, she extensively revised almost all of the prior art and translated our crude sketches into beautiful new art. We hope you agree that our art program re-

mains superbly clear and elegant. Our copy editors, Norma Roche, Liz Pierson, and Jane Murfett, went far beyond what such people usually do. Their knowledge and encyclopedic recall of our book's chapters made our prose sharper and more accurate. Diane Kelly, Susan McGlew, and Shannon Howard effectively coordinated the hundreds of reviews that we described above. David McIntyre was a terrific photo editor, finding over 550 new photographs, including many new ones of his own, that enrich the book's content and visual statement. Jefferson Johnson is responsible for the design elements that make this edition of *Life* not just clear and easy to learn from, but beautiful as well. Christopher Small headed the production department—Joanne Delphia, Joan Gemme, Janice Holabird, and Jefferson Johnson—who contributed in innumerable ways to bringing *Life* to its final form. Jason Dirks once again coordinated the creation of our array of media and supplements, including our superb new Web resources. Carol Wigg, for the ninth time in nine editions, oversaw the editorial process; her influence pervades the entire book.

W. H. Freeman continues to bring *Life* to a wider audience. Associate Director of Marketing Debbie Clare, the Regional Specialists, Regional Managers, and experienced sales force are effective ambassadors and skillful transmitters of the features and unique strengths of our book. We depend on their expertise and energy to keep us in touch with how *Life* is perceived by its users. And thanks also to the Freeman media group for eBook and BioPortal production.

Finally, we are indebted to Andy Sinauer. Like ours, his name is on the cover of the book, and he truly cares deeply about what goes into it. Combining decades of professionalism, high standards, and kindness to all who work with him, he is truly our mentor and friend.

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# LIFE's Media and Supplements

## BIOPORTAL featuring Prep-U

yourBioPortal.com

BioPortal is the new gateway to all of *Life*'s state-of-the-art online resources for students and instructors. BioPortal includes the breakthrough quizzing engine, Prep-U; a fully interactive eBook; and additional premium learning media. The textbook is tightly integrated with BioPortal via in-text references that connect the printed text and media resources. The result is a powerful, easily-managed online course environment. BioPortal includes the following features and resources:

### ***Life, Ninth Edition eBook***

- Integration of all activities, animated tutorials, and other media resources.
- Quick, intuitive navigation to any section or subsection, as well as any printed book page number.
- In-text links to all glossary entries.
- Easy text highlighting.
- A bookmarking feature that allows for quick reference to any page.
- A powerful Notes feature that allows students to add notes to any page.
- A full glossary and index.
- Full-text search, including an additional option to search the glossary and index.
- Automatic saving of all notes, highlighting, and bookmarks.

### ***Additional eBook features for instructors:***

- Content Customization: Instructors can easily add pages of their own content and/or hide chapters or sections that they do not cover in their course.
- Instructor Notes: Instructors can choose to create an annotated version of the eBook with their own notes on any page. When students in the course log in, they see the instructor's personalized version of the eBook. Instructor notes can include text, Web links, images, links to all BioPortal content, and more.



Built by educators, Prep-U focuses student study time exactly where it should be, through the use of personalized, adaptive quizzes that move students toward a better grasp of the material—and better grades. For *Life*, Ninth Edition, Prep-U is fully integrated into BioPortal, making it easy for instructors to take advantage of this powerful quizzing engine in their course. Features include:

- Adaptive quizzing
- Automatic results reporting into the BioPortal gradebook

- Misconception index
- Comparison to national data

### **Student Resources**

**Diagnostic Quizzing.** The diagnostic quiz for each chapter of *Life* assesses student understanding of that chapter, and generates a Personalized Study Plan to effectively focus student study time. The plan includes links to specific textbook sections, animated tutorials, and activities.

**Interactive Summaries.** For each chapter, these dynamic summaries combine a review of important concepts with links to all of the key figures from the chapter as well as all of the relevant animated tutorials, activities, and key terms.

**Animated Tutorials.** Over 100 in-depth animated tutorials, in a new format for the Ninth Edition, present complex topics in a clear, easy-to-follow format that combines a detailed animation with an introduction, conclusion, and quiz.

**Activities.** Over 120 interactive activities help students learn important facts and concepts through a wide range of exercises, such as labeling steps in processes or parts of structures, building diagrams, and identifying different types of organisms.

**NEW! Interactive Tutorials.** New for the Ninth Edition, these tutorial modules help students master key concepts through hands-on activities that allow them to learn through action. With these tutorials, students can solve problem scenarios by applying concepts from the text, by working with experimental techniques, and by using interactive models to discover how biological mechanisms work. Each tutorial includes a self-assessment quiz that can be assigned.

**Interactive Quizzes.** Each question includes an image from the textbook, thorough feedback on both correct and incorrect answer choices, references to textbook pages, and links to eBook pages, for quick review.

**BioNews from Scientific American.** BioNews makes it easy for instructors to bring the dynamic nature of the biological sciences and up-to-the-minute currency into their course. Accessible from within BioPortal, BioNews is a continuously updated feed of current news, podcasts, magazine articles, science blog entries, “strange but true” stories, and more.

**NEW! BioNavigator.** This unique visual resource is an innovative way to access the wide variety of *Life* media resources. Starting from the whole-Earth view, instructors and students can zoom to any level of biological inquiry, encountering links to a wealth of animations, activities, and tutorials on the full range of topics along the way.

**Working with Data.** Built around some of the original experiments depicted in the Investigating Life figures, these exercises help build quantitative skills and encourage student in-

terest in how scientists do research, by looking at real experimental data and answering questions based on those data.

**Flashcards.** For each chapter of the book, there is a set of flashcards that allows the student to review all the key terminology from the chapter. Students can review the terms in study mode, and then quiz themselves on a list of terms.

**Experiment Links.** For each Investigating Life figure in the textbook, BioPortal includes an overview of the experiment featured in the figure and related research or applications that followed, a link to the original paper, and links to additional information related to the experiment.

**Key Terms.** The key terminology introduced in each chapter is listed, with definitions and audio pronunciations from the glossary.

**Suggested Readings.** For each chapter of the book, a list of suggested readings is provided as a resource for further study.

**Glossary.** The language of biology is often difficult for students taking introductory biology to master, so BioPortal includes a full glossary that features audio pronunciations of all terms.

**Statistics Primer.** This brief introduction to the use of statistics in biological research explains why statistics are integral to biology, and how some of the most common statistical methods and techniques are used by biologists in their work.

**Math for Life.** A collection of mathematical shortcuts and references to help students with the quantitative skills they need in the laboratory.

**Survival Skills.** A guide to more effective study habits. Topics include time management, note-taking, effective highlighting, and exam preparation.

## Instructor Resources

### Assessment

- Diagnostic Quizzing provides instant class comprehension feedback to instructors, along with targeted lecture resources for those areas requiring the most attention.
- Question banks include questions ranked according to Bloom's taxonomy.
- Question filtering: Allows instructors to select questions based on Bloom's category and/or textbook section.
- Easy-to-use customized assessment tools allow instructors to quickly create quizzes and many other types of assignments using any combination of the questions and resources provided along with their own materials.
- Comprehensive question banks include questions from the test bank, study guide, textbook self-quizzes, and diagnostic quizzes.

### Media Resources (see Instructor's Media Library below for details)

- Videos
- PowerPoint® Presentations (Textbook Figures, Lectures, Layered Art)

- Supplemental Photos
- Clicker Questions
- Instructor's Manual
- Lecture Notes

### Course Management

- Complete course customization capabilities
- Custom resources/document posting
- Robust Gradebook
- Communication Tools: Announcements, Calendar, Course Email, Discussion Boards

*Note:* The printed textbook, the eBook, BioPortal, and Prep-U can all be purchased individually as stand-alone items, in addition to being available in a package with the printed textbook.

## Student Supplements

### Study Guide (ISBN 978-1-4292-3569-3)

Jacalyn Newman, *University of Pittsburgh*; Edward M. Dzialowski, *University of North Texas*; Betty McGuire, *Cornell University*; Lindsay Goodloe, *Cornell University*; and Nancy Guild, *University of Colorado*

For each chapter of the textbook, the *Life* Study Guide offers a variety of study and review tools. The contents of each chapter are broken down into both a detailed review of the Important Concepts covered and a boiled-down Big Picture snapshot. New for the Ninth Edition, Diagram Exercises help students synthesize what they have learned in the chapter through exercises such as ordering concepts, drawing graphs, linking steps in processes, and labeling diagrams. In addition, Common Problem Areas and Study Strategies are highlighted. A set of study questions (both multiple-choice and short-answer) allows students to test their comprehension. All questions include answers and explanations.

### Lecture Notebook (ISBN 978-1-4292-3583-9)

This invaluable printed resource consists of all the artwork from the textbook (more than 1,000 images with labels) presented in the order in which they appear in the text, with ample space for note-taking. Because the Notebook has already done the drawing, students can focus more of their attention on the concepts. They will absorb the material more efficiently during class, and their notes will be clearer, more accurate, and more useful when they study from them later.

### Companion Website [www.thelifewire.com](http://www.thelifewire.com)

(Also available as a CD, which can be optionally packaged with the textbook.)

For those students who do not have access to BioPortal, the *Life*, Ninth Edition Companion Website is available free of charge (no access code required). The site features a variety of resources, including animations, flashcards, activities, study ideas, help with math and statistics, and more.

## CatchUp Math & Stats

Michael Harris, Gordon Taylor, and Jacquelyn Taylor (ISBN 978-1-4292-0557-3)

This primer will help your students quickly brush up on the quantitative skills they need to succeed in biology. Presented in brief, accessible units, the book covers topics such as working with powers, logarithms, using and understanding graphs, calculating standard deviation, preparing a dilution series, choosing the right statistical test, analyzing enzyme kinetics, and many more.

## Student Handbook for Writing in Biology, Third Edition

Karen Knisely, *Bucknell University* (ISBN 978-1-4292-3491-7)

This book provides practical advice to students who are learning to write according to the conventions in biology. Using the standards of journal publication as a model, the author provides, in a user-friendly format, specific instructions on: using biology databases to locate references; paraphrasing for improved comprehension; preparing lab reports, scientific papers, posters; preparing oral presentations in PowerPoint®, and more.

## Bioethics and the New Embryology: Springboards for Debate

Scott F. Gilbert, Anna Tyler, and Emily Zackin (ISBN 978-0-7167-7345-0)

Our ability to alter the course of human development ranks among the most significant changes in modern science and has brought embryology into the public domain. The question that must be asked is: Even if we can do such things, should we?

## BioStats Basics: A Student Handbook

James L. Gould and Grant F. Gould (ISBN 978-0-7167-3416-1)

*BioStats Basics* provides introductory-level biology students with a practical, accessible introduction to statistical research. Engaging and informal, the book avoids excessive theoretical and mathematical detail, and instead focuses on how core statistical methods are put to work in biology.

## Instructor Media & Supplements

### Instructor's Media Library

The *Life*, Ninth Edition Instructor's Media Library (available both online via BioPortal and on disc) includes a wide range of electronic resources to help instructors plan their course, present engaging lectures, and effectively assess student comprehension. The Media Library includes the following resources:

**Textbook Figures and Tables.** Every image and table from the textbook is provided in both JPEG (high- and low-resolution) and PDF formats. Each figure is provided both with and without balloon captions, and large, complex figures are provided in both a whole and split version.

**Unlabeled Figures.** Every figure is provided in an unlabeled format, useful for student quizzing and custom presentation development.

**Supplemental Photos.** The supplemental photograph collection contains over 1,500 photographs (in addition to those in the text), giving instructors a wealth of additional imagery to draw upon.

**Animations.** Over 100 detailed animations, revised and enlarged for the Ninth Edition, all created from the textbook's art program, and viewable in either narrated or step-through mode.

**Videos.** A collection of over 200 video segments that covers topics across the entire textbook and helps demonstrate the complexity and beauty of life. Includes the Cell Visualization Videos.

**PowerPoint® Resources.** For each chapter of the textbook, several different PowerPoint presentations are available. These give instructors the flexibility to build presentations in the manner that best suits their needs. Included are:

- Textbook Figures and Tables
- Lecture Presentation
- Figures with Editable Labels
- Layered Art Figures
- Supplemental Photos
- Videos
- Animations

**Clicker Questions.** A set of questions written specifically to be used with classroom personal response systems, such as the iClicker system, is provided for each chapter. These questions are designed to reinforce concepts, gauge student comprehension, and engage students in active participation.

**Chapter Outlines, Lecture Notes,** and the complete **Test File** are all available in Microsoft Word® format for easy use in lecture and exam preparation.

**Intuitive Browser Interface** provides a quick and easy way to preview and access all of the content on the Instructor's Media Library.

### Instructor's Resource Kit

The *Life*, Ninth Edition Instructor's Resource Kit includes a wealth of information to help instructors in the planning and teaching of their course. The Kit includes:

#### **Instructor's Manual**, featuring (by chapter):

- A "What's New" guide to the Ninth Edition
- Brief chapter overview
- Chapter outline
- Key terms section with all of the boldface terms from the text

**Lecture Notes.** Detailed notes for each chapter, which can serve as the basis for lectures, including references to figures and media resources.

**Media Guide.** A visual guide to the extensive media resources available with the Ninth Edition of *Life*. The guide includes thumbnails and descriptions of every video, animation, lecture PowerPoint®, and supplemental photo in the Media Library, all organized by chapter.

### Overhead Transparencies

This set includes over 1,000 transparencies—including all of the four-color line art and all of the tables from the text—along with convenient binders. All figures have been formatted and color-enhanced for clear projection in a wide range of conditions. Labels and images have been resized for improved readability.

### Test File

Catherine Ueckert, *Northern Arizona University*; Norman Johnson, *University of Massachusetts*; Paul Nolan, *The Citadel*; Nicola Plowes, *Arizona State University*

The Test File offers more than 5,000 questions, covering the full range of topics presented in the textbook. All questions are referenced to textbook sections and page numbers, and are ranked according to Bloom's taxonomy. Each chapter includes a wide range of multiple choice and fill-in-the-blank questions. In addition, each chapter features a set of diagram questions that involve the student in working with illustrations of structures, graphs, steps in processes, and more. The electronic versions of the Test File (within BioPortal, the Instructor's Media Library, and the Computerized Test Bank CD) also include all of the textbook end-of-chapter Self-Quiz questions, all of the BioPortal Diagnostic Quiz questions, and all of the Study Guide multiple-choice questions.

### Computerized Test Bank

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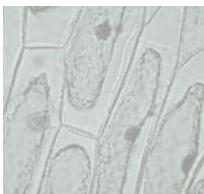
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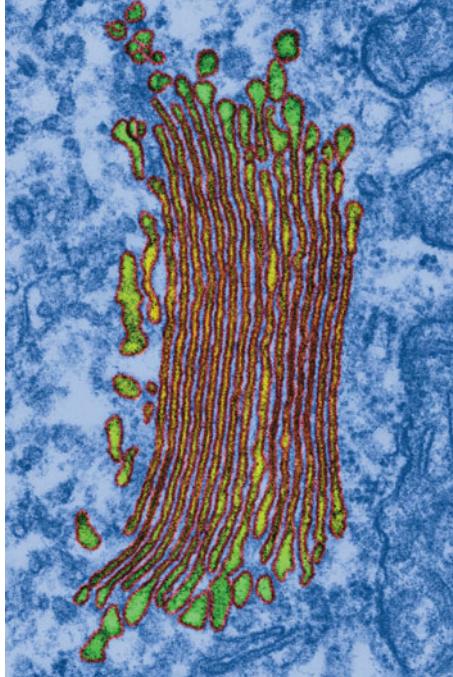
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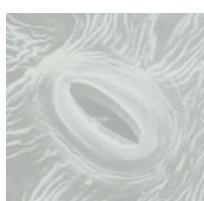
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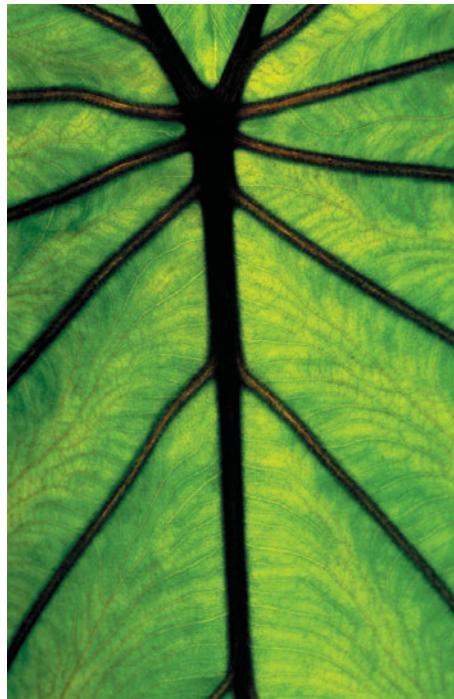
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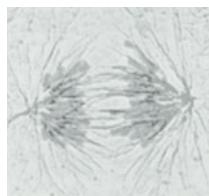
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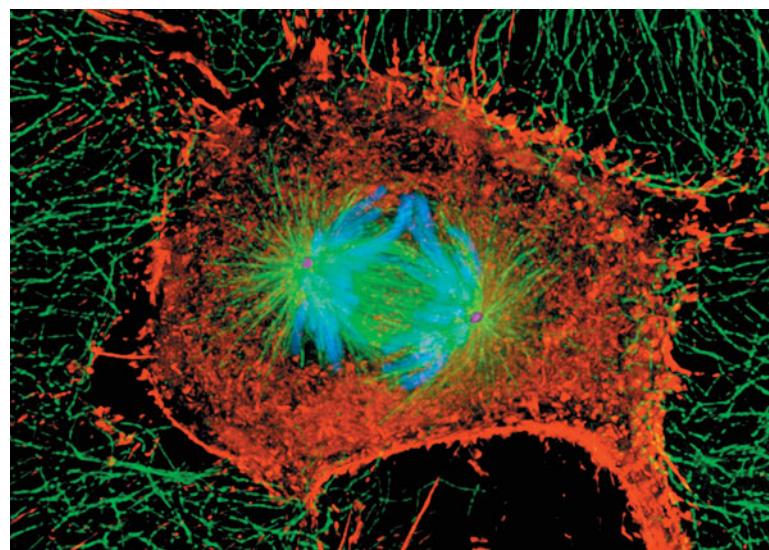
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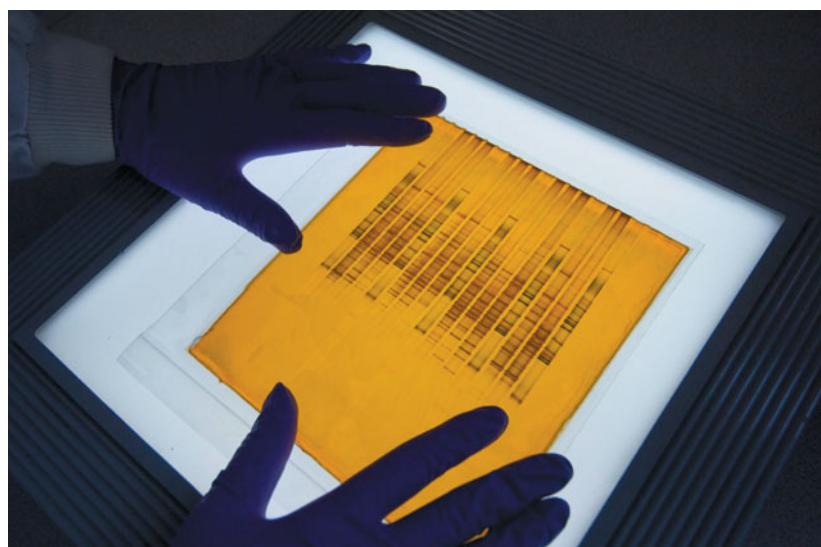
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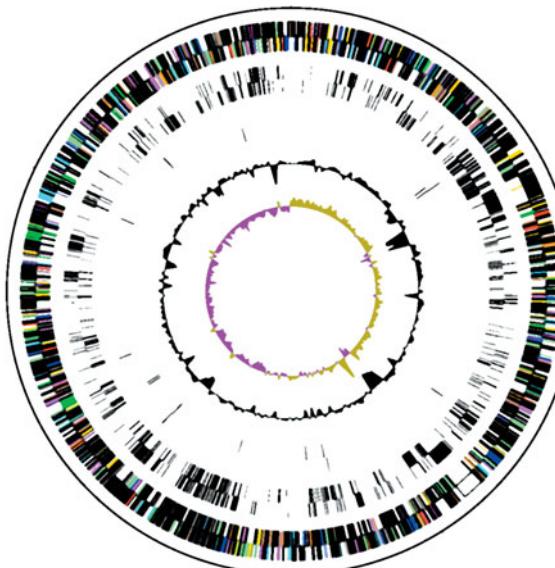
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## PART SIX THE PATTERNS AND PROCESSES OF EVOLUTION

### 21 Evidence and Mechanisms of Evolution 440

#### 21.1 What Facts Form the Basis of Our Understanding of Evolution? 441

Charles Darwin articulated the principle of natural selection 442  
Adaptation has two meanings 444  
Population genetics provides an underpinning for Darwin's theory 444  
Most populations are genetically variable 445  
Evolutionary change can be measured by allele and genotype frequencies 446  
The genetic structure of a population changes over time, unless certain restrictive conditions exist 447  
Deviations from Hardy–Weinberg equilibrium show that evolution is occurring 448

#### 21.2 What Are the Mechanisms of Evolutionary Change? 448

Mutations generate genetic variation 448  
Gene flow may change allele frequencies 449  
Genetic drift may cause large changes in small populations 449  
Nonrandom mating can change genotype frequencies 451

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Natural selection can change or stabilize populations 452  
Sexual selection influences reproductive success 453

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Neutral mutations accumulate in populations 456  
Sexual recombination amplifies the number of possible genotypes 456  
Frequency-dependent selection maintains genetic variation within populations 457

Heterozygote advantage maintains polymorphic loci 457  
Much genetic variation in species is maintained in geographically distinct populations 457  
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Comparisons among species require an evolutionary perspective 467

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Phylogenies are reconstructed from many sources of data 470  
Mathematical models expand the power of phylogenetic reconstruction 471  
The accuracy of phylogenetic methods can be tested 471

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Phylogenies allow us to compare and contrast living organisms 474  
Ancestral states can be reconstructed 475  
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Evolutionary history is the basis for modern biological classification 477  
Several codes of biological nomenclature govern the use of scientific names 478

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Species are reproductively isolated lineages on the tree of life 483

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Gene incompatibilities can produce reproductive isolation in two daughter species 484  
Reproductive isolation develops with increasing genetic divergence 485  
Geographic barriers give rise to allopatric speciation 485  
Sympatric speciation occurs without physical barriers 486

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Postzygotic barriers can isolate species after fertilization 491  
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Genes and proteins are compared through sequence alignment 500  
Models of sequence evolution are used to calculate evolutionary divergence 501

Experimental studies examine molecular evolution directly 502

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Much of evolution is neutral 506

Positive and purifying selection can be detected in the genome 506  
Genome size and organization also evolve 507

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Most new functions arise following gene duplication 510  
Some gene families evolve through concerted evolution 511

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Gene evolution is used to study protein function 513  
In vitro evolution produces new molecules 514  
Molecular evolution is used to study and combat diseases 514



Radioisotope dating methods have been expanded and refined 521

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Oxygen concentrations in Earth's atmosphere have changed over time 523  
Earth's climate has shifted between hot/humid and cold/dry conditions 524  
Volcanoes have occasionally changed the history of life 525  
Extraterrestrial events have triggered changes on Earth 525

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Several processes contribute to the paucity of fossils 526  
Precambrian life was small and aquatic 527  
Life expanded rapidly during the Cambrian period 527  
Many groups of organisms that arose during the Cambrian later diversified 528  
Geographic differentiation increased during the Mesozoic era 532  
Modern biota evolved during the Cenozoic era 533  
The tree of life is used to reconstruct evolutionary events 533

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Prokaryotes generally form complex communities 539

Prokaryotes have distinctive cell walls 541

Prokaryotes have distinctive modes of locomotion 541

Prokaryotes reproduce asexually, but genetic recombination can occur 542

Prokaryotes can communicate 542

Prokaryotes have amazingly diverse metabolic pathways 543

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The small size of prokaryotes has hindered our study of their phylogeny 545

The nucleotide sequences of prokaryotes reveal their evolutionary relationships 545

Lateral gene transfer can lead to discordant gene trees 545

The great majority of prokaryote species have never been studied 546

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Spirochetes move by means of axial filaments 547

Chlamydias are extremely small parasites 548

Some high-GC Gram-positives are valuable sources of antibiotics 548

Cyanobacteria are important photoautotrophs 548

The low-GC Gram-positives include the smallest cellular organisms 549

The proteobacteria are a large and diverse group 550

Archaea differ in several important ways from bacteria 551

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 Cellular features support the monophyly of eukaryotes 561  
 The modern eukaryotic cell arose in several steps 564  
 Chloroplasts are a study in endosymbiosis 565  
 Lateral gene transfer accounts for the presence of some prokaryotic genes in eukaryotes 566

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 Protists have diverse means of locomotion 567  
 Protists employ vacuoles in several ways 567  
 The cell surfaces of protists are diverse 568

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Alveolates have sacs under their plasma membrane 575  
 Stramenopiles have two unequal flagella, one with hairs 577  
 Red algae have a distinctive accessory photosynthetic pigment 579  
 Chlorophytes, charophytes, and land plants contain chlorophylls *a* and *b* 580  
 Diplomonads and parabasalids are excavates that lack mitochondria 581  
 Heteroloboseans alternate between amoeboid forms and forms with flagella 581  
 Euglenids and kinetoplastids have distinctive mitochondria and flagella 581  
 Foraminiferans have created vast limestone deposits 582  
 Radiolarians have thin, stiff pseudopods 582  
 Amoebozoans use lobe-shaped pseudopods for locomotion 583

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 Life cycles of land plants feature alternation of generations 592

The sporophytes of nonvascular land plants are dependent on gametophytes 592

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Vascular tissues transport water and dissolved materials 594  
 Vascular plants have been evolving for almost half a billion years 595  
 The earliest vascular plants lacked roots and leaves 596  
 The vascular plants branched out 596  
 Roots may have evolved from branches 596  
 Monilophytes and seed plants have true leaves 597  
 Heterospory appeared among the vascular plants 597

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 Water- and sugar-transport mechanisms first emerged in the mosses 600  
 Hornworts have distinctive chloroplasts and sporophytes without stalks 600  
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 Horsetails, whisk ferns, and ferns constitute a clade 602

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 A change in anatomy enabled seed plants to grow to great heights 611

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Recent analyses have revealed the oldest split among the angiosperms	620

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The body of a multicellular fungus is composed of hyphae	629
Fungi are in intimate contact with their environment	630
Fungi reproduce both sexually and asexually	630

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Fungi may engage in parasitic and predatory interactions	632
Some fungi engage in relationships beneficial to both partners	633
Endophytic fungi protect some plants from pathogens, herbivores, and stress	635

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A few basic developmental patterns differentiate major animal groups	648

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The structure of the body cavity influences movement	649
Segmentation improves control of movement	650
Appendages have many uses	650

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Filter feeders capture small prey	652
Herbivores eat plants	652
Predators capture and subdue large prey	652
Parasites live in or on other organisms	653
Detrivores live off the remains of other organisms	654

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Most animal life cycles have at least one dispersal stage	655
No life cycle can maximize all benefits	655
Parasite life cycles evolve to facilitate dispersal and overcome host defenses	656
Colonial organisms are composed of genetically identical, physiologically integrated individuals	656

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Placozoans are abundant but rarely observed	660
Ctenophores are radially symmetrical and diploblastic	660
Cnidarians are specialized carnivores	661

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Cilia-bearing lophophores and trophophores evolved among the lophotrochozoans	668
Ecdysozoans must shed their cuticles	669
Arrow worms retain some ancestral developmental features	670

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Flatworms and rotifers are structurally diverse relatives 672  
 Ribbon worms have a long, protrusible feeding organ 673  
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 Annelids have segmented bodies 674  
 Mollusks have undergone a dramatic evolutionary radiation 676

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Several marine groups have relatively few species 679  
 Nematodes and their relatives are abundant and diverse 680

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Arthropod relatives have fleshy, unjointed appendages 682  
 Jointed appendages first appeared in the trilobites 682  
 Myriapods have many legs 683  
 Most chelicerates have four pairs of legs 683  
 Crustaceans are diverse and abundant 684

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 A dorsal supporting structure replaces the notochord in vertebrates 699  
 The vertebrate body plan can support large, active animals 700

Fins and swim bladders improved stability and control over locomotion 701

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Jointed fins enhanced support for fishes 703  
 Amphibians adapted to life on land 704  
 Amniotes colonized dry environments 706  
 Reptiles adapted to life in many habitats 707  
 Crocodilians and birds share their ancestry with the dinosaurs 708  
 The evolution of feathers allowed birds to fly 708  
 Mammals radiated after the extinction of dinosaurs 709  
 Most mammals are therians 710

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Human ancestors evolved bipedal locomotion 715  
 Human brains became larger as jaws became smaller 716  
 Humans developed complex language and culture 716



## **PART EIGHT**

# **FLOWERING PLANTS: FORM AND FUNCTION**

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The root system anchors the plant and takes up water and dissolved minerals 721  
 The stem supports leaves and flowers 722  
 Leaves are the primary sites of photosynthesis 722

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Cell walls and vacuoles help determine plant form 723  
 The structure of cell walls allows plants to grow 723

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 Cells of the xylem transport water and dissolved minerals 728  
 Cells of the phloem transport the products of photosynthesis 728

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Plants increase in size through primary and secondary growth 728  
 A hierarchy of meristems generates the plant body 729  
 Indeterminate primary growth originates in apical meristems 730  
 The root apical meristem gives rise to the root cap and the root primary meristems 730  
 The products of the root's primary meristems become root tissues 730

The products of the stem's primary meristems become stem tissues 731

Leaves are determinate organs produced by shoot apical meristems 732

Many eudicot stems and roots undergo secondary growth 733

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 Aquaporins facilitate the movement of water across membranes 742  
 Uptake of mineral ions requires membrane transport proteins 742

Water and ions pass to the xylem by way of the apoplast and symplast 743

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Xylem sap is not pumped by living cells 745

Root pressure alone does not account for xylem transport 745

The transpiration-cohesion-tension mechanism accounts for xylem transport 746

A pressure chamber measures tension in the xylem sap 747

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The pressure flow model appears to account for translocation in the phloem 751

The pressure flow model has been experimentally tested 752



Nitrogen fixers make all other life possible 763

Nitrogenase catalyzes nitrogen fixation 763

Some plants and bacteria work together to fix nitrogen 764

Legumes and rhizobia communicate using chemical signals 765

Biological nitrogen fixation does not always meet agricultural needs 765

Plants and bacteria participate in the global nitrogen cycle 766

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Carnivorous plants supplement their mineral nutrition 767

Parasitic plants take advantage of other plants 767

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Deficiency symptoms reveal inadequate nutrition 757

Hydroponic experiments identified essential elements 758

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Soils form through the weathering of rock 760

Soils are the source of plant nutrition 760

Fertilizers and lime are used in agriculture 761

Plants affect soil fertility and pH 761

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Mycorrhizae expand the root system of plants 762

Soil bacteria are essential in getting nitrogen from air to plant cells 762

Seed germination begins with the uptake of water 774

The embryo must mobilize its reserves 774

Several hormones and photoreceptors help regulate plant growth 774

Signal transduction pathways are involved in all stages of plant development 775

Studies of *Arabidopsis thaliana* have increased our understanding of plant signal transduction 775

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Gibberellins are plant hormones 777

Gibberellins have many effects on plant growth and development 777

Gibberellins act by initiating the breakdown of transcriptional repressors 778

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Auxin transport is polar and requires carrier proteins 781

Auxin transport mediates responses to light and gravity 781

Auxin affects plant growth in several ways 782

At the molecular level, auxin and gibberellins act similarly 784

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Ethylene is a gaseous hormone that hastens leaf senescence and fruit ripening 786

Brassinosteroids are plant steroid hormones 786

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In early development, the seed germinates and forms a growing seedling 773

Environment cues can initiate seed germination 773

Seed dormancy affords adaptive advantages 774

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- Phototropins, cryptochromes, and zeaxanthin are blue-light receptors 788
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- The flower is an angiosperm's structure for sexual reproduction 795
- Flowering plants have microscopic gametophytes 796
- Pollination in the absence of water is an evolutionary adaptation 798
- Flowering plants prevent inbreeding 798
- A pollen tube delivers sperm cells to the embryo sac 799
- Angiosperms perform double fertilization 799
- Embryos develop within seeds 800
- Seed development is under hormonal control 801
- Fruits assist in seed dispersal 801

### **38.2 What Determines the Transition from the Vegetative to the Flowering State? 802**

- Apical meristems can become inflorescence meristems 803
- A cascade of gene expression leads to flowering 803
- Photoperiodic cues can initiate flowering 804
- Plants vary in their responses to photoperiodic cues 804
- The length of the night is the key photoperiodic cue determining flowering 804

- The flowering stimulus originates in a leaf 805
- Florigen is a small protein 807
- Flowering can be induced by temperature or gibberellin 808
- Some plants do not require an environmental cue to flower 808

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- Plants can seal off infected parts to limit damage 816
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- Receptor-elicitor binding evokes the hypersensitive response 817
- Systemic acquired resistance is a form of long-term "immunity" 818
- Plants develop specific immunity to RNA viruses 818

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- Mechanical defenses against herbivores are widespread 819
- Plants produce chemical defenses against herbivores 820

- Some secondary metabolites play multiple roles 821
- Plants respond to herbivory with induced defenses 821
- Why don't plants poison themselves? 822
- The plant doesn't always win the arms race 823

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- Plants can acclimate to drought stress 826
- Plants have ways of coping with temperature extremes 826

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## PART NINE ANIMALS: FORM AND FUNCTION

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An internal environment makes complex multicellular animals possible 833

Physiological systems maintain homeostasis 834

Cells, tissues, organs, and systems are specialized to serve homeostatic needs 835

Organs consist of multiple tissues 837

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Animals acclimatize to seasonal temperatures 839

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Endotherms produce heat metabolically 839

Ectotherms and endotherms respond differently to changes in temperature 840

Energy budgets reflect adaptations for regulating body temperature 841

Both ectotherms and endotherms control blood flow to the skin 842

Some fishes elevate body temperature by conserving metabolic heat 843

Some ectotherms regulate heat production 843

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Basal metabolic rates are correlated with body size and environmental temperature 844

Endotherms respond to cold by producing heat and adapt to cold by reducing heat loss 845

Evaporation of water can dissipate heat, but at a cost 846

The mammalian thermostat uses feedback information 846

Fever helps the body fight infections 847

Turning down the thermostat 847

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Chemical signals can act locally or at a distance 853

Hormonal communication has a long evolutionary history 853

Hormones can be divided into three chemical groups 856

Hormone receptors can be membrane-bound or intracellular 856

Hormone action depends on the nature of the target cell and its receptors 857

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The pituitary connects the nervous and endocrine systems 858

The anterior pituitary is controlled by hypothalamic neurohormones 860

Negative feedback loops regulate hormone secretion 861

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The thyroid gland secretes thyroxine 861

Three hormones regulate blood calcium concentrations 863

PTH lowers blood phosphate levels 864

Insulin and glucagon regulate blood glucose concentrations 864

The adrenal gland is two glands in one 865

Sex steroids are produced by the gonads 867

Melatonin is involved in biological rhythms and photoperiodicity 868

Many chemicals may act as hormones 868

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Hormones can be detected and measured with immunoassays 868

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Blood and lymph tissues play important roles in defense 875

White blood cells play many defensive roles 875

Immune system proteins bind pathogens or signal other cells 875

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Barriers and local agents defend the body against invaders 877

Other nonspecific defenses include specialized proteins and cellular processes 878

Inflammation is a coordinated response to infection or injury 878

Inflammation can cause medical problems 879

Cell signaling pathways stimulate the body's defenses 879

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Adaptive immunity has four key features 880

Two types of specific immune responses interact: an overview 881

Genetic changes and clonal selection generate the specific immune response 882

Immunity and immunological memory result from clonal selection 883

Vaccines are an application of immunological memory 883

Animals distinguish self from nonself and tolerate their own antigens 884

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- Different antibodies share a common structure 885
- There are five classes of immunoglobulins 886
- Monoclonal antibodies have many uses 886

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- T cell receptors bind to antigens on cell surfaces 888
- MHC proteins present antigen to T cells 888
- T-helper cells and MHC II proteins contribute to the humoral immune response 889
- Cytotoxic T cells and MHC I proteins contribute to the cellular immune response 889
- Regulatory T cells suppress the humoral and cellular immune responses 889
- MHC proteins are important in tissue transplants 891

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- The constant region is involved in immunoglobulin class switching 893

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- Autoimmune diseases are caused by reactions against self antigens 895
- AIDS is an immune deficiency disorder 895

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- Budding and regeneration produce new individuals by mitosis 900
- Parthenogenesis is the development of unfertilized eggs 901

#### **43.2 How Do Animals Reproduce Sexually? 902**

- Gametogenesis produces eggs and sperm 902
- Fertilization is the union of sperm and egg 905
- Getting eggs and sperm together 906
- An individual animal can function as both male and female 907
- The evolution of vertebrate reproductive systems parallels the move to land 907
- Animals with internal fertilization are distinguished by where the embryo develops 908

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- Male sex organs produce and deliver semen 909
- Male sexual function is controlled by hormones 911

- Female sex organs produce eggs, receive sperm, and nurture the embryo 912

The ovarian cycle produces a mature egg 913

The uterine cycle prepares an environment for the fertilized egg 913

Hormones control and coordinate the ovarian and uterine cycles 914

In pregnancy, hormones from the extraembryonic membranes take over 915

Childbirth is triggered by hormonal and mechanical stimuli 916

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- Humans use a variety of methods to control fertility 917
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#### **44.1 How Does Fertilization Activate Development? 923**

- The sperm and the egg make different contributions to the zygote 923
- Rearrangements of egg cytoplasm set the stage for determination 924
- Cleavage repackages the cytoplasm 925
- Early cell divisions in mammals are unique 926
- Specific blastomeres generate specific tissues and organs 927

#### **44.2 How Does Gastrulation Generate Multiple Tissue Layers? 928**

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- Gastrulation in the frog begins at the gray crescent 929
- The dorsal lip of the blastopore organizes embryo formation 930
- Transcription factors underlie the organizer's actions 931
- The organizer changes its activity as it migrates from the dorsal lip 932
- Reptilian and avian gastrulation is an adaptation to yolked eggs 933
- Placental mammals retain the avian-reptilian gastrulation pattern but lack yolk 934



#### 44.3 How Do Organs and Organ Systems Develop? 935

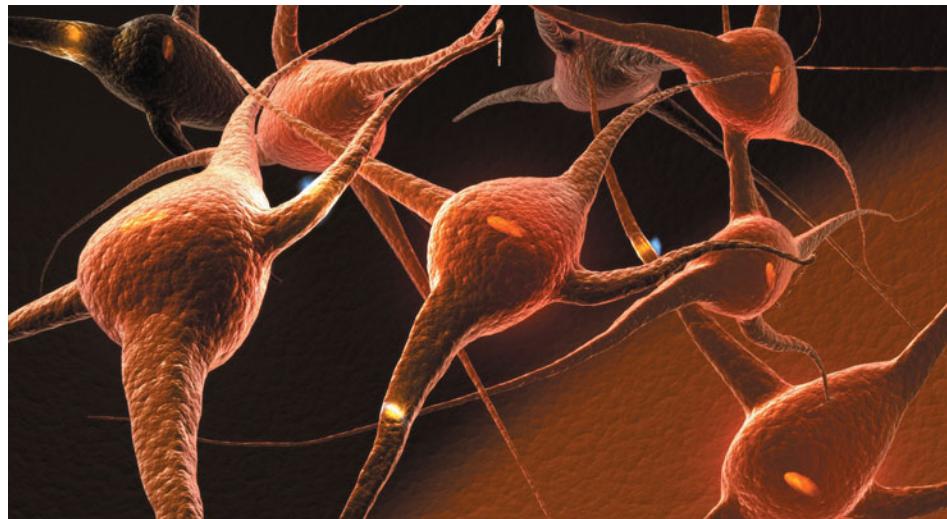
- The stage is set by the dorsal lip of the blastopore 935
- Body segmentation develops during neurulation 935
- Hox genes control development along the anterior-posterior axis 936

#### 44.4 How is the Growing Embryo Sustained? 937

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- Developmental changes continue throughout life 940



## 45 Neurons and Nervous Systems 943

#### 45.1 What Cells Are Unique to the Nervous System? 944

- Neural networks range in complexity 944
- Neurons are the functional units of nervous systems 945
- Glia are also important components of nervous systems 947

#### 45.2 How Do Neurons Generate and Transmit Electrical Signals? 948

- Simple electrical concepts underlie neural function 948
- Membrane potentials can be measured with electrodes 948
- Ion transporters and channels generate membrane potentials 948
- Ion channels and their properties can now be studied directly 951
- Gated ion channels alter membrane potential 952
- Graded changes in membrane potential can integrate information 952
- Sudden changes in  $\text{Na}^+$  and  $\text{K}^+$  channels generate action potentials 953
- Action potentials are conducted along axons without loss of signal 955

Action potentials can jump along axons 955

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- The neuromuscular junction is a model chemical synapse 956
- The arrival of an action potential causes the release of neurotransmitter 956
- Synaptic functions involve many proteins 957
- The postsynaptic membrane responds to neurotransmitter 957
- Synapses between neurons can be excitatory or inhibitory 958
- The postsynaptic cell sums excitatory and inhibitory input 958
- Synapses can be fast or slow 958
- Electrical synapses are fast but do not integrate information well 959
- The action of a neurotransmitter depends on the receptor to which it binds 959
- Glutamate receptors may be involved in learning and memory 960
- To turn off responses, synapses must be cleared of neurotransmitter 960
- The diversity of receptors makes drug specificity possible 961

Sensation depends on which neurons receive action potentials from sensory cells 967

Many receptors adapt to repeated stimulation 967

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- Arthropods are good models for studying chemoreception 968
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- The vomeronasal organ contains chemoreceptors 969
- Gustation is the sense of taste 969

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- Hair cells are sensitive to being bent 974
- Hair cells detect forces of gravity and momentum 975
- Hair cells are evolutionarily conserved 975

#### 46.4 How Do Sensory Systems Detect Light? 976

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- Rod cells respond to light 976
- Invertebrates have a variety of visual systems 978
- Image-forming eyes evolved independently in vertebrates and cephalopods 979
- The vertebrate retina receives and processes visual information 980

## 46 Sensory Systems 964

#### 46.1 How Do Sensory Cells Convert Stimuli into Action Potentials? 965

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# 47 The Mammalian Nervous System: Structure and Higher Function 985

## 47.1 How Is the Mammalian Nervous System Organized? 986

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- The spinal cord transmits and processes information 988
- The reticular system alerts the forebrain 989
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- Regions of the telencephalon interact to produce consciousness and control behavior 990
- The human brain is off the curve 992

## 47.2 How Is Information Processed by Neural Networks? 993

- The autonomic nervous system controls involuntary physiological functions 993
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## 47.3 Can Higher Functions Be Understood in Cellular Terms? 998

- Sleep and dreaming are reflected in electrical patterns in the cerebral cortex 999
- Language abilities are localized in the left cerebral hemisphere 1000
- Some learning and memory can be localized to specific brain areas 1000
- We still cannot answer the question "What is consciousness?" 1002

# 48 Musculoskeletal Systems 1006

## 48.1 How Do Muscles Contract? 1007

- Sliding filaments cause skeletal muscle to contract 1007
- Actin-myosin interactions cause filaments to slide 1009
- Actin-myosin interactions are controlled by calcium ions 1010
- Cardiac muscle is similar to and different from skeletal muscle 1012
- Smooth muscle causes slow contractions of many internal organs 1012
- Single skeletal muscle twitches are summed into graded contractions 1014

## 48.2 What Determines Muscle Performance? 1015

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- A muscle has an optimal length for generating maximum tension 1016
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- Muscle ATP supply limits performance 1017
- Insect muscle has the greatest rate of cycling 1018

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# 49 Gas Exchange in Animals 1025

## 49.1 What Physical Factors Govern Respiratory Gas Exchange? 1026

- Diffusion is driven by concentration differences 1026
- Fick's law applies to all systems of gas exchange 1027
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- High temperatures create respiratory problems for aquatic animals 1028
- O<sub>2</sub> availability decreases with altitude 1028
- CO<sub>2</sub> is lost by diffusion 1028

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- Transporting gases to and from exchange surfaces optimizes partial pressure gradients 1029
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- Fish gills use countercurrent flow to maximize gas exchange 1030
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Tubular guts have an opening at each end 1075

Digestive enzymes break down complex food molecules 1076

**51.3 How Does the Vertebrate Gastrointestinal System Function? 1077**

The vertebrate gut consists of concentric tissue layers 1077  
Mechanical activity moves food through the gut and aids digestion 1078  
Chemical digestion begins in the mouth and the stomach 1079  
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The stomach gradually releases its contents to the small intestine 1080  
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**51 Nutrition, Digestion, and Absorption 1067****51.1 What Do Animals Require from Food? 1068**

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Sources of energy can be stored in the body 1070  
Food provides carbon skeletons for biosynthesis 1070  
Animals need mineral elements for a variety of functions 1071  
Animals must obtain vitamins from food 1072  
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### **52.4 How Do Vertebrates Maintain Salt and Water Balance? 1097**

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The loop of Henle creates a concentration gradient in the renal medulla 1102

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Ethologists probed the causes of behavior 1116

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## PART TEN ECOLOGY

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- Ecologists study biotic and abiotic components of ecosystems 1142

## 54.2 Why Do Climates Vary Geographically? 1142

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- Solar energy input determines atmospheric circulation patterns 1142
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- Organisms adapt to climatic challenges 1144

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- Temperate deciduous forests change with the seasons 1149
- Temperate grasslands are widespread 1150
- Hot deserts form around 30° latitude 1151
- Cold deserts are high and dry 1152
- Chaparral has hot, dry summers and wet, cool winters 1153
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# 56 Species Interaction and Coevolution 1185

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- Predator-prey interactions result in a range of adaptations 1189
- Herbivory is a widespread interaction 1190
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# *Life*

The Science of Biology

NINTH EDITION

# Studying Life

## Why are frogs croaking?

**A**mphibians—frogs, toads, and salamanders—have been around for a long time. They watched the dinosaurs come and go. But today amphibian populations around the world are in dramatic decline, with more than a third of the world's amphibian species threatened with extinction. Why?

Biologists work to answer this question by making observations and doing experiments. A number of factors may be involved, and one possible cause may be the effects of agricultural pesticides and herbicides. Several studies have shown that many of these chemicals tested at realistic concentrations do not kill amphibians. But Tyrone Hayes, a biologist at the University of California at Berkeley, probed deeper.

Hayes focused on atrazine, the most widely used herbicide in the world and a common contaminant in fresh water. More than 70 million pounds of atrazine are applied to farmland in the United States every year, and it is used in at least 20 countries. Atrazine is usually applied in the spring, when many amphibians are breeding and thou-

sands of tadpoles swim in the ditches, ponds, and streams that receive runoff from farms.

In his laboratory, Hayes and his associates raised frog tadpoles in water containing no atrazine and in water with concentrations ranging from 0.01 parts per billion (ppb) up to 25 ppb. The U.S. Environmental Protection Agency considers environmental levels of atrazine of 10 to 20 ppb of no concern; the level it considers safe in drinking water is 3 ppb. Rainwater in Iowa has been measured to contain 40 ppb. In Switzerland, where the use of atrazine is illegal, the chemical has been measured at approximately 1 ppb in rainwater.

In the Hayes laboratory, concentrations as low as 0.1 ppb had a dramatic effect on tadpole development: it feminized the males. In some of the adult males that developed from these larvae, the vocal structures used in mating calls were smaller than normal, female sex organs developed, and eggs were found growing in the testes. In other studies, normal adult male frogs exposed to 25 ppb had a tenfold reduction in testosterone levels and did not produce sperm. You can imagine the disastrous effects these developmental and hormonal changes could have on the capacity of frogs to breed and reproduce.

But Hayes's experiments were performed in the laboratory, with a species of frog bred for laboratory use. Would his results be the same in nature? To find out, he and his students traveled from Utah to Iowa, sampling water and collecting frogs. They analyzed the water



**Frogs Are Having Serious Problems** An alarming number of species of frogs, such as this tiny leaf frog (*Agalychnis calcarifer*) from Ecuador, are in danger of becoming extinct. The numerous possible reasons for the decline in global amphibian populations have been a subject of widespread scientific investigation.



**A Biologist at Work** Tyrone Hayes grew up near the great Congaree Swamp in South Carolina collecting turtles, snakes, frogs, and toads. Now a professor of biology at the University of California at Berkeley, he has more than 3,000 frogs in his laboratory and studies hormonal control of their development.

for atrazine and examined the frogs. In the only site where atrazine was undetectable in the water, the frogs were normal; in all the other sites, male frogs had abnormalities of the sex organs.

Like other biologists, Hayes made observations. He then made predictions based on those observations, and designed and carried out experiments to test his predictions. Some of the conclusions from his experiments, described at the end of this chapter, could have profound implications not only for amphibians but also for other animals, including humans.

**IN THIS CHAPTER** we identify and examine the most common features of living organisms and put those features into the context of the major principles that underlie all biology. Next we offer a brief outline of how life evolved and how the different organisms on Earth are related. We then turn to the subjects of biological inquiry and the scientific method. Finally we consider how knowledge discovered by biologists influences public policy.

## CHAPTER OUTLINE

- 1.1 What Is Biology?
- 1.2 How Is All Life on Earth Related?
- 1.3 How Do Biologists Investigate Life?
- 1.4 How Does Biology Influence Public Policy?

### 1.1 What Is Biology?

**Biology** is the scientific study of living things. Biologists define “living things” as all the diverse organisms descended from a single-celled ancestor that evolved almost 4 billion years ago. Because of their common ancestry, living organisms share many characteristics that are not found in the nonliving world. Living organisms:

- consist of one or more cells
- contain genetic information
- use genetic information to reproduce themselves
- are genetically related and have evolved
- can convert molecules obtained from their environment into new biological molecules
- can extract energy from the environment and use it to do biological work
- can regulate their internal environment

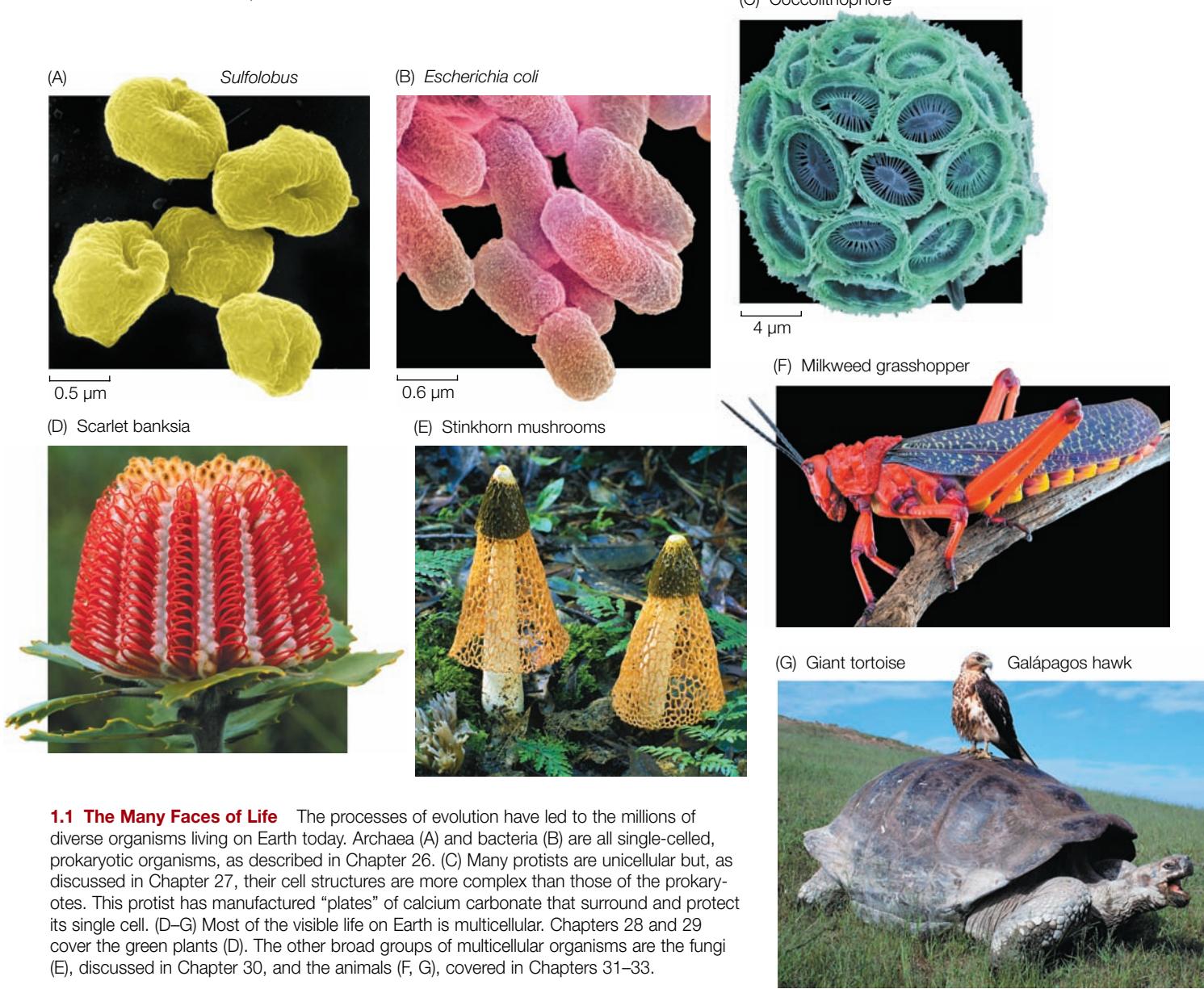
This simple list, however, belies the incredible complexity and diversity of life. Some forms of life may not display all of these characteristics all of the time. For example, the seed of a desert plant may go for many years without extracting energy from the environment, converting molecules, regulating its internal environment, or reproducing; yet the seed is alive.

And what about viruses? Viruses do not consist of cells, and they cannot carry out physiological functions on their own; they must parasitize host cells to do those jobs for them. Yet viruses contain genetic information, and they certainly mutate and evolve (as we know, because evolving flu viruses require constant changes in the vaccines we create to combat them). The existence of viruses depends on cells, and it is highly probable that viruses evolved from cellular life forms. So, are viruses alive? What do you think?

This book explores the characteristics of life, how these characteristics vary among organisms, how they evolved, and how they work together to enable organisms to survive and reproduce. *Evolution* is a central theme of biology and therefore of this book. Through differential survival and reproduction, living systems evolve and become adapted to Earth’s many environments. The processes of evolution have generated the enormous diversity that we see today as life on Earth.

#### Cells are the basic unit of life

We lay the chemical foundation for our study of life in the next three chapters, after which we will turn to cells and the processes by which they live, reproduce, age, and die. Some organisms are *unicellular*, consisting of a single cell that carries out



**1.1 The Many Faces of Life** The processes of evolution have led to the millions of diverse organisms living on Earth today. Archaea (A) and bacteria (B) are all single-celled, prokaryotic organisms, as described in Chapter 26. (C) Many protists are unicellular but, as discussed in Chapter 27, their cell structures are more complex than those of the prokaryotes. This protist has manufactured “plates” of calcium carbonate that surround and protect its single cell. (D–G) Most of the visible life on Earth is multicellular. Chapters 28 and 29 cover the green plants (D). The other broad groups of multicellular organisms are the fungi (E), discussed in Chapter 30, and the animals (F, G), covered in Chapters 31–33.

all the functions of life (**Figure 1.1A–C**). Others are *multicellular*, made up of many cells that are specialized for different functions (**Figure 1.1D–G**). Viruses are *acellular*, although they depend on cellular organisms.

The discovery of cells was made possible by the invention of the microscope in the 1590s by the Dutch spectacle makers Hans and Zaccharias Janssen (father and son). In the mid- to late 1600s, Antony van Leeuwenhoek of Holland and Robert Hooke of England both made improvements on the Janssens' technology and used it to study living organisms. Van Leeuwenhoek discovered that drops of pond water teemed with single-celled organisms, and he made many other discoveries as he progressively improved his microscopes over a long lifetime of research. Hooke put pieces of plants under his microscope and observed that they were made up of repeated units he called *cells* (**Figure 1.2**). In 1676, Hooke wrote that van Leeuwenhoek had observed “a vast number of small animals in his Excrements which were most abounding when he was troubled with a Loosenesse and very few or none when he was well.” This simple observation

represents the discovery of bacteria—and makes one wonder why scientists do some of the things they do.

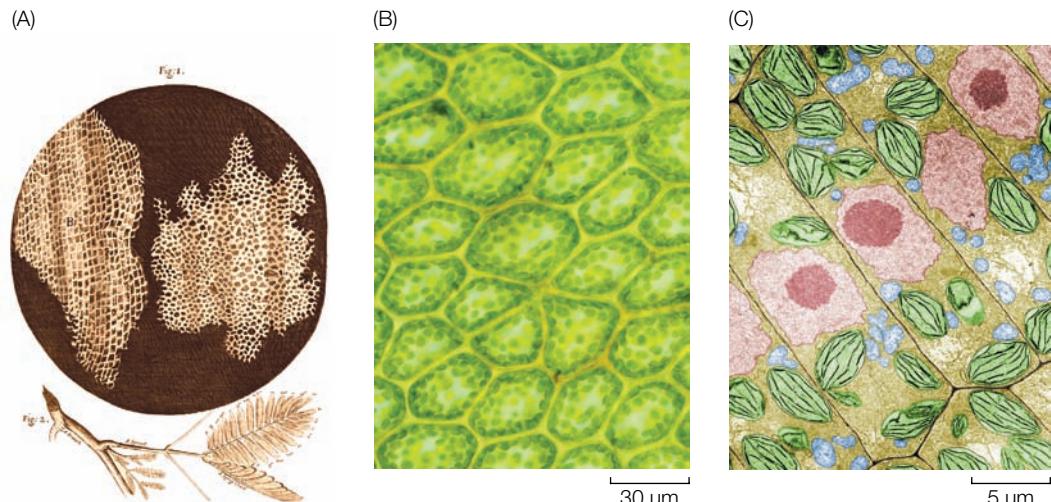
More than a hundred years passed before studies of cells advanced significantly. As they were dining together one evening in 1838, Matthias Schleiden, a German biologist, and Theodor Schwann, from Belgium, discussed their work on plant and animal tissues, respectively. They were struck by the similarities in their observations and came to the conclusion that the basic structural elements of plants and animals were essentially the same. They formulated their conclusion as the **cell theory**, which states that:

- Cells are the basic structural and physiological units of all living organisms.
- Cells are both distinct entities and building blocks of more complex organisms.

But Schleiden and Schwann also believed (wrongly) that cells emerged by the self-assembly of nonliving materials, much as crystals form in a solution of salt. This conclusion was in ac-

## 1.2 Cells Are the Building Blocks of Life

The development of microscopes revealed the microbial world to seventeenth-century scientists such as Robert Hooke, who proposed the concept of cells based on his observations. (A) Hooke drew the cells of a slice of plant tissue (cork) as he saw them under his optical microscope. (B) A modern optical, or “light,” microscope reveals the intricacies of cells in a leaf. (C) Transmission electron microscopes (TEMs) allow scientists to see even smaller objects. TEMs do not visualize color; here color has been added to a black-and-white micrograph of cells in a duckweed stem.



cordance with the prevailing view of the day, which was that life can arise from non-life by spontaneous generation—mice from dirty clothes, maggots from dead meat, or insects from pond water.

The debate continued until 1859, when the French Academy of Sciences sponsored a contest for the best experiment to prove or disprove spontaneous generation. The prize was won by the great French scientist Louis Pasteur, who demonstrated that sterile broth directly exposed to the dirt and dust in air developed a culture of microorganisms, but a similar container of broth not directly exposed to air remained sterile (see Figure 4.7). Pasteur’s experiment did not prove that it was microorganisms in the air that caused the broth to become infected, but it did uphold the conclusion that life must be present in order for new life to be generated.

Today scientists accept the fact that all cells come from pre-existing cells and that the functional properties of organisms derive from the properties of their cells. Since cells of all kinds share both essential mechanisms and a common ancestry that goes back billions of years, modern cell theory has additional elements:

- All cells come from preexisting cells.
- All cells are similar in chemical composition.
- Most of the chemical reactions of life occur in aqueous solution within cells.
- Complete sets of genetic information are replicated and passed on during cell division.
- Viruses lack cellular structure but remain dependent on cellular organisms.

At the same time Schleiden and Schwann were building the foundation for the cell theory, Charles Darwin was beginning to understand how organisms undergo evolutionary change.

### All of life shares a common evolutionary history

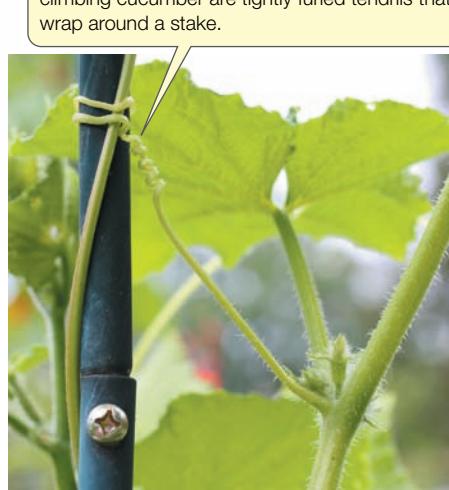
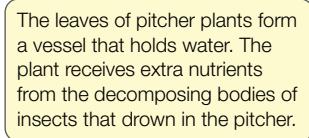
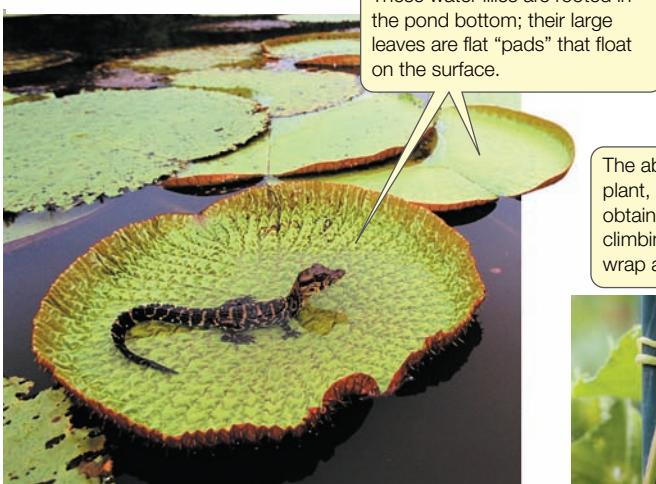
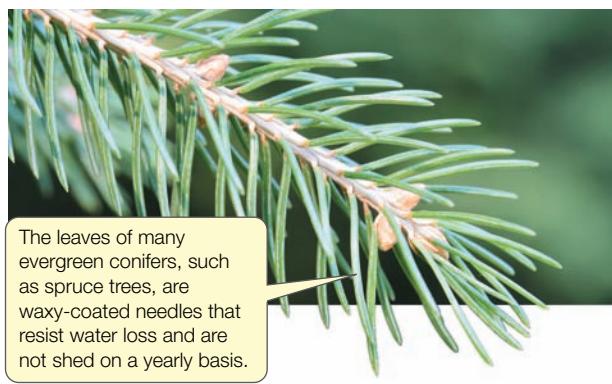
**Evolution**—change in the genetic makeup of biological populations through time—is the major unifying principle of biology.

Charles Darwin compiled factual evidence for evolution in his 1859 book *On the Origin of Species*. Since then, biologists have gathered massive amounts of data supporting Darwin’s theory that all living organisms are descended from a common ancestor. Darwin also proposed one of the most important processes that produce evolutionary change. He argued that differential survival and reproduction among individuals in a population, which he termed **natural selection**, could account for much of the evolution of life.

Although Darwin proposed that living organisms are descended from common ancestors and are therefore related to one another, he did not have the advantage of understanding the mechanisms of genetic inheritance. Even so, he observed that offspring resembled their parents; therefore, he surmised, such mechanisms had to exist. That simple fact is the basis for the concept of a **species**. Although the precise definition of a species is complicated, in its most widespread usage it refers to a group of organisms that can produce viable and fertile offspring with one another.

But offspring do differ from their parents. Any population of a plant or animal species displays variation, and if you select breeding pairs on the basis of some particular trait, that trait is more likely to be present in their offspring than in the general population. Darwin himself bred pigeons, and was well aware of how pigeon fanciers selected breeding pairs to produce offspring with unusual feather patterns, beak shapes, or body sizes (see Figure 21.2). He realized that if humans could select for specific traits in domesticated animals, the same process could operate in nature; hence the term *natural selection* as opposed to artificial (human-imposed) selection.

How would natural selection function? Darwin postulated that different probabilities of survival and reproductive success would do the job. He reasoned that the reproductive capacity of plants and animals, if unchecked, would result in unlimited growth of populations, but we do not observe such growth in nature; in most species, only a small percentage of offspring survive to reproduce. Thus any trait that confers even a small increase in the probability that its possessor will survive and reproduce would be spread in the population.



**1.3 Adaptations to the Environment** The leaves of all plants are specialized for photosynthesis—the sun-light-powered transformation of water and carbon dioxide into larger structural molecules called carbohydrates. The leaves of different plants, however, display many different adaptations to their individual environments.

Because organisms with certain traits survive and reproduce best under specific sets of conditions, natural selection leads to **adaptations**: structural, physiological, or behavioral traits that enhance an organism's chances of survival and reproduction in its environment (Figure 1.3). In addition to natural selection, evolutionary processes such as sexual selection (selection due to mate choice) and genetic drift (the random fluctuation of gene frequencies in a population due to chance events) contribute to the rise of diverse adaptations. These processes operating over evolutionary history have led to the remarkable array of life on Earth.

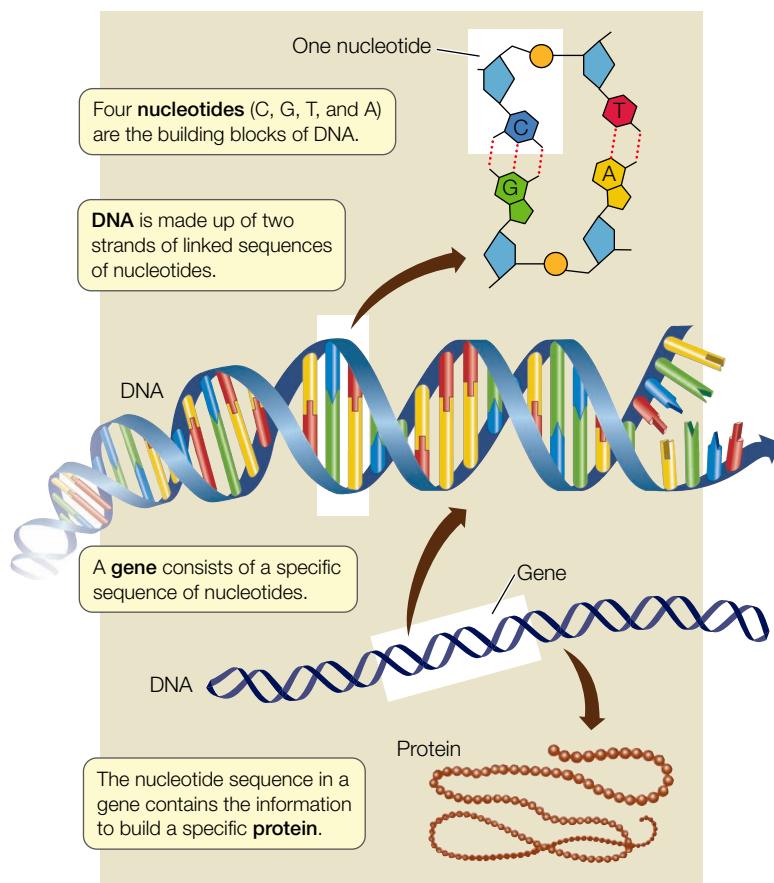
If all cells come from preexisting cells, and if all the diverse species of organisms on Earth are related by descent with modification from a common ancestor, then what is the source of information that is passed from parent to daughter cells and from parental organisms to their offspring?

### Biological information is contained in a genetic language common to all organisms

Cells are the basic building blocks of organisms, but even a single cell is complex, with many internal structures and many functions that depend on information. The information required

for a cell to function and interact with other cells—the “blueprint” for existence—is contained in the cell’s **genome**, the sum total of all the DNA molecules it contains. **DNA** (deoxyribonucleic acid) molecules are long sequences of four different sub-units called **nucleotides**. The sequence of the nucleotides contains genetic information. **Genes** are specific segments of DNA encoding the information the cell uses to make **proteins** (Figure 1.4). Protein molecules govern the chemical reactions within cells and form much of an organism’s structure.

By analogy with a book, the nucleotides of DNA are like the letters of an alphabet. Protein molecules are the sentences. Combinations of proteins that form structures and control biochemical processes are the paragraphs. The structures and processes that are organized into different systems with specific tasks (such as digestion or transport) are the chapters of the book, and the complete book is the organism. If you were to write out your own genome using four letters to represent the four nucleotides, you would write more than 3 billion letters. Using the size type you are reading now, your genome would fill about a thousand books the size of this one. The mechanisms of evolution, including natural selection, are the authors and editors of all the books in the library of life.



**1.4 DNA Is Life's Blueprint** The instructions for life are contained in the sequences of nucleotides in DNA molecules. Specific DNA nucleotide sequences comprise genes. The average length of a single human gene is 16,000 nucleotides. The information in each gene provides the cell with the information it needs to manufacture molecules of a specific protein.

All the cells of a multicellular organism contain the same genome, yet different cells have different functions and form different structures—contractile proteins form in muscle cells, hemoglobin in red blood cells, digestive enzymes in gut cells, and so on. Therefore, different types of cells in an organism must express different parts of the genome. How cells control gene expression in ways that enable a complex organism to develop and function is a major focus of current biological research.

The genome of an organism consists of thousands of genes. If the nucleotide sequence of a gene is altered, it is likely that the protein that gene encodes will be altered. Alterations of the genome are called *mutations*. Mutations occur spontaneously; they can also be induced by outside factors, including chemicals and radiation. Most mutations are either harmful or have no effect, but occasionally a mutation improves the functioning of the organism under the environmental conditions it encounters. Such beneficial mutations are the raw material of evolution and lead to adaptations.

### Cells use nutrients to supply energy and to build new structures

Living organisms acquire *nutrients* from the environment. Nutrients supply the organism with energy and raw materials for carrying out biochemical reactions. Life depends on thousands

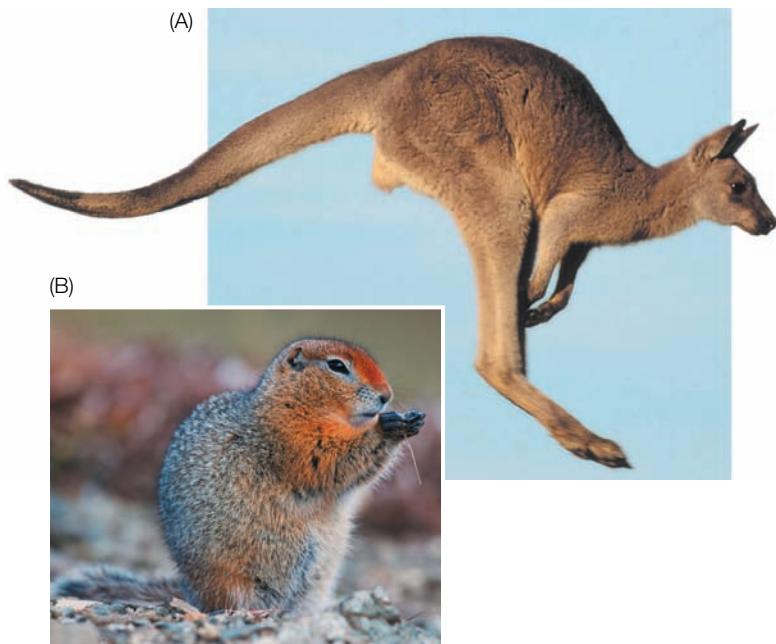
of biochemical reactions that occur inside cells. Some of these reactions break down nutrient molecules into smaller chemical units, and in the process some of the energy contained in the chemical bonds of the nutrients is captured by high-energy molecules that can be used to do different kinds of cellular work.

One obvious kind of work cells do is mechanical—moving molecules from one cellular location to another, moving whole cells or tissues, or even moving the organism itself, as muscles do (Figure 1.5A). The most basic cellular work is the building, or *synthesis*, of new complex molecules and structures from smaller chemical units. For example, we are all familiar with the fact that carbohydrates eaten today may be deposited in the body as fat tomorrow (Figure 1.5B). Still another kind of work is the electrical work that is the essence of information processing in nervous systems. The sum total of all the chemical transformations and other work done in all the cells of an organism is its **metabolism**, or **metabolic rate**.

The myriad of biochemical reactions that go on in cells are integrally linked in that the products of one are the raw materials of the next. These complex networks of reactions must be integrated and precisely controlled; when they are not, the result is disease.

### Living organisms regulate their internal environment

Multicellular organisms have an *internal environment* that is not cellular. That is, their individual cells are bathed in extracellular fluids, from which they receive nutrients and into which they excrete waste products of metabolism. The cells of multicellu-



**1.5 Energy Can Be Used Immediately or Stored** (A) Animal cells break down and release the energy contained in the chemical bonds of food molecules to do mechanical work—in this kangaroo's case, to jump. (B) The cells of this Arctic ground squirrel have broken down the complex carbohydrates in plants and converted their molecules into fats, which are stored in the animal's body to provide an energy supply for the cold months.

lar organisms are specialized, or *differentiated*, to contribute in some way to the maintenance of the internal environment. With the evolution of specialization, differentiated cells lost many of the functions carried out by single-celled organisms, and must depend on the internal environment for essential services.

To accomplish their specialized tasks, assemblages of differentiated cells are organized into *tissues*. For example, a single muscle cell cannot generate much force, but when many cells combine to form the tissue of a working muscle, considerable force and movement can be generated (see Figure 1.5B). Different tissue types are organized to form *organs* that accomplish specific functions. For example, the heart, brain, and stomach are each constructed of several types of tissues. Organs whose functions are interrelated can be grouped into *organ systems*; the stomach, intestine, and esophagus, for example, are parts of the digestive system. The functions of cells, tissues, organs, and organ systems are all integral to the multicellular *organism*. We cover the biology of organisms in Parts Eight and Nine of this book.

### Living organisms interact with one another

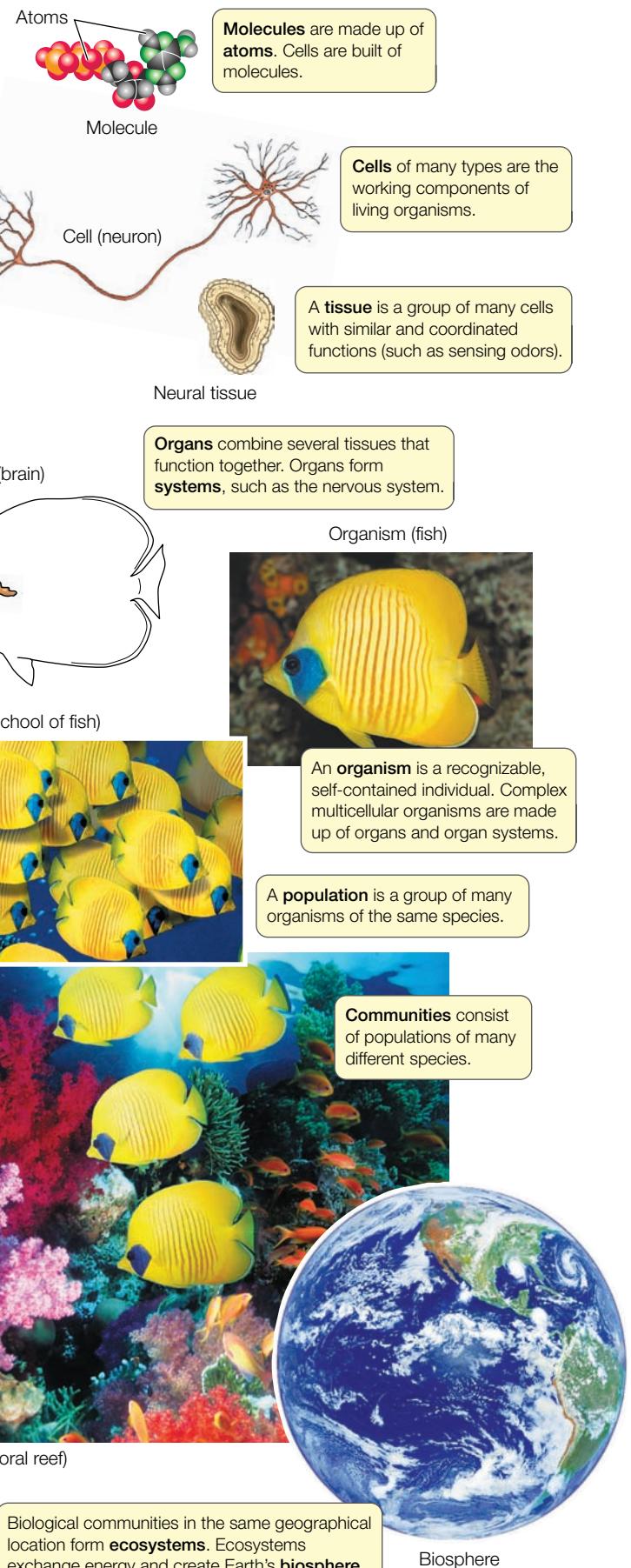
The internal hierarchy of the individual organism is matched by the external hierarchy of the biological world (Figure 1.6). Organisms do not live in isolation. A group of individuals of the same species that interact with one another is a *population*, and populations of all the species that live and interact in the same area are called a *community*. Communities together with their abiotic environment constitute an *ecosystem*.

Individuals in a population interact in many different ways. Animals eat plants and other animals (usually members of another species) and compete with other species for food and other resources. Some animals will prevent other individuals of their own species from exploiting a resource, whether it be food, nesting sites, or mates. Animals may also *cooperate* with members of their species, forming social units such as a termite colony or a flock of birds. Such interactions have resulted in the evolution of social behaviors such as communication.

Plants also interact with their external environment, which includes other plants, animals, and microorganisms. All terrestrial plants depend on complex partnerships with fungi, bacteria, and animals. Some of these partnerships are necessary to obtain nutrients, some to produce fertile seeds, and still others to disperse seeds. Plants compete with each other

### 1.6 Biology Is Studied at Many Levels of Organization

Life's properties emerge when DNA and other molecules are organized in cells. Energy flows through all the biological levels shown here.



for light and water, and they have ongoing evolutionary interactions with the animals that eat them, evolving anti-predation adaptations or ways to attract the animals that assist in their reproduction. The interactions of populations of different plant and animal species in a community are major evolutionary forces that produce specialized adaptations.

Communities interacting over a broad geographic area with distinguishing physical features form ecosystems; examples might include an Arctic tundra, a coral reef, or a tropical rainforest. The ways in which species interact with one another and with their environment in communities and in ecosystems is the subject of *ecology* and of Part Ten of this book.

### Discoveries in biology can be generalized

Because all life is related by descent from a common ancestor, shares a genetic code, and consists of similar building blocks—cells—knowledge gained from investigations of one type of organism can, with care, be generalized to other organisms. Biologists use **model systems** for research, knowing that they can extend their findings to other organisms, including humans. For example, our basic understanding of the chemical reactions in cells came from research on bacteria but is applicable to all cells, including those of humans. Similarly, the biochemistry of photosynthesis—the process by which plants use sunlight to produce biological molecules—was largely worked out from experiments on *Chlorella*, a unicellular green alga (see Figure 10.13). Much of what we know about the genes that control plant development is the result of work on *Arabidopsis thaliana*, a relative of the mustard plant. Knowledge about how animals develop has come from work on sea urchins, frogs, chickens, roundworms, and fruit flies. And recently, the discovery of a major gene controlling human skin color came from work on zebrafish. Being able to generalize from model systems is a powerful tool in biology.

### 1.1 RECAP

**Living organisms are made of (or depend on) cells, are related by common descent and evolve, contain genetic information and use it to reproduce, extract energy from their environment and use it to do biological work, synthesize complex molecules to construct biological structures, regulate their internal environment, and interact with one another.**

- Describe the relationship between evolution by natural selection and the genetic code. **See pp. 6–7**
- Why can the results of biological research on one species often be generalized to very different species? **See p. 9**

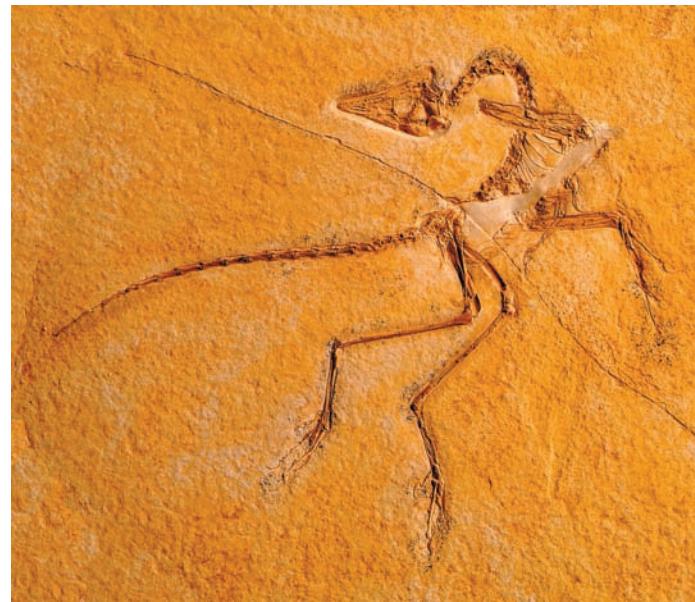
Now that you have an overview of the major features of life that you will explore in depth in this book, you can ask how and when life first emerged. In the next section we will summarize briefly the history of life from the earliest simple life forms to the complex and diverse organisms that inhabit our planet today.

## 1.2 How Is All Life on Earth Related?

What do biologists mean when they say that all organisms are *genetically related*? They mean that species on Earth share a *common ancestor*. If two species are similar, as dogs and wolves are, then they probably have a common ancestor in the fairly recent past. The common ancestor of two species that are more different—say, a dog and a deer—probably lived in the more distant past. And if two organisms are very different—such as a dog and a clam—then we must go back to the *very* distant past to find their common ancestor. How can we tell how far back in time the common ancestor of any two organisms lived? In other words, how do we discover the evolutionary relationships among organisms?

For many years, biologists have investigated the history of life by studying the *fossil record*—the preserved remains of organisms that lived in the distant past (Figure 1.7). Geologists supplied knowledge about the ages of fossils and the nature of the environments in which they lived. Biologists then inferred the evolutionary relationships among living and fossil organisms by comparing their anatomical similarities and differences. Frequently big gaps existed in the fossil record, forcing biologists to predict the nature of the “missing links” between two lineages of organisms. As the fossil record became more complete, those missing links were filled in.

Molecular methods for comparing genomes, described in Chapter 24, are enabling biologists to more accurately establish the degrees of relationship between living organisms and to use that information to interpret the fossil record. Molecular information can occasionally be gleaned from fossil specimens, such as recently deciphered genetic material from fossil bones of Ne-



**1.7 Fossils Give Us a View of Past Life** This fossil, formed some 150 million years ago, is that of an *Archaeopteryx*, the earliest known representative of the birds. Birds evolved from the same group of reptiles as the modern crocodiles.

anderthals that led to the conclusion that even though Neanderthals and modern humans coexisted, they did not interbreed.

In general, the greater the differences between the genomes of two species, the more distant their common ancestor. Using molecular techniques, biologists are exploring fundamental questions about life. What were the earliest forms of life? How did simple organisms give rise to the great diversity of organisms alive today? Can we reconstruct a family tree of life?

### Life arose from non-life via chemical evolution

Geologists estimate that Earth formed between 4.6 and 4.5 billion years ago. At first, the planet was not a very hospitable place. It was some 600 million years or more before the earliest life evolved. If we picture the history of Earth as a 30-day month, life first appeared somewhere toward the end of the first week (**Figure 1.8**).

When we consider how life might have arisen from nonliving matter, we must take into account the properties of the young

Earth's atmosphere, oceans, and climate, all of which were very different than they are today. Biologists postulate that complex biological molecules first arose through the random physical association of chemicals in that environment. Experiments simulating the conditions on early Earth have confirmed that the generation of complex molecules under such conditions is possible, even probable. The critical step for the evolution of life, however, had to be the appearance of molecules that could reproduce themselves and also serve as templates for the synthesis of large molecules with complex but stable shapes. The variation of the shapes of these large, stable molecules (described in Chapters 3 and 4) enabled them to participate in increasing numbers and kinds of chemical reactions with other molecules.

### Cellular structure evolved in the common ancestor of life

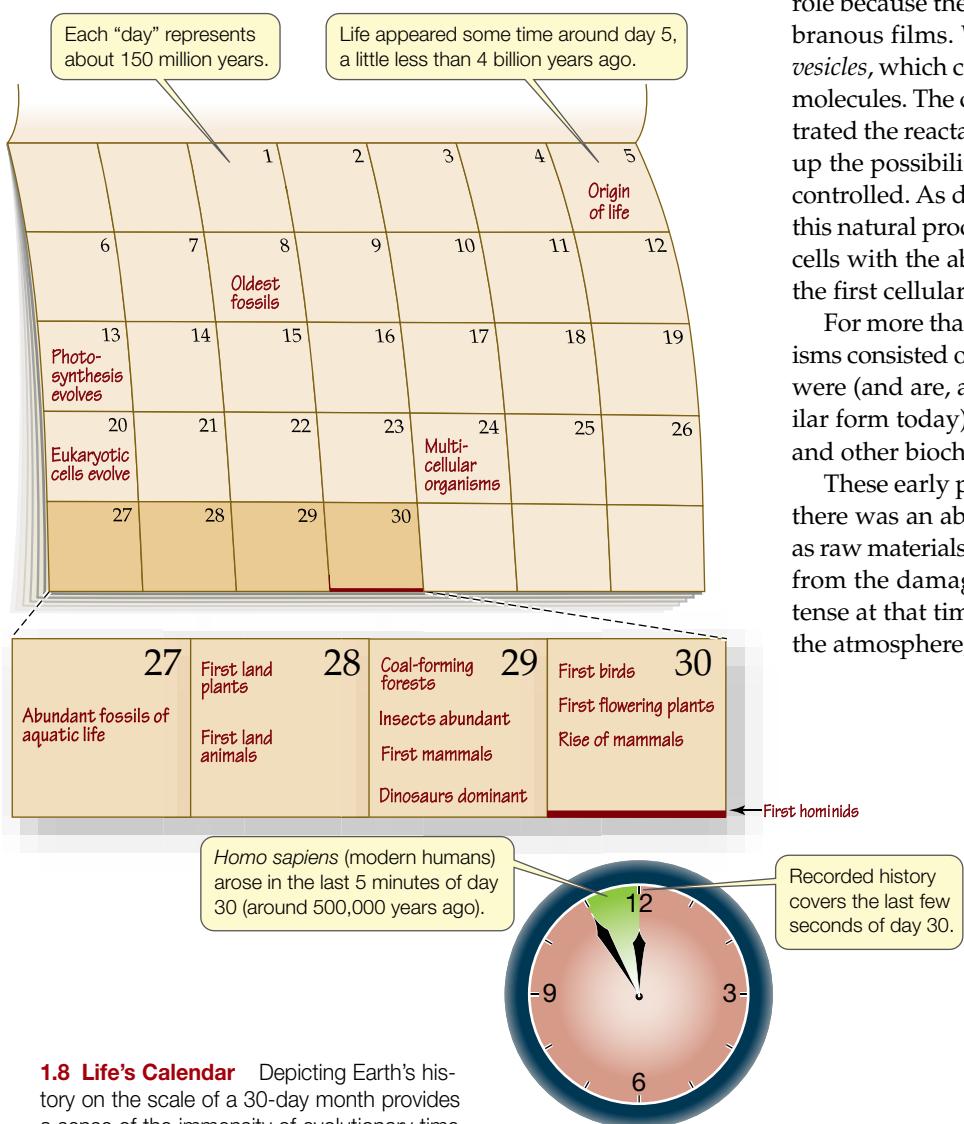
The second critical step in the origin of life was the enclosure of complex biological molecules by *membranes* that contained them in a compact internal environment separate from the surrounding external environment. Fatlike molecules played a critical role because they are not soluble in water and they form membranous films. When agitated, these films can form spherical *vesicles*, which could have enveloped assemblages of biological molecules. The creation of an internal environment that concentrated the reactants and products of chemical reactions opened up the possibility that those reactions could be integrated and controlled. As described in Section 4.4, scientists postulate that this natural process of membrane formation resulted in the first cells with the ability to replicate themselves—the evolution of the first cellular organisms.

For more than 2 billion years after cells originated, all organisms consisted of only one cell. These first unicellular organisms were (and are, as multitudes of their descendants exist in similar form today) **prokaryotes**. Prokaryotic cells consist of DNA and other biochemicals enclosed in a membrane.

These early prokaryotes were confined to the oceans, where there was an abundance of complex molecules they could use as raw materials and sources of energy. The ocean shielded them from the damaging effects of ultraviolet light, which was intense at that time because there was little or no oxygen ( $O_2$ ) in the atmosphere, and hence no protective ozone ( $O_3$ ) layer.

### Photosynthesis changed the course of evolution

To fuel their cellular metabolism, the earliest prokaryotes took in molecules directly from their environment and broke these small molecules down to release and use the energy contained in their chemical bonds. Many modern species of prokaryotes still function this way, and very successfully. During the early eons of life on Earth, there was no oxygen in the atmosphere. In fact, oxygen was toxic to the life forms that existed then.





### 1.9 Photosynthetic Organisms Changed Earth's Atmosphere

These strands are composed of many cells of cyanobacteria. This modern species (*Oscillatoria tenuis*) may be very similar to the early photosynthetic prokaryotes responsible for the buildup of oxygen in Earth's atmosphere.

About 2.7 billion years ago, the evolution of **photosynthesis** changed the nature of life on Earth. The chemical reactions of photosynthesis transform the energy of sunlight into a form of biological energy that can power the synthesis of large molecules (see Chapter 10). These large molecules are the building blocks of cells, and they can be broken down to provide metabolic energy. Photosynthesis is the basis of much of life on Earth today because its energy-capturing processes provide food for other organisms.

Early photosynthetic cells were probably similar to present-day prokaryotes called *cyanobacteria* (Figure 1.9). Over time, photosynthetic prokaryotes became so abundant that vast quantities of O<sub>2</sub>, which is a by-product of photosynthesis, slowly began to accumulate in the atmosphere. Oxygen was poisonous to many of the prokaryotes that lived at that time. Those organisms that did tolerate oxygen, however, were able to proliferate as the presence of oxygen opened up vast new avenues of evolution. *Aerobic metabolism* (energy production based on the conversion of O<sub>2</sub>) is more efficient than *anaerobic* (non-O<sub>2</sub>-using) *metabolism*, and today it is used by the majority of Earth's organisms. Aerobic metabolism allowed cells to grow larger.

Oxygen in the atmosphere also made it possible for life to move onto land. For most of life's history, ultraviolet (UV) radiation falling on Earth's surface was too intense to allow life to exist outside the shielding water. But the accumulation of photosynthetically generated oxygen in the atmosphere for more than 2 billion years gradually produced a layer of ozone in the upper atmosphere. By about 500 million years ago, the ozone layer was sufficiently dense and absorbed enough UV radiation to make it possible for organisms to leave the protection of the water and live on land.

### Eukaryotic cells evolved from prokaryotes

Another important step in the history of life was the evolution of cells with discrete intracellular compartments, called **organelles**, which were capable of taking on specialized cellular functions. This event happened about 3 weeks into our calendar of Earth's history (see Figure 1.8). One of these organelles, the dense-appearing *nucleus* (Latin *nux*, "nut" or "core"), came to contain the cell's genetic information and gives these cells their name: **eukaryotes** (Greek *eu*, "true"; *karyon*, "kernel" or "core"). The eukaryotic cell is completely distinct from the cells of prokaryotes (*pro*, "before"), which lack nuclei and other internal compartments.

Some organelles are hypothesized to have originated by **endosymbiosis** when cells ingested smaller cells. The *mitochondria* that generate a cell's energy probably evolved from engulfed prokaryotic organisms. And *chloroplasts*—organelles specialized to conduct photosynthesis—could have originated when photosynthetic prokaryotes were ingested by larger eukaryotes. If the larger cell failed to break down this intended food object, a partnership could have evolved in which the ingested prokaryote provided the products of photosynthesis and the host cell provided a good environment for its smaller partner.

### Multicellularity arose and cells became specialized

Until just over a billion years ago, all the organisms that existed—whether prokaryotic or eukaryotic—were unicellular. An important evolutionary step occurred when some eukaryotes failed to separate after cell division, remaining attached to each other. The permanent association of cells made it possible for some cells to specialize in certain functions, such as reproduction, while other cells specialized in other functions, such as absorbing nutrients and distributing them to neighboring cells. This **cellular specialization** enabled multicellular eukaryotes to increase in size and become more efficient at gathering resources and adapting to specific environments.

### Biologists can trace the evolutionary tree of life

If all the species of organisms on Earth today are the descendants of a single kind of unicellular organism that lived almost 4 billion years ago, how have they become so different? A simplified answer is that as long as individuals within a population mate with one another, structural and functional changes can evolve within that population, but the population will remain one species. However, if something happens to isolate some members of a population from the others, the structural and functional differences between the two groups may accumulate over time. The two groups may diverge to the point where their members can no longer reproduce with each other and are thus distinct species. We discuss this evolutionary process, called *speciation*, in Chapter 23.

Biologists give each species a distinctive scientific name formed from two Latinized names (a **binomial**). The first name identifies the species' *genus*—a group of species that share a recent common ancestor. The second is the name of the species. For

example, the scientific name for the human species is *Homo sapiens*: *Homo* is our genus and *sapiens* our species. *Homo* is Latin for “man”; *sapiens* is from the Latin for word for “wise” or “rational.”

Tens of millions of species exist on Earth today. Many times that number lived in the past but are now extinct. Many millions of speciation events created this vast diversity, and the unfolding of these events can be diagrammed as an evolutionary “tree” whose branches describe the order in which populations split and eventually evolved into new species, as described in Chapter 22. Much of biology is based on comparisons among species, and these comparisons are useful precisely because we can place species in an evolutionary context relative to one another. Our ability to do this has been greatly enhanced in recent decades by our ability to sequence and compare the genomes of different species.

Genome sequencing and other molecular techniques have allowed *systematists*—scientists who study the evolution and classification of life’s diverse organisms—to augment evolutionary knowledge based on the fossil record with a vast array of molecular evidence. The result is the ongoing compilation of *phylogenetic trees* that document and diagram evolutionary relationships as part of an overarching tree of life, the broadest categories of which are shown in **Figure 1.10**. (The tree is expanded in this book’s Appendix; you can also explore the tree interactively at <http://tolweb.org/tree/>.)

Although many details remain to be clarified, the broad outlines of the tree of life have been determined. Its branching patterns are based on a rich array of evidence from fossils, struc-

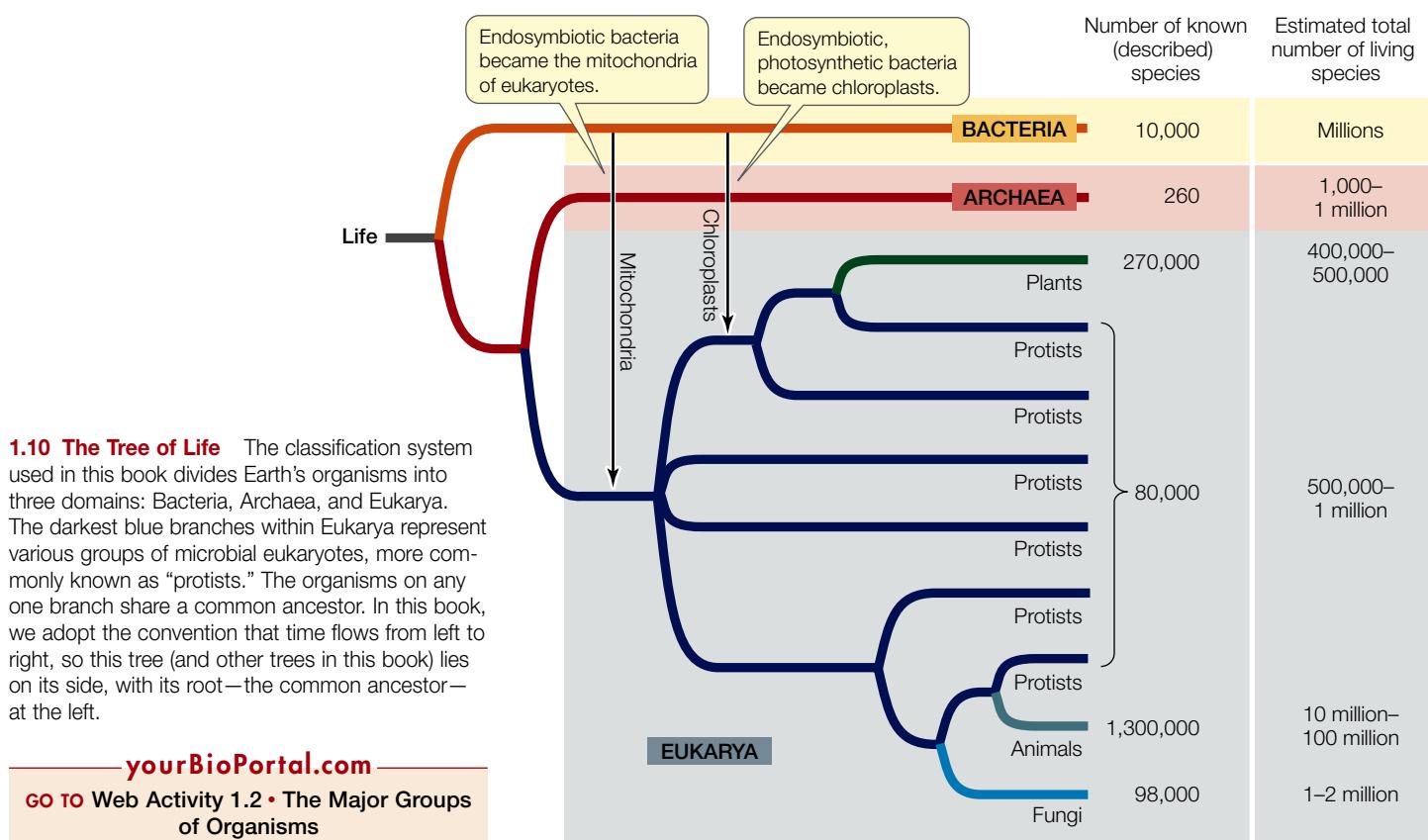
tures, metabolic processes, behavior, and molecular analyses of genomes. Molecular data in particular have been used to separate the tree into three major **domains**: Archaea, Bacteria, and Eukarya. The organisms of each domain have been evolving separately from those in the other domains for more than a billion years.

Organisms in the domains **Archaea** and **Bacteria** are single-celled prokaryotes. However, members of these two groups differ so fundamentally in their metabolic processes that they are believed to have separated into distinct evolutionary lineages very early. Species belonging to the third domain—**Eukarya**—have eukaryotic cells whose mitochondria and chloroplasts may have originated from the ingestion of prokaryotic cells, as described on page 11.

The three major groups of multicellular eukaryotes—plants, fungi, and animals—each evolved from a different group of the eukaryotes generally referred to as *protists*. The chloroplast-containing, photosynthetic protist that gave rise to plants was completely distinct from the protist that was ancestral to both animals and fungi, as can be seen from the branching pattern of Figure 1.10. Although most protists are unicellular (and thus sometimes called *microbial eukaryotes*), multicellularity has evolved in several protist lineages.

### The tree of life is predictive

There are far more species alive on Earth than biologists have discovered and described to date. In fact, most species on Earth



have yet to be discovered by humans (see Section 32.4 for a discussion of how we know this). When we encounter a new species, its placement on the tree of life immediately tells us a great deal about its biology. In addition, understanding relationships among species allows biologists to make predictions about species that have not yet been studied, based on our knowledge of those that have.

For example, until phylogenetic methods were developed, it took years of investigation to isolate and identify most newly encountered human pathogens, and even longer to discover how these pathogens moved into human populations. Today, pathogens that cause diseases such as the flu are identified quickly on the basis of their evolutionary relationships. Placement in an evolutionary tree also gives us clues about the disease's biology, possible effective treatments, and the origin of the pathogen (see Chapters 21 and 22).

## 1.2 RECAP

The first cellular life on Earth was prokaryotic and arose about 4 billion years ago. The complexity of the organisms that exist today is the result of several important evolutionary events, including the evolution of photosynthesis, eukaryotic cells, and multicellularity. The genetic relationships of all organisms can be shown as a branching tree of life.

- Discuss the evolutionary significance of photosynthesis. **See pp. 10–11**
- What do the domains of life represent? What are the major groups of eukaryotes? **See p. 12 and Figure 1.10**

In February of 1676, Robert Hooke received a letter from the physicist Sir Isaac Newton in which Newton famously re-



marked, "If I have seen a little further, it is by standing on the shoulders of giants." We all stand on the shoulders of giants, building on the research of earlier scientists. By the end of this course, you will know more about evolution than Darwin ever could have, and you will know infinitely more about cells than Schleiden and Schwann did. Let's look at the methods biologists use to expand our knowledge of life.

## 1.3 How Do Biologists Investigate Life?

Regardless of the many different tools and methods used in research, all scientific investigations are based on *observation* and *experimentation*. In both, scientists are guided by the *scientific method*, one of the most powerful tools of modern science.

### Observation is an important skill

Biologists have always observed the world around them, but today our ability to observe is greatly enhanced by technologies such as electron microscopes, DNA chips, magnetic resonance imaging, and global positioning satellites. These technologies have improved our ability to observe at all levels, from the distribution of molecules in the body to the distribution of fish in the oceans. For example, not too long ago marine biologists were only able to observe the movement of fish in the ocean by putting physical tags on the fish, releasing them, and hoping that a fisherman would catch that fish and send back the tag—and even that would reveal only where the fish ended up. Today we can attach electronic recording devices to fish that continuously record not only where the fish is, but also how deep it swims and the temperature and salinity of the water around it (**Figure 1.11**). The tags download this information to a satellite, which relays it back to researchers. Suddenly we are acquiring a great deal of knowledge about the distribution of life in the oceans—information that is relevant to studies of climate change.

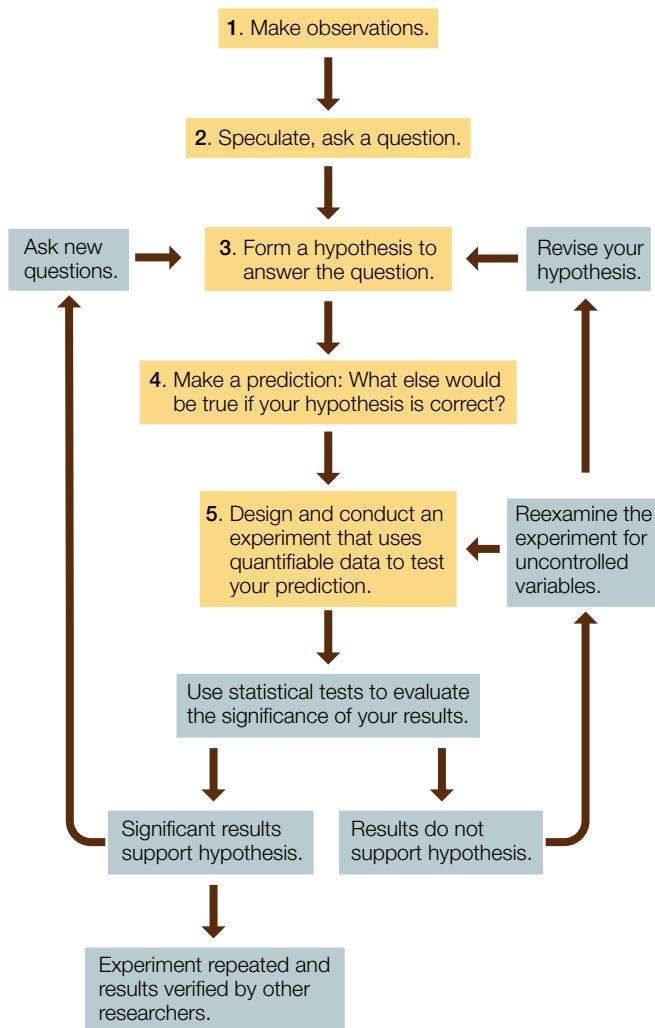
Technologies that enable us to *quantify* observations are very important in science. For example, for hundreds of years species were classified by generally qualitative descriptions of the physical differences between them. There was no way of objectively calculating evolutionary distances between organisms, and biologists had to depend on the fossil record for insight. Today our ability to rapidly analyze DNA sequences enables quantitative estimates of evolutionary distances, as described in Parts Five and Six of this book. The ability to gather quantitative observations adds greatly to the biologist's ability to make strong conclusions.

**1.11 Tuna Tracking** Marine biologist Barbara Block attaches computerized data recording tags (inset) to a live bluefin tuna before returning it to the ocean. Such tags make it possible to track an individual tuna wherever it travels in the world's oceans.

### The scientific method combines observation and logic

Observations lead to questions, and scientists make additional observations and do experiments to answer those questions. The conceptual approach that underlies most modern scientific investigations is the **scientific method**. This powerful tool, also called the *hypothesis–prediction (H–P) method*, has five steps: (1) making *observations*; (2) asking *questions*; (3) forming *hypotheses*, or tentative answers to the questions; (4) making *predictions* based on the hypotheses; and (5) *testing* the predictions by making additional observations or conducting experiments (Figure 1.12).

After posing a question, a scientist uses *inductive logic* to propose a tentative answer. Inductive logic involves taking observations or facts and creating a new proposition that is compatible with those observations or facts. Such a tentative proposition is called a **hypothesis**. In formulating a hypothesis, scientists put together the facts they already know to formulate one or more possible answers to the question. For example, at the opening of



**1.12 The Scientific Method** The process of observation, speculation, hypothesis, prediction, and experimentation is the cornerstone of modern science. Answers gleaned through experimentation lead to new questions, more hypotheses, further experiments, and expanding knowledge.

this chapter you learned that scientists have observed the rapid decline of amphibian populations worldwide and are asking why. Some scientists have hypothesized that a fungal disease is a cause; other scientists have hypothesized that increased exposure to ultraviolet radiation is a cause. Tyrone Hayes hypothesized that exposure to agricultural chemicals could be a cause. He knew that the most widely used chemical herbicide is atrazine; that it is mostly applied in the spring, when amphibians are breeding; and that atrazine is a common contaminant in the waters in which amphibians live as they develop into adults.

The next step in the scientific method is to apply a different form of logic—*deductive logic*—to make predictions based on the hypothesis. Deductive logic starts with a statement believed to be true and then goes on to predict what facts would also have to be true to be compatible with that statement. Based on his hypothesis, Tyrone Hayes predicted that frog tadpoles exposed to atrazine would show adverse effects of the chemical once they reached adulthood.

### Good experiments have the potential to falsify hypotheses

Once predictions are made from a hypothesis, experiments can be designed to test those predictions. The most informative experiments are those that have the ability to show that the prediction is wrong. If the prediction is wrong, the hypothesis must be questioned, modified, or rejected.

There are two general types of experiments, both of which compare data from different groups or samples. A *controlled experiment* manipulates one or more of the factors being tested; *comparative experiments* compare unmanipulated data gathered from different sources. As described at the opening of this chapter, Tyrone Hayes and his colleagues conducted both types of experiment to test the prediction that the herbicide atrazine, a contaminant in freshwater ponds and streams throughout the world, affects the development of frogs.

In a **controlled experiment**, we start with groups or samples that are as similar as possible. We predict on the basis of our hypothesis that some critical factor, or **variable**, has an effect on the phenomenon we are investigating. We devise some method to manipulate *only that variable* in an “experimental” group and compare the resulting data with data from an unmanipulated “control” group. If the predicted difference occurs, we then apply statistical tests to ascertain the probability that the manipulation created the difference (as opposed to the difference being the result of random chance). Figure 1.13 describes one of the many controlled experiments performed by the Hayes laboratory to quantify the effects of atrazine on male frogs.

The basis of controlled experiments is that one variable is manipulated while all others are held constant. The variable that is manipulated is called the *independent variable*, and the response that is measured is the *dependent variable*. A good controlled experiment is not easy to design because biological variables are so interrelated that it is difficult to alter just one.

A **comparative experiment** starts with the prediction that there will be a difference between samples or groups based on the hypothesis. In comparative experiments, however, we can-

# INVESTIGATING LIFE

## 1.13 Controlled Experiments Manipulate a Variable

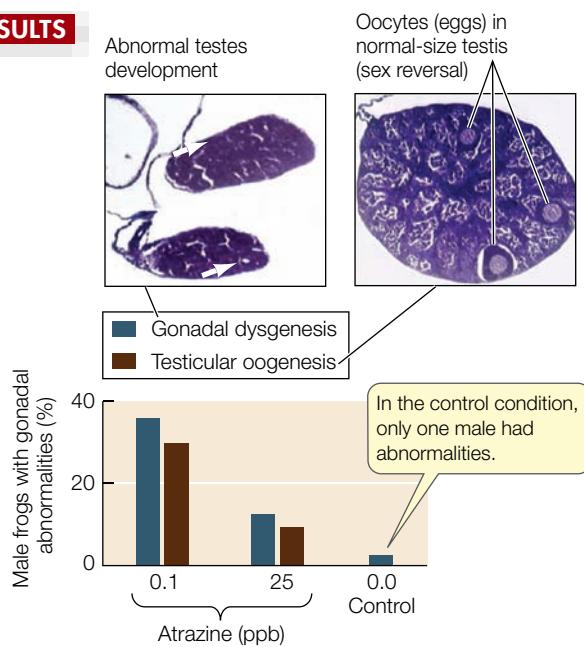
The Hayes laboratory created controlled environments that differed only in the concentrations of atrazine in the water. Eggs from leopard frogs (*Rana pipiens*) raised specifically for laboratory use were allowed to hatch and the tadpoles were separated into experimental tanks containing water with different concentrations of atrazine.

**HYPOTHESIS** Exposure to atrazine during larval development causes abnormalities in the reproductive system of male frogs.

### METHOD

- Establish 9 tanks in which all attributes are held constant except the water's atrazine concentrations. Establish 3 atrazine conditions (3 replicate tanks per condition): 0 ppb (control condition), 0.1 ppb, and 25 ppb.
- Place *Rana pipiens* tadpoles from laboratory-reared eggs in the 9 tanks (30 tadpoles per replicate).
- When tadpoles have transitioned into adults, sacrifice the animals and evaluate their reproductive tissues.
- Test for correlation of degree of atrazine exposure with the presence of abnormalities in the reproductive systems of male frogs.

### RESULTS



**CONCLUSION** Exposure to atrazine at concentrations as low as 0.1 ppb induces abnormalities in the male reproductive systems of frogs. The effect is not proportional to the level of exposure.

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not control the variables; often we cannot even identify all the variables that are present. We are simply gathering and comparing data from different sample groups.

When his controlled experiments indicated that atrazine indeed affects reproductive development in frogs, Hayes and his colleagues performed a comparative experiment. They collected frogs and water samples from eight widely separated sites across the United States and compared the incidence of abnormal frogs from environments with very different levels of atrazine (Figure 1.14). Of course, the sample sites differed in many ways besides the level of atrazine present.

The results of experiments frequently reveal that the situation is more complex than the hypothesis anticipated, thus raising new questions. In the Hayes experiments, for example, there was no clear direct relationship between the *amount* of atrazine present and the percentage of abnormal frogs: there were fewer abnormal frogs at the highest concentrations of atrazine than at lower concentrations. There are no “final answers” in science. Investigations consistently reveal more complexity than we expect. The scientific method is a tool to identify, assess, and understand that complexity.

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[GO TO](#) Animated Tutorial 1.1 • The Scientific Method

### Statistical methods are essential scientific tools

Whether we do comparative or controlled experiments, at the end we have to decide whether there is a difference between the samples, individuals, groups, or populations in the study. How do we decide whether a measured difference is enough to support or falsify a hypothesis? In other words, how do we decide in an unbiased, objective way that the measured difference is significant?

Significance can be measured with statistical methods. Scientists use statistics because they recognize that variation is always present in any set of measurements. Statistical tests calculate the probability that the differences observed in an experiment could be due to random variation. The results of statistical tests are therefore probabilities. A statistical test starts with a **null hypothesis**—the premise that no difference exists. When quantified observations, or **data**, are collected, statistical methods are applied to those data to calculate the likelihood that the null hypothesis is correct.

More specifically, statistical methods tell us the probability of obtaining the same results by chance even if the null hypothesis were true. We need to eliminate, insofar as possible, the chance that any differences showing up in the data are merely the result of random variation in the samples tested. Scientists generally conclude that the differences they measure are significant if statistical tests show that the *probability of error* (that is, the probability that the same results can be obtained by mere chance) is 5 percent or lower.

### Not all forms of inquiry are scientific

Science is a unique human endeavor that is bounded by certain standards of practice. Other areas of scholarship share with science the practice of making observations and asking ques-

# INVESTIGATING LIFE

## 1.14 Comparative Experiments Look for Differences among Groups

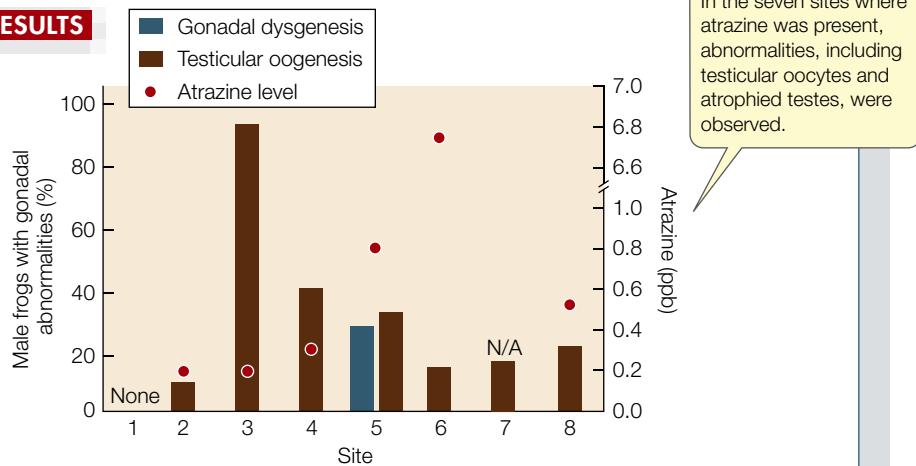
To see whether the presence of atrazine correlates with reproductive system abnormalities in male frogs, the Hayes lab collected frogs and water samples from different locations around the U.S. The analysis that followed was “blind,” meaning that the frogs and water samples were coded so that experimenters working with each specimen did not know which site the specimen came from.

**HYPOTHESIS** Presence of the herbicide atrazine in environmental water correlates with reproductive system abnormalities in frog populations.

### METHOD

1. Based on commercial sales of atrazine, select 4 sites (sites 1–4) less likely and 4 sites (sites 5–8) more likely to be contaminated with atrazine.
2. Visit all sites in the spring (i.e., when frogs have transitioned from tadpoles into adults); collect frogs and water samples.
3. In the laboratory, sacrifice frogs and examine their reproductive tissues, documenting abnormalities.
4. Analyze the water samples for atrazine concentration (the sample for site 7 was not tested).
5. Quantify and correlate the incidence of reproductive abnormalities with environmental atrazine concentrations.

### RESULTS



### CONCLUSION

Reproductive abnormalities exist in frogs from environments in which aqueous atrazine concentration is 0.2 ppb or above. The incidence of abnormalities does not appear to be proportional to atrazine concentration at the time of transition to adulthood.

**FURTHER INVESTIGATION:** The highest proportion of abnormal frogs was found at site 3, located on a wildlife reserve in Wyoming. What kind of data and observations would you need to suggest possible explanations for this extremely high incidence?

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tions, but scientists are distinguished by what they do with their observations and how they answer their questions. Data, subjected to appropriate statistical analysis, are critical in the testing of hypotheses. The scientific method is the most powerful way humans have devised for learning about the world and how it works.

Scientific explanations for natural processes are objective and reliable because the hypotheses proposed *must be testable* and *must have the potential of being rejected* by direct observations and experiments. Scientists must clearly describe the methods they use to test hypotheses so that other scientists can repeat their results. Not all experiments are repeated, but surprising or controversial results are always subjected to independent verification. Scientists worldwide share this process of testing and rejecting hypotheses, contributing to a common body of scientific knowledge.

If you understand the methods of science, you can distinguish science from non-science. Art, music, and literature all contribute to the quality of human life, but they are not science. They do not use the scientific method to establish what is fact. Religion is not science, although religions have historically purported to explain natural events ranging from unusual weather patterns to crop failures to human diseases. Most such phenomena that at one time were mysterious can now be explained in terms of scientific principles.

The power of science derives from the uncompromising objectivity and absolute dependence on evidence that comes from *reproducible and quantifiable observations*. A religious or spiritual explanation of a natural phenomenon may be coherent and satisfying for the person holding that view, but it is not testable, and therefore it is not science. To invoke a supernatural explanation (such as a “creator” or “intelligent designer” with no known bounds) is to depart from the world of science.

Science describes the facts about how the world works, not how it “ought to be.” Many scientific advances that have contributed to human welfare have also raised major ethical issues. Recent developments in genetics and developmental biology, for example, enable us to select the sex of our children, to use stem cells to repair our bodies, and to modify the

human genome. Although scientific knowledge allows us to do these things, science cannot tell us whether or not we should do them, or, if we choose to do so, how we should regulate them.

To make wise decisions about public policy, we need to employ the best possible ethical reasoning in deciding which outcomes we should strive for.

## 1.3 RECAP

The scientific method of inquiry starts with the formulation of hypotheses based on observations and data. Comparative and controlled experiments are carried out to test hypotheses.

- Explain the relationship between a hypothesis and an experiment. **See p. 14 and Figure 1.12**
- What is controlled in a controlled experiment? **See p. 14 and Figure 1.13**
- What features characterize questions that can be answered only by using a comparative approach? **See pp. 14–15 and Figure 1.14**
- Do you understand why arguments must be supported by quantifiable and reproducible data in order to be considered scientific? **See pp. 15–16**

The vast scientific knowledge accumulated over centuries of human civilization allows us to understand and manipulate aspects of the natural world in ways that no other species can. These abilities present us with challenges, opportunities, and above all, responsibilities.

## 1.4 How Does Biology Influence Public Policy?

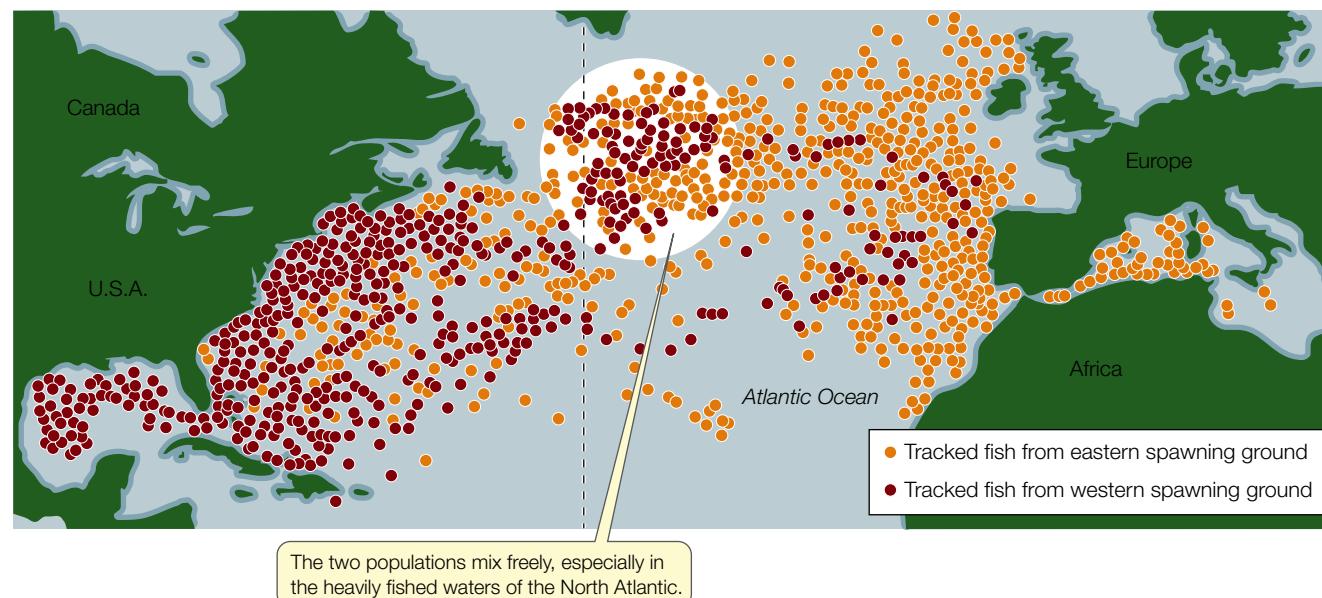
Agriculture and medicine are two important human activities that depend on biological knowledge. Our ancestors unknowingly applied the principles of evolutionary biology when they domesticated plants and animals, and people have speculated about the causes of diseases and searched for methods to combat them since ancient times. Long before the microbial causes of diseases were known, people recognized that infections could

be passed from one person to another, and the isolation of infected persons has been practiced as long as written records have been available.

Today, thanks to the deciphering of genomes and our newfound ability to manipulate them, vast new possibilities exist for controlling human diseases and increasing agricultural productivity, but these capabilities raise ethical and policy issues. How much and in what ways should we tinker with the genes of humans and other species? Does it matter whether the genomes of our crop plants and domesticated animals are changed by traditional methods of controlled breeding and crossbreeding or by the biotechnology of gene transfer? What rules should govern the release of genetically modified organisms into the environment? Science alone cannot provide all the answers, but wise policy decisions must be based on accurate scientific information.

Biologists are increasingly called on to advise government agencies concerning the laws, rules, and regulations by which society deals with the increasing number of challenges that have at least a partial biological basis. As an example of the value of scientific knowledge for the assessment and formulation of public policy, let's return to the tracking study of bluefin tuna introduced in Section 1.3. Prior to this study, both scientists and fishermen knew that bluefins had a western breeding ground in the Gulf of Mexico and an eastern breeding ground in the Mediterranean Sea (**Figure 1.15**). Overfishing had led to declining numbers of fish in the western-breeding populations, to the point of these populations being endangered.

**1.15 Bluefin Tuna Do Not Recognize Boundaries** It was assumed that tuna from western-breeding populations and those from eastern-breeding populations also fed on their respective sides of the Atlantic, so separate fishing quotas were established on either side of 45° W longitude (dashed line) to allow the endangered western population to recover. However, tracking data shows that the two populations *do not* remain separate after spawning, so in fact the established policy does not protect the western population.



Initially it was assumed by scientists, fishermen, and policy makers alike that the eastern and western populations had geographically separate feeding grounds as well as separate breeding grounds. Acting on this assumption, an international commission drew a line down the middle of the Atlantic Ocean and established strict fishing quotas on the western side of the line, with the intent of allowing the western population to recover. New tracking data, however, revealed that in fact the eastern and western bluefin populations mix freely on their feeding grounds across the entire North Atlantic—a swath of ocean that includes the most heavily fished waters in the world. Tuna caught on the eastern side of the line could just as likely be from the western breeding population as the eastern; thus the established policy was not achieving its intended goal.

Policy makers take more things into consideration than scientific knowledge and recommendations. For example, studies on the effects of atrazine on amphibians have led one U.S. group, the Natural Resources Defense Council, to take legal action to have atrazine banned on the basis of the Endangered Species Act. The U.S. Environmental Protection Agency, however, must also consider the potential loss to agriculture that such a ban would create and has continued to approve atrazine's use as long as environmental levels do not exceed 30 to 40 ppb—which is 300 to 400 times the levels shown to induce abnormalities in the Hayes studies. Scientific conclusions do not always prevail in the political world.

Another reason for studying biology is to understand the effects of the vastly increased human population on its environment. Our use of natural resources is putting stress on the ability of Earth's ecosystems to continue to produce the goods and services on which our society depends. Human activities are changing global climates, causing the extinctions of a large number of species like the amphibians featured in this chapter, and spreading new diseases while facilitating the resurgence of old ones. The rapid spread of flu viruses has been facilitated by modern modes of transportation, and the recent resurgence of tuberculosis is the result of the evolution of bacteria that are resistant to antibiotics. Biological knowledge is vital for determining the causes of these changes and for devising wise policies to deal with them.

Beyond issues of policy and pragmatism lies the human “need to know.” Human beings are fascinated by the richness and diversity of life, and most people want to know more about organisms and how they interact. Human curiosity might even be seen as an adaptive trait—it is possible that such a trait could have been selected for if individuals who were motivated to learn about their surroundings were likely to have survived and reproduced better, on average, than their less curious relatives. Far from ending the process, new discoveries and greater knowledge typically engender questions no one thought to ask before. There are vast numbers of questions for which we do not yet have answers, and the most important motivator of most scientists is curiosity.

## CHAPTER SUMMARY

### 1.1 What Is Biology?

- **Biology** is the scientific study of living organisms, including their characteristics, functions, and interactions. Cells are the basic structural and physiological units of life. The **cell theory** states that all life consists of cells and that all cells come from preexisting cells.
- All living organisms are related to one another through descent with modification. **Evolution** by **natural selection** is responsible for the diversity of **adaptations** found in living organisms.
- The instructions for a cell are contained in its **genome**, which consists of **DNA** molecules made up of sequences of **nucleotides**. Specific segments of DNA called **genes** contain the information the cell uses to make **proteins**. **Review Figure 1.4**
- Living organisms regulate their internal environment. They also interact with other organisms of the same and different species. Biologists study life at all these levels of organization. **Review Figure 1.6**, **WEB ACTIVITY 1.1**
- Biological knowledge obtained from a **model system** may be generalized to other species.

### 1.2 How Is All Life on Earth Related?

- Biologists use fossils, anatomical similarities and differences, and molecular comparisons of genomes to reconstruct the history of life. **Review Figure 1.8**

- Life first arose by chemical evolution. Cells arose early in the evolution of life.
- **Photosynthesis** was an important evolutionary step because it changed Earth's atmosphere and provided a means of capturing energy from sunlight.
- The earliest organisms were **prokaryotes**. Organisms called **eukaryotes**, with more complex cells, arose later. Eukaryotic cells have discrete intracellular compartments, called **organelles**, including a nucleus that contains the cell's genetic material.
- The genetic relationships of **species** can be represented as an evolutionary tree. Species are grouped into three **domains**: **Archaea**, **Bacteria**, and **Eukarya**. Archaea and Bacteria are domains of unicellular prokaryotes. Eukarya contains diverse groups of protists (most but not all of which are unicellular) and the multicellular plants, fungi, and animals. **Review Figure 1.10**, **WEB ACTIVITY 1.2**

### 1.3 How Do Biologists Investigate Life?

- The **scientific method** used in most biological investigations involves five steps: making observations, asking questions, forming hypotheses, making predictions, and testing those predictions. **Review Figure 1.12**
- **Hypotheses** are tentative answers to questions. Predictions made on the basis of a hypothesis are tested with additional

observations and two kinds of **experiments: comparative** and **controlled experiments**. Review Figures 1.13 and 1.14, ANIMATED TUTORIAL 1.1

- Statistical methods are applied to **data** to establish whether or not the differences observed are significant or whether they could be the result of chance. These methods start with the **null hypothesis** that there are no differences.

- Science can tell us how the world works, but it cannot tell us what we should or should not do.

#### 1.4 How Does Biology Influence Public Policy?

- Biologists are often called on to advise government agencies on the solution of important problems that have a biological component.

### FOR DISCUSSION

1. Even if we knew the sequences of all of the genes of a single-celled organism and could cause those genes to be expressed in a test tube, it would still be incredibly difficult to create a functioning organism. Why do you think this is so? In light of this fact, what do you think of the statement that the genome contains all of the information for a species?
2. Why is it so important in science that we design and perform tests capable of falsifying a hypothesis?
3. What features characterize questions that can be answered only by using a comparative approach?
4. Cite an example of how you apply aspects of the scientific method to solve problems in your daily life.

### ADDITIONAL INVESTIGATION

1. The abnormalities of frogs in Tyrone Hayes's studies were associated with the presence of a herbicide in the environment. That herbicide did not kill the frogs, but it feminized the males. How would you investigate whether this effect could lead to decreased reproductive capacity for the frog populations in nature?
2. Just as all cells come from preexisting cells, all mitochondria—the cell organelles that convert energy in food to a form of energy that can do biological work—come from preexisting mitochondria. Cells do not synthesize mitochondria from the genetic information in their nuclei. What investigations would you carry out to understand the nature of mitochondria?

### WORKING WITH DATA (GO TO [yourBioPortal.com](#))

**Feminization of Frogs** Analogous to the experiment shown in Figure 1.13, this exercise asks you to graph data about the size of the laryngeal (throat) muscles required to produce male mating calls in the frog *Xenopus laevis*. After plotting data from

frogs exposed to different levels of the herbicide atrazine during their development, you will formulate conclusions about the effects of the herbicide on this physical attribute and speculate about what these effects might mean.

## 2

# Small Molecules and the Chemistry of Life

## A hairy story

"**Y**ou are what you eat—and that is recorded in your hair." Two scientists at the University of Utah are responsible for adding the last phrase to this famous saying about body chemistry. Ecologist Jim Ehleringer and chemist Thure Cerling showed that the composition of human hair reflects the region where a person lives.

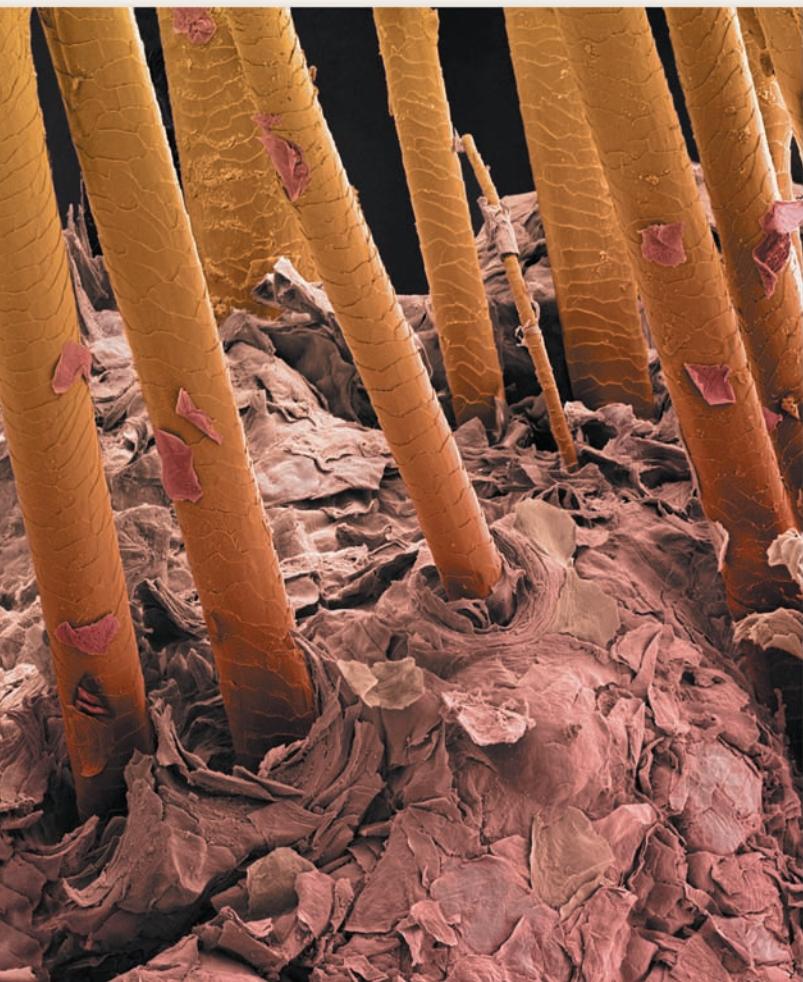
As we pointed out in Chapter 1, living things are made up of the same kinds of atoms that make up the inanimate universe. Two of those atoms are hydrogen (H) and

oxygen (O), which combine to form water ( $H_2O$ ). Both atoms have naturally occurring variants called *isotopes*, which have the same chemical properties but different weights because their nuclei have different numbers of particles called *neutrons*.

When water evaporates from the ocean, it forms clouds that move inland and release rain. Water made up of the heavier H and O isotopes is heavier and tends to fall more readily than water containing the lighter isotopes. Warm rains tend to be heavier than cooler precipitation. People living on the coast or in regions where there are frequent warm rains consume heavier water and foods made from water than people living in cooler, inland areas (assuming, of course, that their beverages and produce come from the same area they live in). And, since you are what you eat, the heavy H and O atoms become part of their bodies.

Our hair contains abundant H and O atoms, many obtained from local water. Ehleringer and Cerling wondered whether the ratios of heavy-to-light H and O in hair reflected the ratio of heavy-to-light  $H_2O$  in the local water. To address this question, Ehleringer's wife and Cerling's children and their friends went on a hair-collecting trip across the United States, collecting hair trimmings from barbershop floors while at the same time filling test tubes with local water. Back at the lab, scientists tested the samples and found that the ratios of heavy to light isotopes in the hair did indeed reflect these same ratios in the local water.

While this information is intrinsically fascinating, it is also potentially useful. For example, police could use hair analysis to evaluate a suspect's alibi: "You say you've been in Montana for the past month? Your hair sample indicates that you were in a warm coastal area." Such conflicting evidence could form the basis of further investigation.



**Hair Tells a Tale** The ratio in hair protein of the heavy isotope  $^{18}O$  to its lighter counterpart  $^{16}O$  reflects the ratios in local water.



**Free Samples** Need hair samples for a research project? Try the local barber shop.

Or anthropologists might analyze hair samples from graves to work out migration patterns of human groups.

The understanding that life is based on chemistry and obeys universal laws of chemistry and physics is relatively new in human history. Until the nineteenth century, a “vital force” (from the Latin *vitalis*, “of life”) was presumed to be responsible for life. This vital force was seen as distinct from the mechanistic forces governing physics and chemistry. Many people still assume that a vital force exists, but the physical–chemical view of life has led to great advances in biological science and is the cornerstone of modern medicine and agriculture.

**IN THIS CHAPTER** we will introduce the constituents of matter: atoms, their variety, their properties, and their capacity to combine with other atoms. We will consider how matter changes, including changes in state (solid to liquid to gas), and changes caused by chemical reactions. We will examine the structure and properties of water and its relationship to chemical acids and bases.

## CHAPTER OUTLINE

- 2.1 How Does Atomic Structure Explain the Properties of Matter?**
- 2.2 How Do Atoms Bond to Form Molecules?**
- 2.3 How Do Atoms Change Partners in Chemical Reactions?**
- 2.4 What Makes Water So Important for Life?**

### 2.1 How Does Atomic Structure Explain the Properties of Matter?

All matter is composed of **atoms**. Atoms are tiny—more than a trillion ( $10^{12}$ ) of them could fit on top of the period at the end of this sentence. Each atom consists of a dense, positively charged **nucleus**, around which one or more negatively charged **electrons** move (Figure 2.1). The nucleus contains one or more positively charged **protons** and may contain one or more **neutrons** with no electrical charge. Atoms and their component particles have volume and mass, which are characteristics of all matter. *Mass* is a measure of the quantity of matter present; the greater the mass, the greater the quantity of matter.

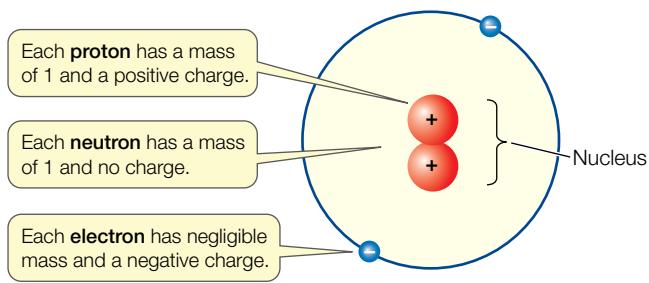
The mass of a proton serves as a standard unit of measure called the *dalton* (named after the English chemist John Dalton) or **atomic mass unit (amu)**. A single proton or neutron has a mass of about 1 dalton (Da), which is  $1.7 \times 10^{-24}$  grams (0.00000000000000000000000017 g). That’s tiny, but an electron is even tinier at  $9 \times 10^{-28}$  g (0.0005 Da). Because the mass of an electron is negligible compared with the mass of a proton or a neutron, the contribution of electrons to the mass of an atom can usually be ignored when measurements and calculations are made. It is electrons, however, that determine how atoms will combine with other atoms to form stable associations.

Each proton has a positive electric charge, defined as +1 unit of charge. An electron has a negative charge equal and opposite to that of a proton (-1). The neutron, as its name suggests, is electrically neutral, so its charge is 0. Charges that are different (+/-) attract each other, whereas charges that are alike (+/+, -/-) repel each other. Atoms are electrically neutral because the number of electrons in an atom equals the number of protons.

#### An element consists of only one kind of atom

An **element** is a pure substance that contains only one kind of atom. The element hydrogen consists only of hydrogen atoms; the element iron consists only of iron atoms. The atoms of each element have certain characteristics or properties that distinguish them from the atoms of other elements. These properties include their mass and how they interact and associate with other atoms.

The more than 100 elements found in the universe are arranged in the *periodic table* (Figure 2.2). Each element has its own one- or two-letter chemical symbol. For example, H stands for hydrogen, C for carbon, and O for oxygen. Some symbols come from other languages: Fe (from the Latin, *ferrum*) stands for iron, Na (Latin, *natrium*) for sodium, and W (German, *wolfram*) for tungsten.



**2.1 The Helium Atom** This representation of a helium atom is called a Bohr model. It exaggerates the space occupied by the nucleus. In reality, although the nucleus accounts for virtually all of the atomic mass, it occupies only about 1/10,000 of the atom's volume. The Bohr model is also inaccurate in that it represents the electron as a discrete particle in a defined orbit around the nucleus.

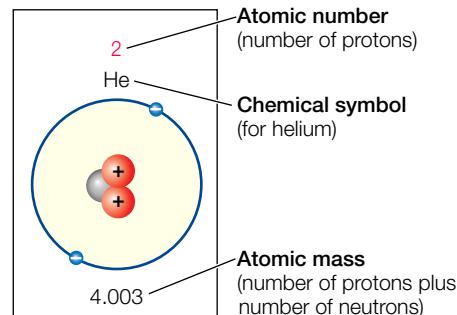
The elements of the periodic table are not found in equal amounts. Stars have abundant amounts of hydrogen and helium. Earth's crust, and the surfaces of the neighboring planets, are almost half oxygen, 28 percent silicon, 8 percent aluminum, and between 2 and 5 percent each of sodium, magnesium, potassium, calcium, and iron. They contain much smaller amounts of the other elements.

About 98 percent of the mass of every living organism (bacterium, turnip, or human) is composed of just six elements: carbon,

bon, hydrogen, nitrogen, oxygen, phosphorus, and sulfur. The chemistry of these six elements will be our primary concern in this chapter, but other elements found in living organisms are important as well. Sodium and potassium, for example, are essential for nerve function; calcium can act as a biological signal; iodine is a component of a vital hormone; and magnesium is bound to chlorophyll in plants. The physical and chemical (reactive) properties of atoms depend on the number of subatomic particles they contain.

**Each element has a different number of protons**

An element differs from other elements by the number of protons in the nucleus of each of its atoms; the number of protons is designated the **atomic number**. This atomic number is unique



<b>1</b> H 1.0079	elements according to their physical and chemical properties. Elements 1–92 occur in nature; elements with atomic numbers above 92 were created in the laboratory.												The six elements highlighted in yellow make up 98% of the mass of most living organisms.					
<b>3</b> Li 6.941	<b>4</b> Be 9.012	Elements in the same vertical columns have similar properties because they have the same number of electrons in their outermost shell.						Elements highlighted in orange are present in small amounts in many organisms.						<b>5</b> B 10.81	<b>6</b> C 12.011	<b>7</b> N 14.007	<b>8</b> O 15.999	<b>9</b> F 18.998
<b>11</b> Na 22.990	<b>12</b> Mg 24.305							<b>13</b> Al 26.982	<b>14</b> Si 28.086	<b>15</b> P 30.974	<b>16</b> S 32.06	<b>17</b> Cl 35.453		<b>10</b> Ne 20.179				
<b>19</b> K 39.098	<b>20</b> Ca 40.08	<b>21</b> Sc 44.956	<b>22</b> Ti 47.88	<b>23</b> V 50.942	<b>24</b> Cr 51.996	<b>25</b> Mn 54.938	<b>26</b> Fe 55.847	<b>27</b> Co 58.933	<b>28</b> Ni 58.69	<b>29</b> Cu 63.546	<b>30</b> Zn 65.38	<b>31</b> Ga 69.72	<b>32</b> Ge 72.59	<b>33</b> As 74.922	<b>34</b> Se 78.96	<b>35</b> Br 79.909	<b>36</b> Kr 83.80	
<b>37</b> Rb 85.4778	<b>38</b> Sr 87.62	<b>39</b> Y 88.906	<b>40</b> Zr 91.22	<b>41</b> Nb 92.906	<b>42</b> Mo 95.94	<b>43</b> Tc (99)	<b>44</b> Ru 101.07	<b>45</b> Rh 102.906	<b>46</b> Pd 106.4	<b>47</b> Ag 107.870	<b>48</b> Cd 112.41	<b>49</b> In 114.82	<b>50</b> Sn 118.69	<b>51</b> Sb 121.75	<b>52</b> Te 127.60	<b>53</b> I 126.904	<b>54</b> Xe 131.30	
<b>55</b> Cs 132.905	<b>56</b> Ba 137.34	<b>71</b> Lu 174.97	<b>72</b> Hf 178.49	<b>73</b> Ta 180.948	<b>74</b> W 183.85	<b>75</b> Re 186.207	<b>76</b> Os 190.2	<b>77</b> Ir 192.2	<b>78</b> Pt 195.08	<b>79</b> Au 196.967	<b>80</b> Hg 200.59	<b>81</b> Tl 204.37	<b>82</b> Pb 207.19	<b>83</b> Bi 208.980	<b>84</b> Po (209)	<b>85</b> At (210)	<b>86</b> Rn (222)	
<b>87</b> Fr (223)	<b>88</b> Ra (260)	<b>103</b> Lr (261)	<b>104</b> Rf (261)	<b>105</b> Db (262)	<b>106</b> Sg (266)	<b>107</b> Bh (264)	<b>108</b> Hs (269)	<b>109</b> Mt (268)	<b>110</b>  (269)	<b>111</b>  (272)	<b>112</b>  (277)	<b>113</b>  (285)	<b>114</b>  (289)	<b>115</b>  	<b>116</b>  	<b>117</b>  (293)	<b>118</b>  	
<b>Lanthanide series</b>		<b>57</b> La 138.906	<b>58</b> Ce 140.12	<b>59</b> Pr 140.9077	<b>60</b> Nd 144.24	<b>61</b> Pm (145)	<b>62</b> Sm 150.36	<b>63</b> Eu 151.96	<b>64</b> Gd 157.25	<b>65</b> Tb 158.924	<b>66</b> Dy 162.50	<b>67</b> Ho 164.930	<b>68</b> Er 167.26	<b>69</b> Tm 168.934	<b>70</b> Yb 173.04			
<b>Actinide series</b>		<b>89</b> Ac 227.028	<b>90</b> Th 232.038	<b>91</b> Pa 231.0359	<b>92</b> U 238.02	<b>93</b> Np 237.0482	<b>94</b> Pu (244)	<b>95</b> Am (243)	<b>96</b> Cm (247)	<b>97</b> Bk (247)	<b>98</b> Cf (251)	<b>99</b> Es (252)	<b>100</b> Fm (257)	<b>101</b> Md (258)	<b>102</b> No (259)			

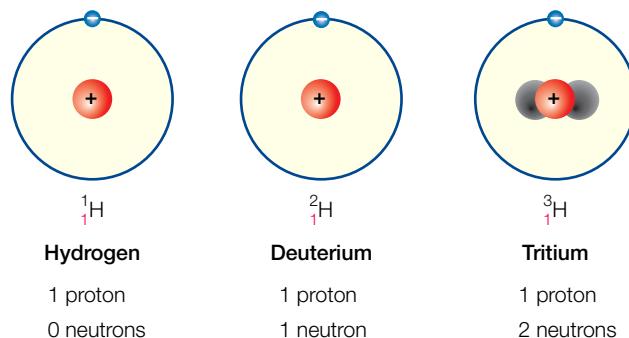
to each element and does not change. The atomic number of helium is 2, and an atom of helium always has two protons; the atomic number of oxygen is 8, and an atom of oxygen always has eight protons.

Along with a definitive number of protons, every element except hydrogen has one or more neutrons in its nucleus. The **mass number** of an atom is the total number of protons and neutrons in its nucleus. The nucleus of a carbon atom contains six protons and six neutrons, and has a mass number of 12. Oxygen has eight protons and eight neutrons, and has a mass number of 16. The mass number is essentially the mass of the atom in daltons (see below).

By convention, we often print the symbol for an element with the atomic number at the lower left and the mass number at the upper left, both immediately preceding the symbol. Thus hydrogen, carbon, and oxygen can be written as  $^1_1\text{H}$ ,  $^{12}_6\text{C}$ , and  $^{16}_8\text{O}$ , respectively.

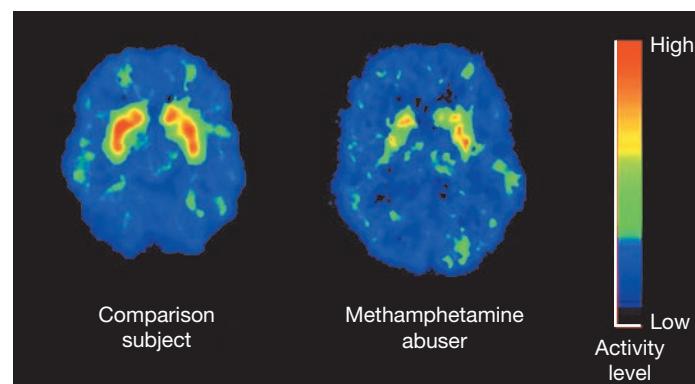
### The number of neutrons differs among isotopes

In some elements, the number of neutrons in the atomic nucleus is not always the same. Different **isotopes** of the same element have the same number of protons, but different numbers of neutrons. Many elements have several isotopes. The isotopes of hydrogen shown below have special names, but the isotopes of most elements do not have distinct names.



The natural isotopes of carbon, for example, are  $^{12}\text{C}$  (six neutrons in the nucleus),  $^{13}\text{C}$  (seven neutrons), and  $^{14}\text{C}$  (eight neutrons). Note that all three (called “carbon-12,” “carbon-13,” and “carbon-14”) have six protons, so they are all carbon. Most carbon atoms are  $^{12}\text{C}$ , about 1.1 percent are  $^{13}\text{C}$ , and a tiny fraction are  $^{14}\text{C}$ . But all have virtually the same chemical reactivity, which is an important property for their use in experimental biology and medicine. An element’s **atomic weight** (or atomic mass) is the average of the mass numbers of a representative sample of atoms of that element, with all the isotopes in their normally occurring proportions. The atomic weight of carbon, taking into account all of its isotopes and their abundances, is thus 12.011. The fractional atomic weight results from averaging the contributing weights of all of the isotopes.

Most isotopes are stable. But some, called **radioisotopes**, are unstable and spontaneously give off energy in the form of  $\alpha$  (alpha),  $\beta$  (beta), or  $\gamma$  (gamma) radiation from the atomic nucleus. Known as *radioactive decay*, this release of energy transforms the original atom. The type of transformation varies depending on



**2.3 Tagging the Brain** In these images from live people, a radioactive-labeled sugar is used to detect differences between the brain activity of a healthy person and that of a person who abuses methamphetamines. The more active a brain region is, the more sugar it takes up. The healthy brain (left) shows more activity in the region involved in memory (the red area) than the drug abuser’s brain does.

the radioisotope, but some can change the number of protons, so that the original atom becomes a different element.

With sensitive instruments, scientists can use the released radiation to detect the presence of radioisotopes. For instance, if an earthworm is given food containing a radioisotope, its path through the soil can be followed using a simple detector called a Geiger counter. Most atoms in living organisms are organized into stable associations called **molecules**. If a radioisotope is incorporated into a molecule, it acts as a tag or label, allowing researchers or physicians to trace the molecule in an experiment or in the body (**Figure 2.3**). Radioisotopes are also used to date fossils, an application described in Section 25.1.

Although radioisotopes are useful in research and in medicine, even a low dose of the radiation they emit has the potential to damage molecules and cells. However, these damaging effects are sometimes used to our advantage; for example, the radiation from  $^{60}\text{Co}$  (cobalt-60) is used in medicine to kill cancer cells.

### The behavior of electrons determines chemical bonding and geometry

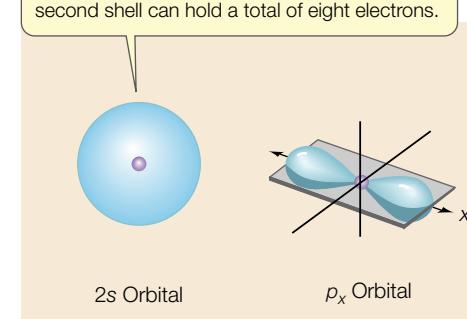
The characteristic number of electrons in an atom determines how it will combine with other atoms. Biologists are interested in how chemical changes take place in living cells. When considering atoms, they are concerned primarily with electrons because the behavior of electrons explains how chemical *reactions* occur. Chemical reactions alter the atomic compositions of substances and thus alter their properties. Reactions usually involve changes in the distribution of electrons between atoms.

The location of a given electron in an atom at any given time is impossible to determine. We can only describe a volume of space within the atom where the electron is likely to be. The region of space where the electron is found at least 90 percent of the time is the electron’s **orbital**. Orbitals have characteristic shapes and orientations, and a given orbital can be occupied by

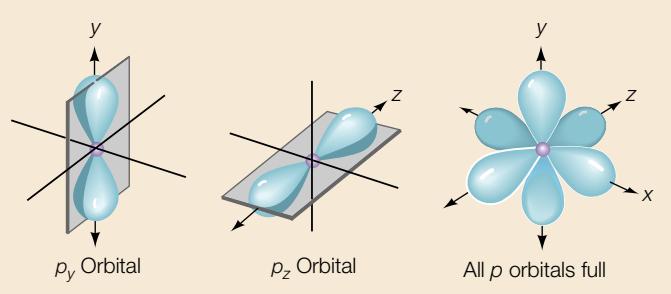
**First shell:**  
The two electrons closest to the nucleus move in a spherical s orbital.



**Second shell:**  
Two electrons occupy the 2s orbital, one of four orbitals in the second shell of electrons. The second shell can hold a total of eight electrons.



**2.4 Electron Shells and Orbitals** Each orbital holds a maximum of two electrons. The s orbitals have a lower energy level and fill with electrons before the p orbitals do.



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GO TO Web Activity 2.1 • Electron Orbitals

Two electrons form a dumbbell-shaped x axis ( $p_x$ ) orbital...

...two more fill the  $p_y$  orbital...

...and two fill the  $p_z$  orbital.

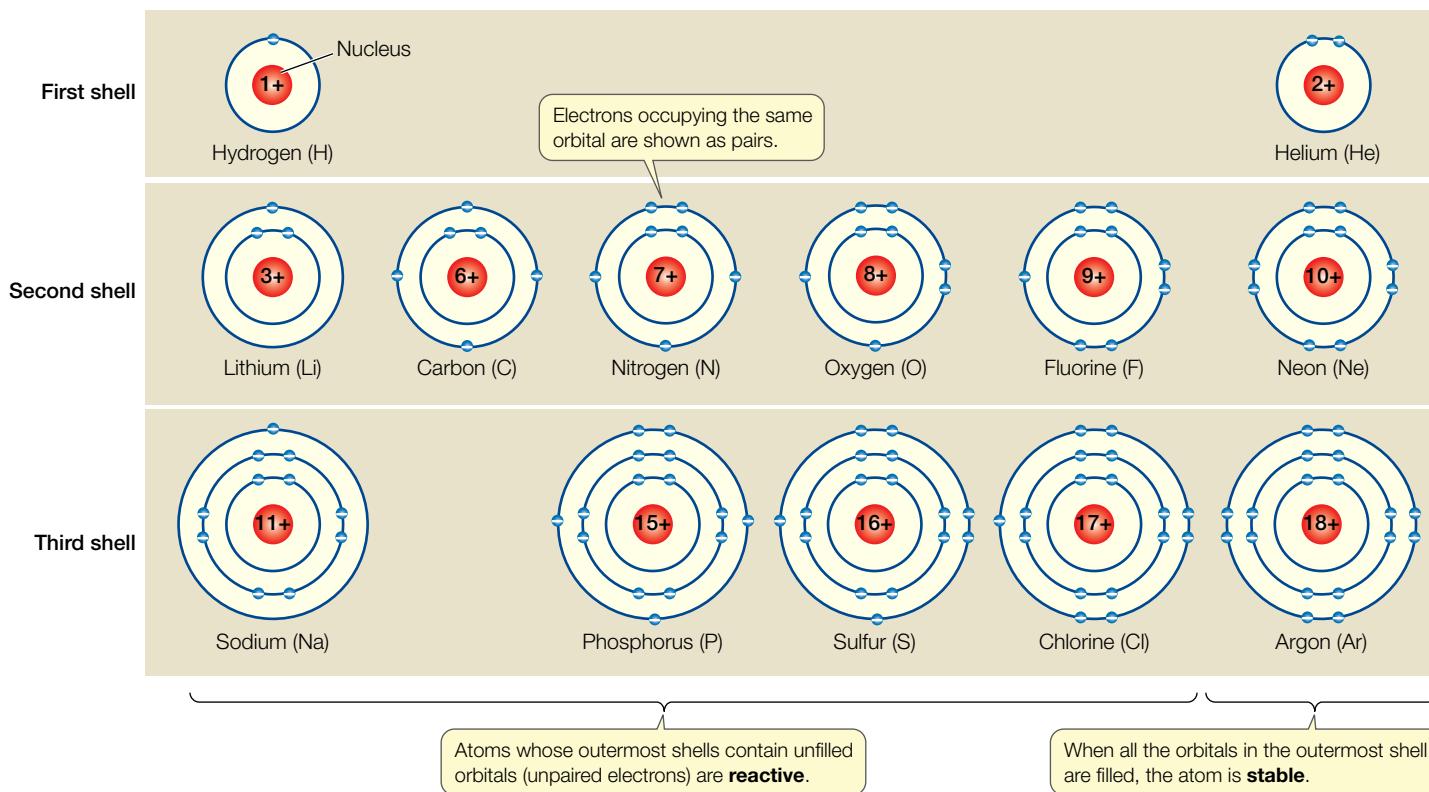
Six electrons fill all three p orbitals.

a maximum of two electrons (Figure 2.4). Thus any atom larger than helium (atomic number 2) must have electrons in two or more orbitals. As we move from lighter to heavier atoms in the periodic chart, the orbitals are filled in a specific sequence, in a series of what are known as **electron shells**, or *energy levels*, around the nucleus.

- **First shell:** The innermost electron shell consists of just one orbital, called an s orbital. A hydrogen atom ( ${}_1\text{H}$ ) has one electron in its first shell; helium ( ${}_2\text{He}$ ) has two. Atoms of all other elements have two or more shells to accommodate orbitals for additional electrons.

- **Second shell:** The second shell contains four orbitals (an s orbital and three p orbitals), and hence holds up to eight electrons. As depicted in Figure 2.4, the s orbitals have the shape of a sphere, while the p orbitals are directed at right angles to one another. The orientations of these orbitals in space contribute to the three-dimensional shapes of molecules when atoms link to other atoms.

**2.5 Electron Shells Determine the Reactivity of Atoms** Each shell can hold a specific maximum number of electrons. Each shell must be filled before electrons can occupy the next shell. The energy level of an electron is higher in a shell farther from the nucleus. An atom with unpaired electrons in its outermost shell can react (bond) with other atoms.



- **Additional shells:** Elements with more than ten electrons have three or more electron shells. The farther a shell is from the nucleus, the higher the energy level is for an electron occupying that shell.

The *s* orbitals fill with electrons first, and their electrons have the lowest energy level. Subsequent shells have different numbers of orbitals, but the outermost shells usually hold only eight electrons. In any atom, the outermost electron shell (the *valence shell*) determines how the atom combines with other atoms—that is, how the atom behaves chemically. When a valence shell with four orbitals contains eight electrons, there are no unpaired electrons, and the atom is *stable*—it will not react with other atoms (Figure 2.5). Examples of chemically stable elements are helium, neon, and argon. On the other hand, atoms that have one or more unpaired electrons in their outer shells are capable of reacting with other atoms.

Atoms with unpaired electrons (i.e., partially filled orbitals) in their outermost electron shells are unstable, and will undergo reactions in order to fill their outermost shells. Reactive atoms can attain stability either by sharing electrons with other atoms or by losing or gaining one or more electrons. In either case, the atoms involved are *bonded* together into stable associations called molecules. The tendency of atoms to form stable molecules so that they have eight electrons in their outermost shells is known as the *octet rule*. Many atoms in biologically important molecules—for example, carbon (C) and nitrogen (N)—follow this rule. An important exception is hydrogen (H), which attains stability when two electrons occupy its single shell (consisting of just one *s* orbital).

## 2.1 RECAP

The living world is composed of the same set of chemical elements as the rest of the universe. An atom consists of a nucleus of protons and neutrons, and a characteristic configuration of electrons in orbitals around the nucleus. This structure determines the atom's chemical properties.

- Describe the arrangement of protons, neutrons, and electrons in an atom. See Figure 2.1
- Use the periodic table to identify some of the similarities and differences in atomic structure among different elements (for example, oxygen, carbon, and helium). How does the configuration of the valence shell influence the placement of an element in the periodic table? See p. 25 and Figures 2.2 and 2.5
- How does bonding help a reactive atom achieve stability? See p. 25 and Figure 2.5

We have introduced the individual players on the biochemical stage—the atoms. We have shown how the energy levels of electrons drive an atomic “quest for stability.” Next we will describe the different types of chemical bonds that can lead to stability, joining atoms together into molecular structures with hosts of different properties.

## 2.2 How Do Atoms Bond to Form Molecules?

A **chemical bond** is an attractive force that links two atoms together in a molecule. There are several kinds of chemical bonds (Table 2.1). In this section we will begin with *covalent bonds*, the strong bonds that result from the sharing of electrons. Next we will examine *ionic bonds*, which form when an atom gains or loses one or more electrons to achieve stability. We will then consider other, weaker, kinds of interactions, including hydrogen bonds, which are enormously important to biology.

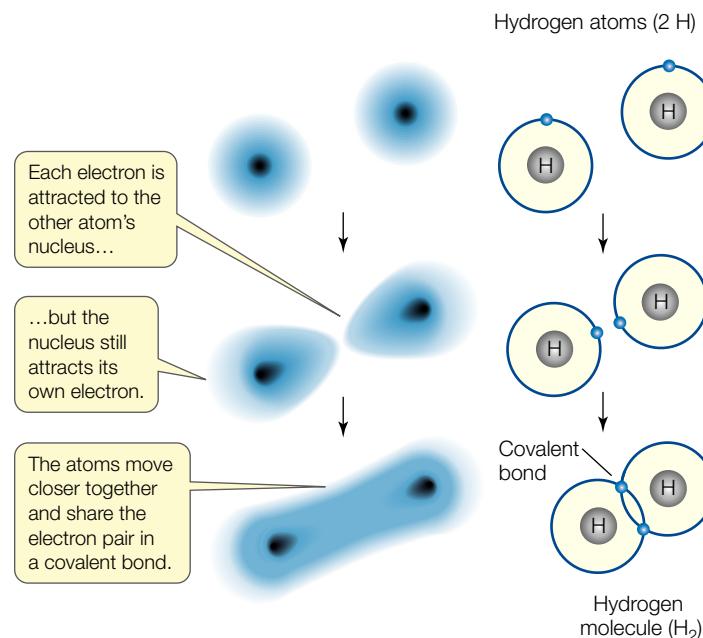
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GO TO Animated Tutorial 2.1 • Chemical Bond Formation

### Covalent bonds consist of shared pairs of electrons

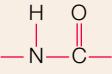
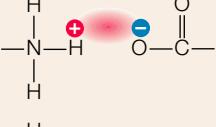
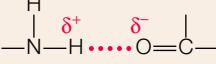
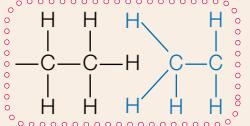
A **covalent bond** forms when two atoms attain stable electron numbers in their outermost shells by *sharing* one or more pairs of electrons. Consider two hydrogen atoms coming into close proximity, each with an unpaired electron in its single shell (Figure 2.6). When the electrons pair up, a stable association is formed, and this links the two hydrogen atoms in a covalent bond, resulting in H<sub>2</sub>.

A **compound** is a substance made up of molecules with two or more elements bonded together in a fixed ratio. Methane gas (CH<sub>4</sub>), water (H<sub>2</sub>O), and table sugar (sucrose, C<sub>12</sub>H<sub>22</sub>O<sub>11</sub>) are examples of compounds. The chemical symbols identify the different elements in a compound, and the subscript numbers indicate how many atoms of each element are present. Every compound has a **molecular weight** (molecular mass) that is the



**2.6 Electrons Are Shared in Covalent Bonds** Two hydrogen atoms can combine to form a hydrogen molecule. A covalent bond forms when the electron orbitals of the two atoms overlap in an energetically stable manner.

**TABLE 2.1**  
**Chemical Bonds and Interactions**

NAME	BASIS OF INTERACTION	STRUCTURE	BOND ENERGY <sup>a</sup> (KCAL/MOL)
Covalent bond	Sharing of electron pairs		50–110
Ionic bond	Attraction of opposite charges		3–7
Hydrogen bond	Sharing of H atom		3–7
Hydrophobic interaction	Interaction of nonpolar substances in the presence of polar substances (especially water)		1–2
van der Waals interaction	Interaction of electrons of nonpolar substances		1

<sup>a</sup>Bond energy is the amount of energy needed to separate two bonded or interacting atoms under physiological conditions.

sum of the atomic weights of all atoms in the molecule. Looking at the periodic table in Figure 2.2, you can calculate the molecular weights of the three compounds listed above to be 16.04, 18.01, and 342.29, respectively. Molecules that make up living organisms range in molecular weight from two to half a billion, and covalent bonds are common to all.

How are covalent bonds formed in a molecule of methane gas ( $\text{CH}_4$ )? The carbon atom in this compound has six electrons: two electrons fill its inner shell, and four unpaired electrons travel in its outer shell. Because its outer shell can hold up to eight electrons, carbon can share electrons with up to four other atoms—it can form four covalent bonds (Figure 2.7A). When an atom of carbon reacts with four hydrogen atoms, methane forms. Thanks to electron sharing, the outer shell of methane’s carbon atom is now filled with eight electrons, a stable configuration. The outer shell of each of the four hydrogen atoms is also filled. Four covalent bonds—four shared electron pairs—

hold methane together. Figure 2.7B shows several different ways to represent the molecular structure of methane. Table 2.2 shows the covalent bonding capacities of some biologically significant elements.

**STRENGTH AND STABILITY** Covalent bonds are very strong, meaning that it takes a lot of energy to break them. At temperatures in which life exists, the covalent bonds of biological molecules are quite stable, as are their three-dimensional structures. However, this stability does not preclude change, as we will discover.

**ORIENTATION** For a given pair of elements—for example, carbon bonded to hydrogen—the length of the covalent bond is always the same. And for a given atom within a molecule, the angle of each covalent bond, with respect to the other bonds, is generally the same. This is true regardless of the type of larger molecule that contains the atom. For example, the four filled orbitals around the carbon atom in methane are always distributed in space so that the bonded hydrogens point to the corners of a regular tetrahedron, with carbon in the center (see Figure 2.7B). Even when carbon is bonded to four atoms other than hydrogen, this three-dimensional orientation is more or less maintained. The orientation of covalent bonds in space gives the molecules their three-dimensional geometry, and the shapes of molecules contribute to their biological functions, as we will see in Section 3.1.

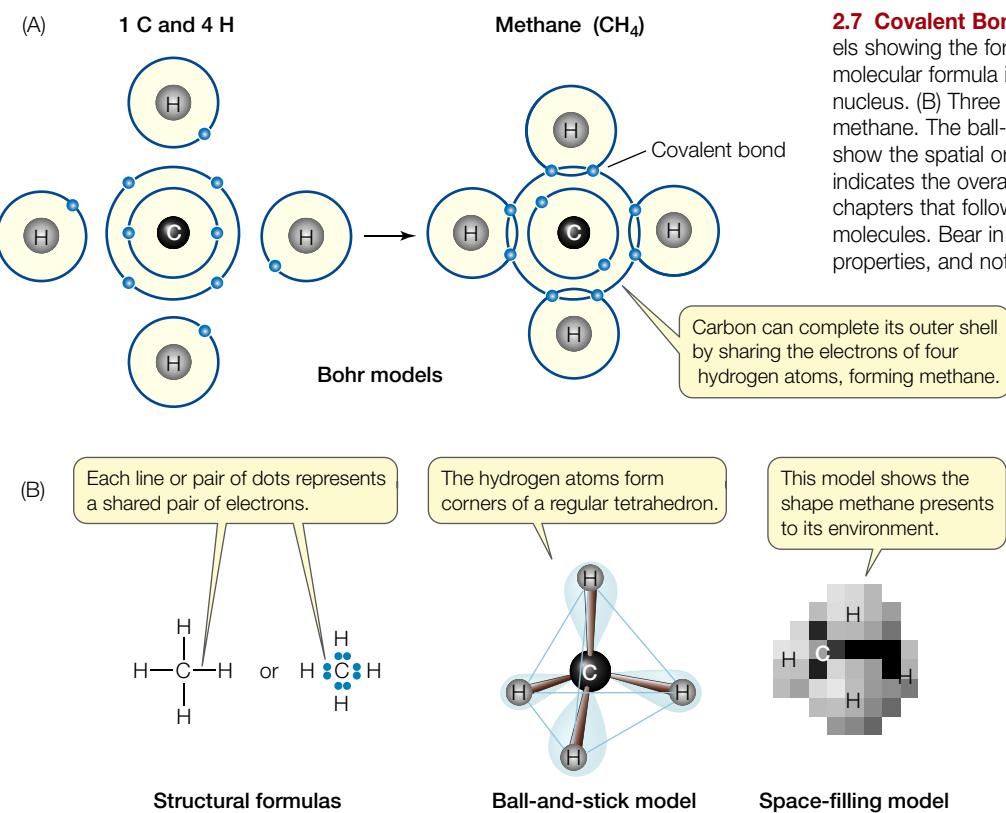
**MULTIPLE COVALENT BONDS** A covalent bond can be represented by a line between the chemical symbols for the linked atoms:

- A *single bond* involves the sharing of a single pair of electrons (for example,  $\text{H}-\text{H}$  or  $\text{C}-\text{H}$ ).

**TABLE 2.2**

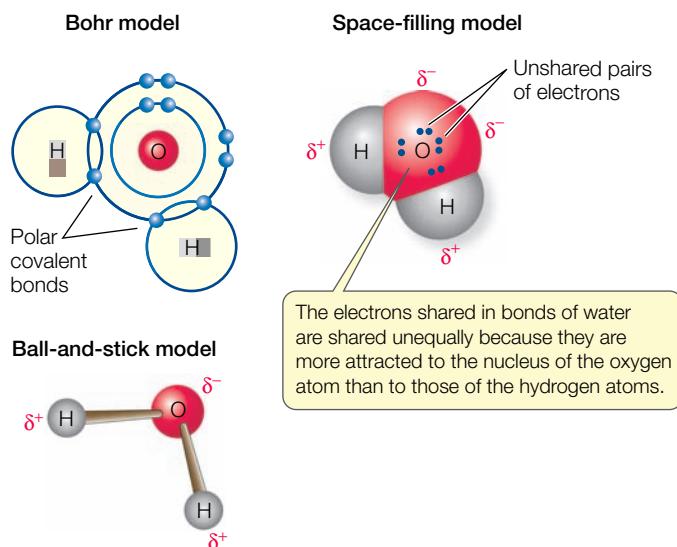
**Covalent Bonding Capabilities of Some Biologically Important Elements**

ELEMENT	USUAL NUMBER OF COVALENT BONDS
Hydrogen (H)	1
Oxygen (O)	2
Sulfur (S)	2
Nitrogen (N)	3
Carbon (C)	4
Phosphorus (P)	5



- A *double bond* involves the sharing of four electrons (two pairs) ( $\text{C}=\text{C}$ ).
- Triple bonds*—six shared electrons—are rare, but there is one in nitrogen gas ( $\text{N}\equiv\text{N}$ ), which is the major component of the air we breathe.

**UNEQUAL SHARING OF ELECTRONS** If two atoms of the same element are covalently bonded, there is an equal sharing of the pair(s) of electrons in their outermost shells. However, when the two atoms are of different elements, the sharing is not nec-



**2.7 Covalent Bonding Can Form Compounds** (A) Bohr models showing the formation of covalent bonds in methane, whose molecular formula is  $\text{CH}_4$ . Electrons are shown in shells around the nucleus. (B) Three additional ways of representing the structure of methane. The ball-and-stick model and the space-filling model show the spatial orientations of the bonds. The space-filling model indicates the overall shape and surface of the molecule. In the chapters that follow, different conventions will be used to depict molecules. Bear in mind that these are models to illustrate certain properties, and not the most accurate portrayal of reality.

essarily equal. One nucleus may exert a greater attractive force on the electron pair than the other nucleus, so that the pair tends to be closer to that atom.

The attractive force that an atomic nucleus exerts on electrons in a covalent bond is called its **electronegativity**. The electronegativity of a nucleus depends on how many positive charges it has (nuclei with more protons are more positive and thus more attractive to electrons) and on the distances between the electrons in the bond and the nucleus (the closer the electrons, the greater the electronegative pull). **Table 2.3** shows the electronegativities (which are calculated to produce dimensionless quantities) of some elements important in biological systems.

If two atoms are close to each other in electronegativity, they will share electrons equally in what is called a *nonpolar covalent bond*. Two oxygen atoms, for example, each with an electronegativity of 3.5, will share electrons equally. So will two hydrogen atoms (each with an electronegativity of 2.1). But when hydrogen bonds with oxygen to form water, the electrons involved are unequally shared: they tend to be nearer to the oxygen nucleus because it is the more electronegative of the two. When electrons are drawn to one nucleus more than to the other, the result is a *polar covalent bond* (Figure 2.8).

**2.8 Water's Covalent Bonds Are Polar** These three representations all illustrate polar covalent bonding in water ( $\text{H}_2\text{O}$ ). When atoms with different electronegativities, such as oxygen and hydrogen, form a covalent bond, the electrons are drawn to one nucleus more than to the other. A molecule held together by such a polar covalent bond has partial ( $\delta^+$  and  $\delta^-$ ) charges at different surfaces. In water, the shared electrons are displaced toward the oxygen atom's nucleus.

**TABLE 2.3**  
**Some Electronegativities**

ELEMENT	ELECTRONEGATIVITY
Oxygen (O)	3.5
Chlorine (Cl)	3.1
Nitrogen (N)	3.0
Carbon (C)	2.5
Phosphorus (P)	2.1
Hydrogen (H)	2.1
Sodium (Na)	0.9
Potassium (K)	0.8

Because of this unequal sharing of electrons, the oxygen end of the hydrogen–oxygen bond has a slightly negative charge (symbolized by  $\delta^-$  and spoken of as “delta negative,” meaning a partial unit of charge), and the hydrogen end has a slightly positive charge ( $\delta^+$ ). The bond is **polar** because these opposite charges are separated at the two ends, or poles, of the bond. The partial charges that result from polar covalent bonds produce polar molecules or polar regions of large molecules. Polar bonds within molecules greatly influence the interactions that they have with other polar molecules. Water ( $H_2O$ ) is a polar compound, and this polarity has significant effects on its physical properties and chemical reactivity, as we will see in later chapters.

### Ionic bonds form by electrical attraction

When one interacting atom is much more electronegative than the other, a complete transfer of one or more electrons may take place. Consider sodium (electronegativity 0.9) and chlorine (3.1). A sodium atom has only one electron in its outermost shell; this condition is unstable. A chlorine atom has seven electrons in its outermost shell—another unstable condition. Since the electronegativity of chlorine is so much greater than that of sodium, any electrons involved in bonding will tend to transfer completely from sodium’s outermost shell to that of chlorine (Figure 2.9). This reaction between sodium and chlorine makes the resulting atoms more stable because they both have eight fully paired electrons in their outer shells. The result is two *ions*.

**Ions** are electrically charged particles that form when atoms gain or lose one or more electrons:

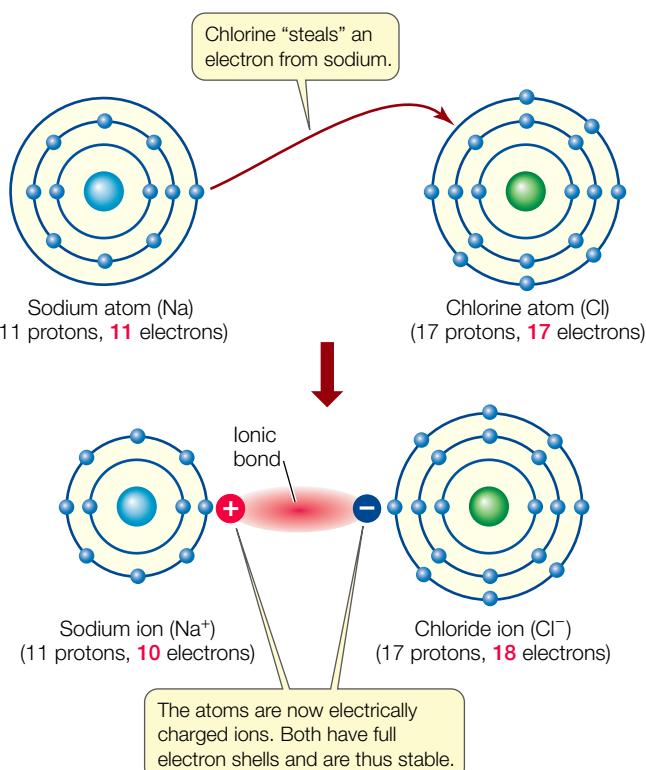
- The sodium ion ( $Na^+$ ) in our example has a +1 unit of charge because it has one less electron than it has protons. The outermost electron shell of the sodium ion is full, with eight electrons, so the ion is stable. Positively charged ions are called **cations**.
- The chloride ion ( $Cl^-$ ) has a -1 unit of charge because it has one more electron than it has protons. This additional electron gives  $Cl^-$  a stable outermost shell with eight electrons. Negatively charged ions are called **anions**.

Some elements can form ions with multiple charges by losing or gaining *more than one* electron. Examples are  $Ca^{2+}$  (the cal-

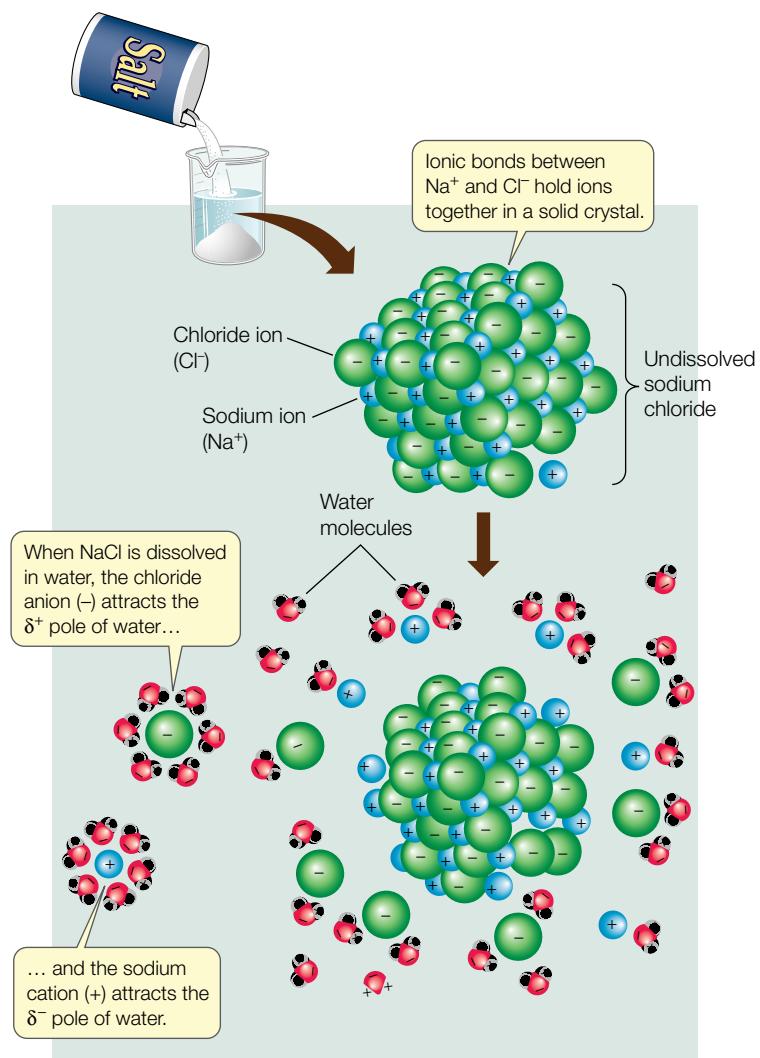
cium ion, a calcium atom that has lost two electrons) and  $Mg^{2+}$  (the magnesium ion). Two biologically important elements can each yield more than one stable ion. Iron yields  $Fe^{2+}$  (the ferrous ion) and  $Fe^{3+}$  (the ferric ion), and copper yields  $Cu^{+}$  (the cuprous ion) and  $Cu^{2+}$  (the cupric ion). Groups of covalently bonded atoms that carry an electric charge are called *complex ions*; examples include  $NH_4^+$  (the ammonium ion),  $SO_4^{2-}$  (the sulfate ion), and  $PO_4^{3-}$  (the phosphate ion). Once formed, ions are usually stable and no more electrons are lost or gained.

**Ionic bonds** are bonds formed as a result of the electrical attraction between ions bearing opposite charges. Ions can form bonds that result in stable solid compounds, which are referred to by the general term *salts*. Examples are sodium chloride ( $NaCl$ ) and potassium phosphate ( $K_3PO_4$ ). In sodium chloride—familiar to us as table salt—cations and anions are held together by ionic bonds. In solids, the ionic bonds are strong because the ions are close together. However, when ions are dispersed in water, the distance between them can be large; the strength of their attraction is thus greatly reduced. Under the conditions in living cells, an ionic attraction is less strong than a nonpolar covalent bond (see Table 2.1).

Not surprisingly, ions can interact with polar molecules, since they both carry electric charges. Such an interaction results when a solid salt such as  $NaCl$  dissolves in water. Water molecules surround the individual ions, separating them (Figure



**2.9 Formation of Sodium and Chloride Ions** When a sodium atom reacts with a chlorine atom, the more electronegative chlorine fills its outermost shell by “stealing” an electron from the sodium. In so doing, the chlorine atom becomes a negatively charged chloride ion ( $Cl^-$ ). With one less electron, the sodium atom becomes a positively charged sodium ion ( $Na^+$ ).



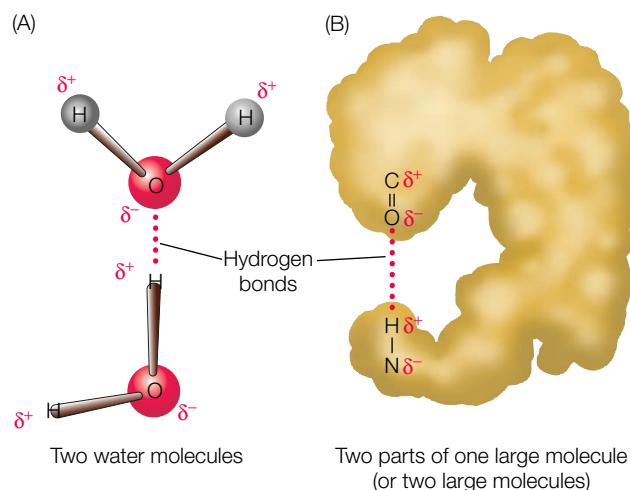
**2.10 Water Molecules Surround Ions** When an ionic solid dissolves in water, polar water molecules cluster around the cations and anions, preventing them from re-associating.

**2.10.** The negatively charged chloride ions attract the positive poles of the water molecules, while the positively charged sodium ions attract the negative poles of the water molecules. This is one of the special properties of water molecules, due to their polarity.

### Hydrogen bonds may form within or between molecules with polar covalent bonds

In liquid water, the negatively charged oxygen ( $\delta^-$ ) atom of one water molecule is attracted to the positively charged hydrogen ( $\delta^+$ ) atoms of another water molecule (Figure 2.11A). The bond resulting from this attraction is called a **hydrogen bond**. Hydrogen bonds are not restricted to water molecules; they may also form between a strongly electronegative atom and a hydrogen atom that is covalently bonded to a different electronegative atom, as shown in Figure 2.11B.

A hydrogen bond is weaker than most ionic bonds because its formation is due to partial charges ( $\delta^+$  and  $\delta^-$ ). It is much weaker than a covalent bond between a hydrogen atom and an oxygen atom (see Table 2.1). Although individual hydrogen bonds are weak, many of them can form within one molecule or



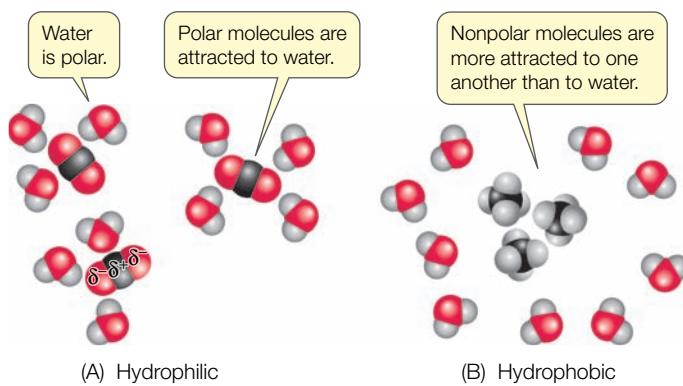
### 2.11 Hydrogen Bonds Can Form Between or Within Molecules

(A) A hydrogen bond between two molecules is an attraction between a negative charge on one molecule and the positive charge on a hydrogen atom of the second molecule. (B) Hydrogen bonds can form between different parts of the same large molecule.

between two molecules. In these cases, the hydrogen bonds together have considerable strength, and greatly influence the structure and properties of substances. Later in this chapter we'll see how hydrogen bonding between water molecules contributes to many of the properties that make water so significant for living systems. Hydrogen bonds also play important roles in determining and maintaining the three-dimensional shapes of giant molecules such as DNA and proteins (see Section 3.2).

### Polar and nonpolar substances: Each interacts best with its own kind

Just as water molecules can interact with one another through hydrogen bonds, any molecule that is polar can interact with other polar molecules through the weak ( $\delta^+$  to  $\delta^-$ ) attractions of hydrogen bonds. If a polar molecule interacts with water in this way, it is called **hydrophilic** ("water-loving") (Figure 2.12A).



**2.12 Hydrophilic and Hydrophobic** (A) Molecules with polar covalent bonds are attracted to polar water (they are hydrophilic). (B) Molecules with nonpolar covalent bonds show greater attraction to one another than to water (they are hydrophobic).

Nonpolar molecules tend to interact with other nonpolar molecules. For example, carbon (electronegativity 2.5) forms nonpolar bonds with hydrogen (electronegativity 2.1), and molecules containing only hydrogen and carbon atoms—called *hydrocarbon molecules*—are nonpolar. In water these molecules tend to aggregate with one another rather than with the polar water molecules. Therefore, nonpolar molecules are known as **hydrophobic** (“water-hating”), and the interactions between them are called *hydrophobic interactions* (**Figure 2.12B**). Of course, hydrophobic substances do not really “hate” water; they can form weak interactions with it, since the electronegativities of carbon and hydrogen are not exactly the same. But these interactions are far weaker than the hydrogen bonds between the water molecules, so the nonpolar substances tend to aggregate.

The interactions between nonpolar substances are enhanced by **van der Waals forces**, which occur when the atoms of two nonpolar molecules are in close proximity. These brief interactions result from random variations in the electron distribution in one molecule, which create opposite charge distributions in the adjacent molecule. Although a single van der Waals interaction is brief and weak, the sum of many such interactions over the entire span of a large nonpolar molecule can result in substantial attraction. This makes nonpolar molecules stick together in the polar (aqueous) environment inside organisms. We will see this many times, for example in the structure of biological membranes.

## 2.2 RECAP

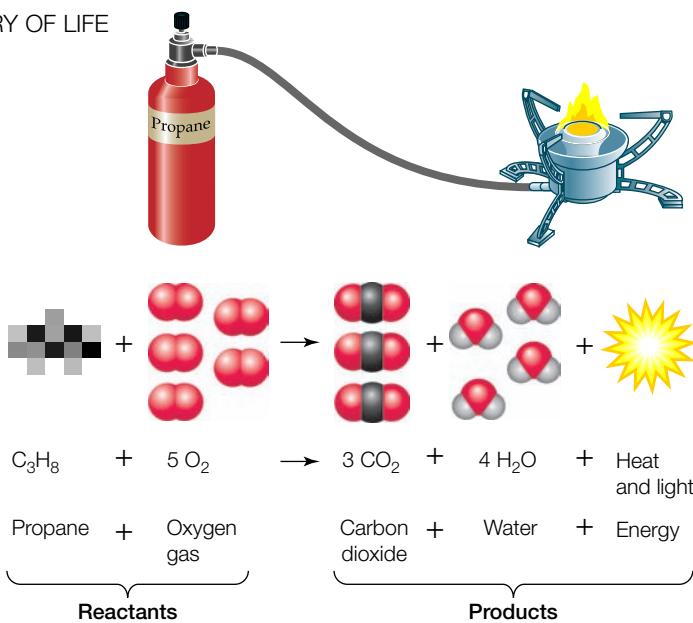
Some atoms form strong covalent bonds with other atoms by sharing one or more pairs of electrons. Unequal sharing of electrons produces polarity. Other atoms become ions by losing or gaining electrons, and they interact with other ions or polar molecules.

- Why is a covalent bond stronger than an ionic bond? **See pp. 26–28 and Table 2.1**
  - How do variations in electronegativity result in the unequal sharing of electrons in polar molecules? **See pp. 27–28 and Figure 2.8**
  - What is a hydrogen bond and how is it important in biological systems? **See p. 29 and Figure 2.11**

The bonding of atoms into molecules is not necessarily a permanent affair. The dynamic of life involves constant change, even at the molecular level. Let's look at how molecules interact with one another—how they break up, how they find new partners, and what the consequences of those changes can be.

## 2.3 How Do Atoms Change Partners in Chemical Reactions?

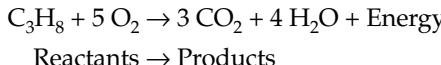
A **chemical reaction** occurs when moving atoms collide with sufficient energy to combine or change their bonding partners. Consider the combustion reaction that takes place in the flame of a propane stove. When propane ( $C_3H_8$ ) reacts with oxygen gas ( $O_2$ ), the carbon atoms become bonded to oxygen atoms instead



## 2.13 Bonding Partners and Energy May Change in a Chemical

**Reaction** One molecule of propane from this burner reacts with five molecules of oxygen gas to give three molecules of carbon dioxide and four molecules of water. This reaction releases energy in the form of heat and light.

of hydrogen atoms, and the hydrogen atoms become bonded to oxygen instead of carbon (**Figure 2.13**). As the covalently bonded atoms change partners, the composition of the matter changes; propane and oxygen gas become carbon dioxide and water. This chemical reaction can be represented by the equation



In this equation, the propane and oxygen are the **reactants**, and the carbon dioxide and water are the **products**. In fact, this is a special type of reaction called an oxidation-reduction reaction. Electrons and protons are transferred from propane (the reducing agent) to oxygen (the oxidizing agent) to form water. You will see this kind of reaction involving electron/proton transfer many times in later chapters.

The products of a chemical reaction have very different properties from the reactants. In the case shown in Figure 2.13, the reaction is *complete*: all the propane and oxygen are used up in forming the two products. The arrow symbolizes the direction of the chemical reaction. The numbers preceding the molecular formulas indicate how many molecules are used or produced.

Note that in this and all other chemical reactions, *matter is neither created nor destroyed*. The total number of carbon atoms on the left (3) equals the total number of carbon atoms on the right (3). In other words, the equation is *balanced*. However, there is another aspect of this reaction: the heat and light of the stove's flame reveal that the reaction between propane and oxygen releases a great deal of energy.

**Energy** is defined as the capacity to do work, but in the context of chemical reactions, it can be thought of as the capacity for change. Chemical reactions do not create or destroy energy, but *changes in the form of energy* usually accompany chemical reactions.

In the reaction between propane and oxygen, a large amount of heat energy is released. This energy was present in another form, called *potential chemical energy*, in the covalent bonds within

the propane and oxygen gas molecules. Not all reactions release energy; indeed, many chemical reactions require that energy be supplied from the environment. Some of this energy is then stored as potential chemical energy in the bonds formed in the products. We will see in future chapters how reactions that release energy and reactions that require energy can be linked together.

Many chemical reactions take place in living cells, and some of these have a lot in common with the oxidation-reduction reaction that happens in the combustion of propane. In cells, the reactants are different (they may be sugars or fats), and the reactions proceed by many intermediate steps that permit the released energy to be harvested and put to use by the cells. But the products are the same: carbon dioxide and water. We will discuss energy changes, oxidation-reduction reactions, and several other types of chemical reactions that are prevalent in living systems in Part Three of this book.

## 2.3 RECAP

In a chemical reaction, a set of reactants is converted to a set of products with different chemical compositions. This is accomplished by breaking and making bonds. Reactions may release energy or require its input.

- Explain how a chemical equation is balanced. See p. 30 and Figure 2.13
- How can the form of energy change during a chemical reaction? See p. 30

We will present and discuss energy changes, oxidation-reduction reactions, and several other types of chemical reactions that are prevalent in living systems in Part Two of this book. First, however, we must understand the unique properties of the substance in which most biochemical reactions take place: water.

## 2.4 What Makes Water So Important for Life?

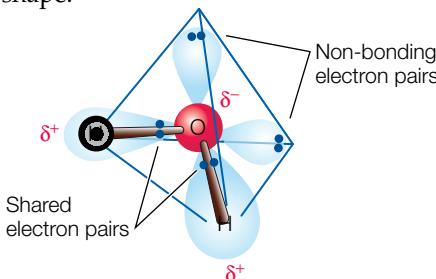
Water is an unusual substance with unusual properties. Under conditions on Earth, water exists in solid, liquid, and gas forms, all of which have relevance to living systems. Water allows chemical reactions to occur inside living organisms, and it is necessary for the formation of certain biological structures. In this section we will explore how the structure and interactions of water molecules make water essential to life.

### 2.14 Hydrogen Bonding and the Properties of Water

Hydrogen bonding exists between the molecules of water in both its liquid and solid states. Ice is more structured but less dense than liquid water, which is why ice floats. Water forms a gas when its hydrogen bonds are broken and the molecules move farther apart.

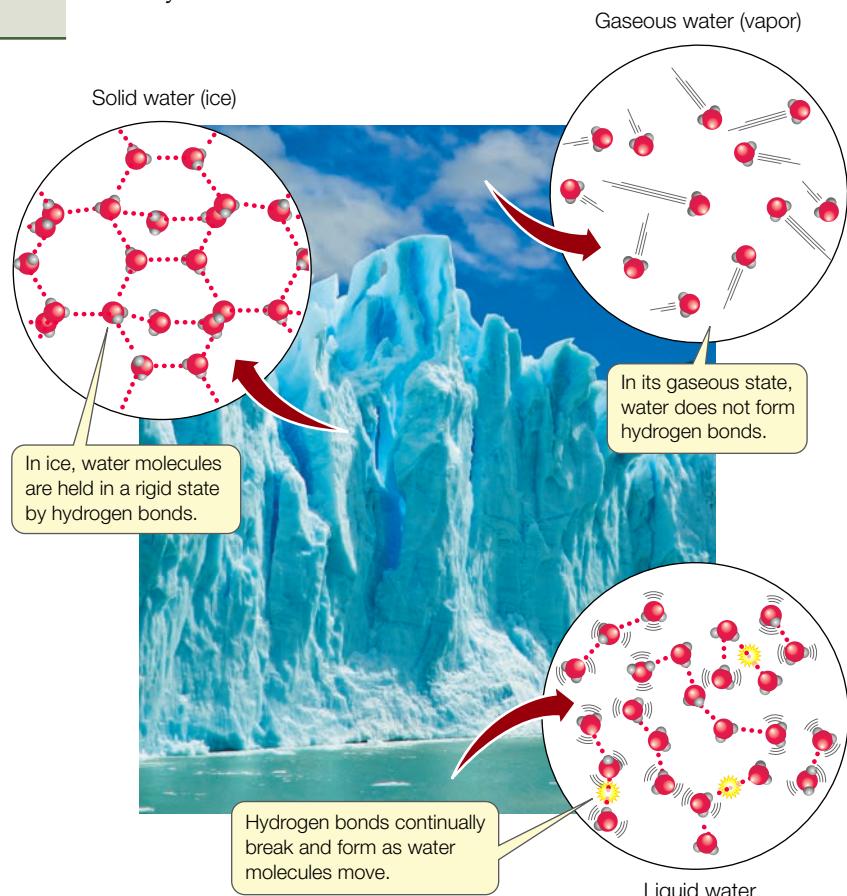
### Water has a unique structure and special properties

The molecule  $\text{H}_2\text{O}$  has unique chemical features. As we have already learned, water is a polar molecule that can form hydrogen bonds. The four pairs of electrons in the outer shell of the oxygen atom repel one another, giving the water molecule a tetrahedral shape:



These chemical features explain some of the interesting properties of water, such as the ability of ice to float, the melting and freezing temperatures of water, the ability of water to store heat, the formation of water droplets, and water's ability to dissolve—and not dissolve—many substances.

**ICE FLOATS** In water's solid state (ice), individual water molecules are held in place by hydrogen bonds. Each molecule is bonded to four other molecules in a rigid, crystalline structure (**Figure 2.14**). Although the molecules are held firmly in place, they are not as tightly packed as they are in liquid water. In other words, *solid water is less dense than liquid water*, which is why ice floats.



Think of the biological consequences if ice were to sink in water. A pond would freeze from the bottom up, becoming a solid block of ice in winter and killing most of the organisms living there. Once the whole pond is frozen, its temperature could drop well below the freezing point of water. But in fact ice floats, forming an insulating layer on the top of the pond, and reducing heat flow to the cold air above. Thus fish, plants, and other organisms in the pond are not subjected to temperatures lower than 0°C, which is the freezing point of pure water.

**MELTING, FREEZING, AND HEAT CAPACITY** Compared with many other substances that have molecules of similar size, ice requires a great deal of heat energy to melt. This is because so many hydrogen bonds must be broken in order for water to change from solid to liquid. In the opposite process—freezing—a great deal of energy is released to the environment.

This property of water contributes to the surprising constancy of the temperatures found in oceans and other large bodies of water throughout the year. The temperature changes of coastal land masses are also moderated by large bodies of water. Indeed, water helps minimize variations in atmospheric temperature across the planet. This moderating ability is a result of the high *heat capacity* of liquid water, which is in turn a result of its high specific heat.

The **specific heat** of a substance is the amount of heat energy required to raise the temperature of 1 gram of that substance by 1°C. Raising the temperature of liquid water takes a relatively large amount of heat because much of the heat energy is used to break the hydrogen bonds that hold the liquid together. Compared with other small molecules that are liquids, water has a high specific heat.

Water also has a high **heat of vaporization**, which means that a lot of heat is required to change water from its liquid to its gaseous state (the process of *evaporation*). Once again, much of the heat energy is used to break the many hydrogen bonds between the water molecules. This heat must be absorbed from the environment in contact with the water. Evaporation thus has a cooling effect on the environment—whether a leaf, a forest, or an entire land mass. This effect explains why sweating cools the human body: as sweat evaporates from the skin, it uses up some of the adjacent body heat.

**COHESION AND SURFACE TENSION** In liquid water, individual molecules are able to move about. The hydrogen bonds between the molecules continually form and break (see Figure 2.14). Chemists estimate that this occurs about a trillion times a minute for a single water molecule, making it a truly dynamic structure.

At any given time, a water molecule will form an average of 3.4 hydrogen bonds with other water molecules. These hydrogen bonds explain the *cohesive strength* of liquid water. This cohesive strength, or **cohesion**, is defined as the capacity of water molecules to resist coming apart from one another when placed under tension. Water's cohesive strength permits narrow columns of liquid water to move from the roots to the leaves of tall trees. When water evaporates from the leaves, the entire column moves upward in response to the pull of the molecules at the top.



**2.15 Surface Tension** Water droplets form “beads” on the surface of a leaf because hydrogen bonds keep the water molecules together. The leaf is coated in a nonpolar wax that does not interact with the water molecules.

The surface of liquid water exposed to the air is difficult to puncture because the water molecules at the surface are hydrogen-bonded to other water molecules below them (Figure 2.15). This *surface tension* of water permits a container to be filled slightly above its rim without overflowing, and it permits insects to walk on the surface of a pond.

### Water is an excellent solvent—the medium of life

A human body is over 70 percent water by weight, excluding the minerals contained in bones. Water is the dominant component of virtually all living organisms, and most biochemical reactions take place in this watery, or aqueous, environment.

A **solution** is produced when a substance (the **solute**) is dissolved in a liquid (the **solvent**). If the solvent is water, then the solution is an *aqueous solution*. Many of the important molecules in biological systems are polar, and therefore soluble in water. Many important biochemical reactions occur in aqueous solutions within cells. Biologists study these reactions in order to identify the reactants and products and to determine their amounts:

- *Qualitative analyses* deal with the identification of substances involved in chemical reactions. For example, a qualitative analysis would be used to investigate the steps involved, and the products formed, during the combustion of glucose in living tissues.
- *Quantitative analyses* measure concentrations or amounts of substances. For example, a biochemist would seek to describe *how much* of a certain product is formed during the combustion of a given amount of glucose using a quantitative analysis. What follows is a brief introduction to some of the quantitative chemical terms you will see in this book.

Fundamental to quantitative thinking in chemistry and biology is the concept of the mole. A **mole** is the amount of a substance (in grams) that is numerically equal to its molecular weight.

So a mole of table sugar ( $C_{12}H_{22}O_{11}$ ) weighs about 342 grams; a mole of sodium ion ( $Na^+$ ) weighs 23 grams; and a mole of hydrogen gas ( $H_2$ ) weighs 2 grams.

Quantitative analyses do not yield direct counts of molecules. Because the amount of a substance in 1 mole is directly related to its molecular weight, it follows that the number of molecules in 1 mole is constant for all substances. So 1 mole of salt contains the same number of molecules as 1 mole of table sugar. This constant number of molecules in a mole is called **Avogadro's number**, and it is  $6.02 \times 10^{23}$  molecules per mole. Chemists work with moles of substances (which can be weighed out in the laboratory) instead of actual molecules (which are too numerous to be counted). Consider 34.2 grams (just over 1 ounce) of table sugar,  $C_{12}H_{22}O_{11}$ . This is one-tenth of a mole, or as Avogadro puts it,  $6.02 \times 10^{22}$  molecules.

If you have trouble grasping the concept of a mole, compare it with the concept of a dozen. We buy a dozen eggs or a dozen doughnuts, knowing that we will get 12 of whichever we buy, even though they don't weigh the same or take up the same amount of space.

A chemist can dissolve a mole of sugar (342 g) in water to make 1 liter of solution, knowing that the mole contains  $6.02 \times 10^{23}$  individual sugar molecules. This solution—1 mole of a substance dissolved in water to make 1 liter—is called a 1 molar (1 M) solution. When a physician injects a certain molar concentration of a drug into the bloodstream of a patient, a rough calculation can be made of the actual number of drug molecules that will interact with the patient's cells.

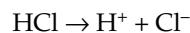
The many molecules dissolved in the water of living tissues are not present at concentrations anywhere near 1 molar. Most are in the micromolar (millionths of a mole per liter of solution;  $\mu M$ ) to millimolar (thousandths of a mole per liter; mM) range. Some, such as hormone molecules, are even less concentrated than that. While these molarities seem to indicate very low concentrations, remember that even a 1  $\mu M$  solution has  $6.02 \times 10^{17}$  molecules of the solute per liter.

### Aqueous solutions may be acidic or basic

When some substances dissolve in water, they release *hydrogen ions* ( $H^+$ ), which are actually single, positively charged protons. Hydrogen ions can attach to other molecules and change their properties. For example, the protons in "acid rain" can damage plants, and you probably have experienced the excess of hydrogen ions that we call "acid indigestion."

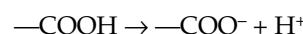
Here we will examine the properties of **acids** (defined as substances that release  $H^+$ ) and **bases** (defined as substances which accept  $H^+$ ). We will distinguish between strong and weak acids and bases and provide a quantitative means for stating the concentration of  $H^+$  in solutions: the pH scale.

**ACIDS RELEASE  $H^+$**  When hydrochloric acid (HCl) is added to water, it dissolves, releasing the ions  $H^+$  and  $Cl^-$ :



Because its  $H^+$  concentration has increased, such a solution is *acidic*.

Acids are substances that *release  $H^+$*  ions in solution. HCl is an acid, as is  $H_2SO_4$  (sulfuric acid). One molecule of sulfuric acid will ionize to yield two  $H^+$  and one  $SO_4^{2-}$ . Biological compounds that contain  $-COOH$  (the carboxyl group) are also acids because



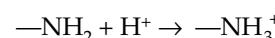
Acids that fully ionize in solution, such as HCl and  $H_2SO_4$  are called *strong acids*. However, not all acids ionize fully in water. For example, if acetic acid ( $CH_3COOH$ ) is added to water, some will dissociate into two ions ( $CH_3COO^-$  and  $H^+$ ), but some of the original acetic acid remains as well. Because the reaction is *not complete*, acetic acid is a *weak acid*.

**BASES ACCEPT  $H^+$**  Bases are substances that *accept  $H^+$*  in solution. Just as with acids, there are strong and weak bases. If NaOH (sodium hydroxide) is added to water, it dissolves and ionizes, releasing  $OH^-$  and  $Na^+$  ions:

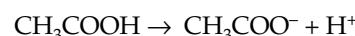


Because the concentration of  $OH^-$  increases and  $OH^-$  absorbs  $H^+$  to form water ( $OH^- + H^+ \rightarrow H_2O$ ), such a solution is *basic*. Because this reaction is complete, NaOH is a *strong base*.

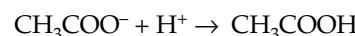
Weak bases include the bicarbonate ion ( $HCO_3^-$ ), which can accept a  $H^+$  ion and become carbonic acid ( $H_2CO_3$ ), and ammonia ( $NH_3$ ), which can accept a  $H^+$  and become an ammonium ion ( $NH_4^+$ ). Biological compounds that contain  $-NH_2$  (the amino group) are also bases because



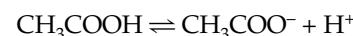
**ACID-BASE REACTIONS MAY BE REVERSIBLE** When acetic acid is dissolved in water, two reactions happen. First, the acetic acid forms its ions:



Then, once the ions are formed, some of them re-form acetic acid:



This pair of reactions is reversible. A **reversible reaction** can proceed in either direction—left to right or right to left—depending on the relative starting concentrations of the reactants and products. The formula for a reversible reaction can be written using a double arrow:

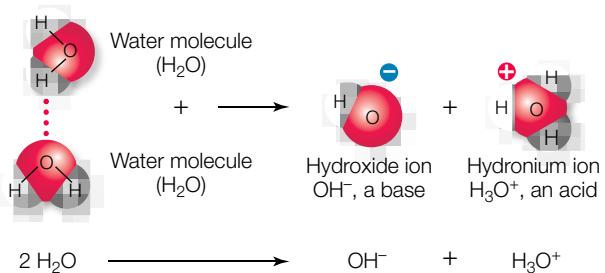


In terms of acids and bases, there are two types of reactions, depending on the extent of the reversibility:

- The ionization of strong acids and bases in water is virtually irreversible.
- The ionization of weak acids and bases in water is somewhat reversible.

**WATER IS A WEAK ACID AND A WEAK BASE** The water molecule has a slight but significant tendency to ionize into a hydroxide ion ( $OH^-$ ) and a hydrogen ion ( $H^+$ ). Actually, two water molecules

participate in this reaction. One of the two molecules “captures” a hydrogen ion from the other, forming a hydroxide ion and a hydronium ion:



The hydronium ion is, in effect, a hydrogen ion bound to a water molecule. For simplicity, biochemists tend to use a modified representation of the ionization of water:



The ionization of water is important to all living creatures. This fact may seem surprising, since only about one water molecule in 500 million is ionized at any given time. But this is less surprising if we focus on the abundance of water in living systems, and the reactive nature of the  $\text{H}^+$  ions produced by ionization.

**pH: HYDROGEN ION CONCENTRATION** Compounds or ions can be acids or bases, and thus, solutions can be acidic or basic. We can measure how acidic or basic a solution is by measuring its concentration of  $\text{H}^+$  in moles per liter (its *molarity*; see page 33). Here are some examples:

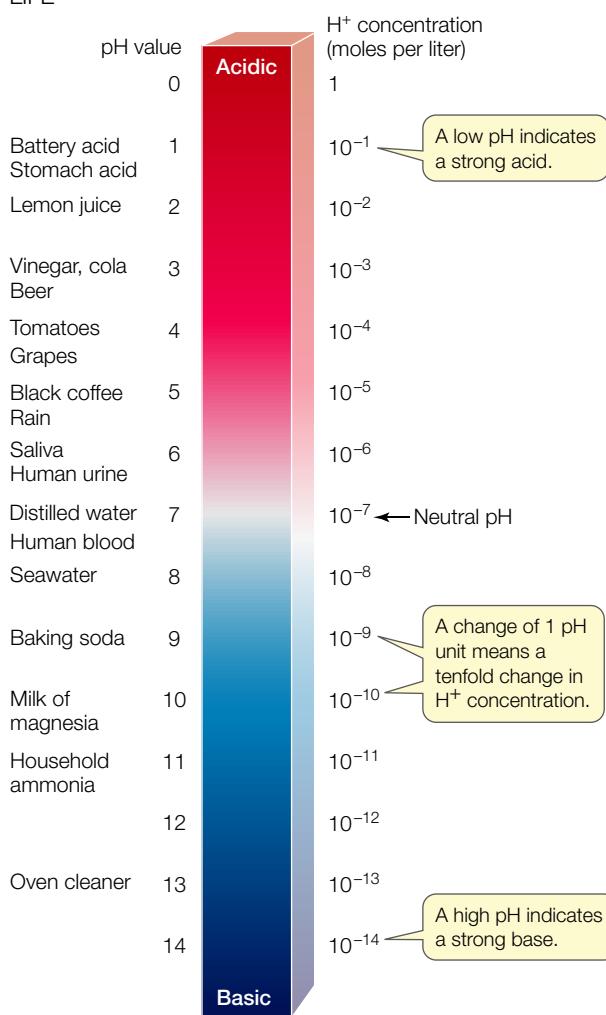
- Pure water has a  $\text{H}^+$  concentration of  $10^{-7} \text{ M}$ .
- A 1 M HCl solution has a  $\text{H}^+$  concentration of 1 M (recall that all the HCl dissociates into its ions).
- A 1 M NaOH solution has a  $\text{H}^+$  concentration of  $10^{-14} \text{ M}$ .

This is a very wide range of numbers to work with—think about the decimals! It is easier to work with the *logarithm* of the  $\text{H}^+$  concentration, because logarithms compress this range: the  $\log_{10}$  of 100, for example is 2, and the  $\log_{10}$  of 0.01 is -2. Because most  $\text{H}^+$  concentrations in living systems are less than 1M, their  $\log_{10}$  values are negative. For convenience, we convert these negative numbers into positive ones, by using the *negative* of the logarithm of the  $\text{H}^+$  molar concentration (the molar concentration is designated by square brackets:  $[\text{H}^+]$ ). This number is called the **pH** of the solution.

Since the  $\text{H}^+$  concentration of pure water is  $10^{-7} \text{ M}$ , its pH is  $-\log(10^{-7}) = -(−7)$ , or 7. A smaller negative logarithm means a larger number. In practical terms, a lower pH means a higher  $\text{H}^+$  concentration, or greater acidity. In 1 M HCl, the  $\text{H}^+$  concentration is 1 M, so the pH is the negative logarithm of 1 ( $-\log 10^0$ ), or 0. The pH of 1 M NaOH is the negative logarithm of  $10^{-14}$ , or 14.

A solution with a pH of less than 7 is acidic—it contains more  $\text{H}^+$  ions than  $\text{OH}^-$  ions. A solution with a pH of 7 is *neutral* (without net charge), and a solution with a pH value greater than 7 is basic. **Figure 2.16** shows the pH values of some common substances.

Why is this discussion of pH so important in biology? Many biologically important molecules contain charged groups



## 2.16 pH Values of Some Familiar Substances

(e.g.,  $-\text{COO}^-$ ) that can interact with the polar regions of water to form their structures. But these groups can combine with  $\text{H}^+$  or other ions in their environment to form uncharged groups (e.g.,  $-\text{COOH}$ , see above). These uncharged groups have much less tendency to interact with water. If such a group is part of a larger molecule, it might now induce the molecule to fold in such a way that it stays away from water because it is hydrophobic. In a more acidic environment, a negatively charged group such as  $-\text{COO}^-$  is more likely to combine with  $\text{H}^+$ . So the pH of a biological tissue is a key to the three-dimensional structures of many of its constituent molecules. Organisms do all they can to minimize changes in the pH of their watery medium. An important way to do this is with buffers.

**BUFFERS** The maintenance of internal constancy—*homeostasis*—is a hallmark of all living things and extends to pH. As we mentioned earlier, if biological molecules lose or gain  $\text{H}^+$  ions their properties can change, thus upsetting homeostasis. Internal constancy is achieved with buffers: solutions that maintain a relatively constant pH even when substantial amounts of acid or base are added. How does this work?

A **buffer** is a solution of a weak acid and its corresponding base—for example, carbonic acid ( $\text{H}_2\text{CO}_3$ ) and bicarbonate ions ( $\text{HCO}_3^-$ ). If an acid is added to a solution containing this buffer,

**2.17 Buffers Minimize Changes in pH** With increasing amounts of added base, the overall slope of a graph of pH is downward. Without a buffer, the slope is steep. Inside the buffering range of an added buffer, however, the slope is shallow. At very high and very low values of pH, where the buffer is ineffective, the slopes are much steeper.

not all the  $\text{H}^+$  ions from the acid stay in solution. Instead, many of them combine with the bicarbonate ions to produce more carbonic acid:



This reaction uses up some of the  $\text{H}^+$  ions in the solution and decreases the acidifying effect of the added acid. If a base is added, the reaction essentially reverses. Some of the carbonic acid ionizes to produce bicarbonate ions and more  $\text{H}^+$ , which counteracts some of the added base. In this way, the buffer minimizes the effect that an added acid or base has on pH. This buffering system is present in the blood, where it is important for preventing significant changes in pH that could disrupt the ability of the blood to carry vital oxygen to tissues. A given amount of acid or base causes a smaller pH change in a buffered solution than in a non-buffered one (Figure 2.17).

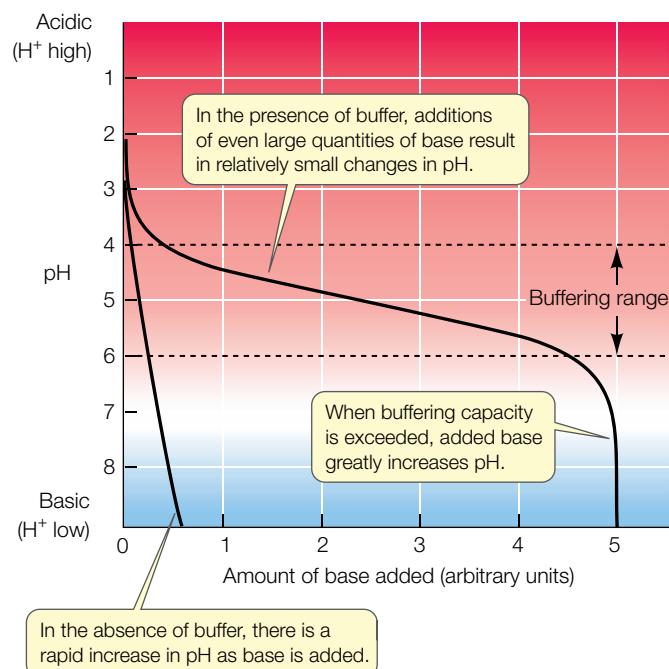
Buffers illustrate an important chemical principle of reversible reactions, called the *law of mass action*. Addition of a reactant on one side of a reversible system drives the reaction in the direction that uses up that compound. In the case of buffers, addition of an acid drives the reaction in one direction; addition of a base drives the reaction in the other direction.

We use a buffer to relieve the common problem of indigestion. The lining of the stomach constantly secretes hydrochloric acid, making the stomach contents acidic. Excessive stomach acid inhibits digestion and causes discomfort. We can relieve this discomfort by ingesting a salt such as  $\text{NaHCO}_3$  ("bicarbonate of soda"), which acts as a buffer.

## 2.4 RECAP

Most of the chemistry of life occurs in water, which has molecular properties that make it suitable for its important biochemical roles. A special property of water is its ability to ionize (release hydrogen ions). The presence of hydrogen ions in solution can change the properties of biological molecules.

- Describe some of the biologically important properties of water arising from its molecular structure. See pp. 31–32 and Figure 2.14
- What is a solution, and why do we call water "the medium of life"? See pp. 32–33
- What is the relationship between hydrogen ions, acids, and bases? Explain what the pH scale measures. See pp. 33–34 and Figure 2.16
- How does a buffer work, and why is buffering important to living systems? See pp. 34–35 and Figure 2.17



## An Overview and a Preview

Now that we have covered the major properties of atoms and molecules, let's review them and see how these properties relate to the major molecules of biological systems.

- *Molecules vary in size.* Some are small, such as those of hydrogen gas ( $\text{H}_2$ ) and methane ( $\text{CH}_4$ ). Others are larger, such as a molecule of table sugar ( $\text{C}_{12}\text{H}_{22}\text{O}_{11}$ ), which has 45 atoms. Still others, especially proteins and nucleic acids, are gigantic, containing tens of thousands or even millions of atoms.
- *All molecules have a specific three-dimensional shape.* For example, the orientations of the bonding orbitals around the carbon atom give the methane molecule ( $\text{CH}_4$ ) the shape of a regular tetrahedron (see Figure 2.7B). Larger molecules have complex shapes that result from the numbers and kinds of atoms present, and the ways in which they are linked together. Some large molecules, such as the protein hemoglobin (the oxygen carrier in red blood cells), have compact, ball-like shapes. Others, such as the protein called keratin that makes up your hair, have long, thin, ropelike structures. Their shapes relate to the roles these molecules play in living cells.
- *Molecules are characterized by certain chemical properties* that determine their biological roles. Chemists use the characteristics of composition, structure (three-dimensional shape), reactivity, and solubility to distinguish a pure sample of one molecule from a sample of a different molecule. The presence of certain groups of atoms can impart distinctive chemical properties to a molecule.

Between the small molecules discussed in this chapter and the world of the living cell are the macromolecules. These larger molecules—proteins, lipids, carbohydrates, and nucleic acids—will be discussed in the next two chapters.

## CHAPTER SUMMARY

### 2.1 How Does Atomic Structure Explain the Properties of Matter?

- Matter is composed of atoms. Each **atom** consists of a positively charged **nucleus** made up of **protons** and **neutrons**, surrounded by **electrons** bearing negative charges. **Review Figure 2.1**
- The number of protons in the nucleus defines an **element**. There are many elements in the universe, but only a few of them make up the bulk of living organisms: C, H, O, P, N, and S. **Review Figure 2.2**
- Isotopes** of an element differ in their numbers of neutrons. **Radioisotopes** are radioactive, emitting radiation as they break down.
- Electrons are distributed in **shells**, which are volumes of space defined by specific numbers of orbitals. Each **orbital** contains a maximum of two electrons. **Review Figures 2.4 and 2.5**, **WEB ACTIVITY 2.1**
- In losing, gaining, or sharing electrons to become more stable, an atom can combine with other atoms to form a **molecule**.

### 2.2 How Do Atoms Bond to Form Molecules?

#### SEE ANIMATED TUTORIAL 2.1

- A **chemical bond** is an attractive force that links two atoms together in a molecule. **Review Table 2.1**
- A **compound** is a substance made up of molecules with two or more elements bonded together in a fixed ratio, such as water ( $\text{H}_2\text{O}$ ) or table sugar ( $\text{C}_6\text{H}_{12}\text{O}_6$ ).
- Covalent bonds** are strong bonds formed when two atoms share one or more pairs of electrons. **Review Figure 2.6**
- When two atoms of unequal electronegativity bond with each other, a **polar** covalent bond is formed. The two ends, or poles, of the bond have partial charges ( $\delta^+$  or  $\delta^-$ ). **Review Figure 2.8**
- Ions** are electrically charged bodies that form when an atom gains or loses one or more electrons in order to form more stable electron configurations. **Anions** and **cations** are negatively and positively charged ions, respectively. Different charges attract, and like charges repel each other.
- Ionic bonds** are electrical attractions between oppositely charged ions. Ionic bonds are strong in solids (salts), but weaken when the ions are separated from one another in solution. **Review Figure 2.9**
- A **hydrogen bond** is a weak electrical attraction that forms between a  $\delta^+$  hydrogen atom in one molecule and a  $\delta^-$  atom in another molecule (or in another part of a large molecule). Hydrogen bonds are abundant in water.

- Nonpolar molecules interact very little with polar molecules, including water. Nonpolar molecules are attracted to one another by very weak bonds called **van der Waals forces**.

### 2.3 How Do Atoms Change Partners in Chemical Reactions?

- In **chemical reactions**, atoms combine or change their bonding partners. **Reactants** are converted into **products**.
- Some chemical reactions release **energy** as one of their products; other reactions can occur only if energy is provided to the reactants.
- Neither matter nor energy is created or destroyed in a chemical reaction, but both change form. **Review Figure 2.13**
- Some chemical reactions, especially in biology, are reversible. That is, the products formed may be converted back to the reactants.
- In living cells, chemical reactions take place in multiple steps so that the released energy can be harvested for cellular activities.

### 2.4 What Makes Water So Important for Life?

- Water's molecular structure and its capacity to form hydrogen bonds give it unique properties that are significant for life. **Review Figure 2.14**
- The high **specific heat** of water means that water gains or loses a great deal of heat when it changes state. Water's high **heat of vaporization** ensures effective cooling when water evaporates.
- The **cohesion** of water molecules refers to their capacity to resist coming apart from one another. Hydrogen bonds between water molecules play an essential role in these properties.
- A **solution** is produced when a solid substance (the **solute**) dissolves in a liquid (the **solvent**). Water is the critically important solvent for life.
- Acids** are solutes that release hydrogen ions in aqueous solutions. **Bases** accept hydrogen ions.
- The **pH** of a solution is the negative logarithm of its hydrogen ion concentration. Values lower than pH 7 indicate that a solution is acidic; values above pH 7 indicate a basic solution. **Review Figure 2.16**
- A **buffer** is a mixture of a weak acid and a base that limits changes in the pH of a solution when acids or bases are added.

## SELF-QUIZ

- The atomic number of an element
  - equals the number of neutrons in an atom.
  - equals the number of protons in an atom.
  - equals the number of protons minus the number of neutrons.
  - equals the number of neutrons plus the number of protons.
  - depends on the isotope.
- The atomic weight (atomic mass) of an element
  - equals the number of neutrons in an atom.
  - equals the number of protons in an atom.
  - equals the number of electrons in an atom.
  - equals the number of neutrons plus the number of protons.
  - depends on the relative abundances of its electrons and neutrons.
- Which of the following statements about the isotopes of an element is *not* true?
  - They all have the same atomic number.
  - They all have the same number of protons.
  - They all have the same number of neutrons.
  - They all have the same number of electrons.
  - They all have identical chemical properties.

4. Which of the following statements about covalent bonds is *not* true?
  - a. A covalent bond is stronger than a hydrogen bond.
  - b. A covalent bond can form between atoms of the same element.
  - c. Only a single covalent bond can form between two atoms.
  - d. A covalent bond results from the sharing of electrons by two atoms.
  - e. A covalent bond can form between atoms of different elements.
5. Hydrophobic interactions
  - a. are stronger than hydrogen bonds.
  - b. are stronger than covalent bonds.
  - c. can hold two ions together.
  - d. can hold two nonpolar molecules together.
  - e. are responsible for the surface tension of water.
6. Which of the following statements about water is *not* true?
  - a. It releases a large amount of heat when changing from liquid into vapor.
  - b. Its solid form is less dense than its liquid form.
  - c. It is the most effective solvent for polar molecules.
  - d. It is typically the most abundant substance in a living organism.
  - e. It takes part in some important chemical reactions.
7. The reaction  $\text{HCl} \rightarrow \text{H}^+ + \text{Cl}^-$  in the human stomach is an example of the
  - a. cleavage of a hydrophobic bond.
  - b. formation of a hydrogen bond.
  - c. elevation of the pH of the stomach.
  - d. formation of ions by dissolving an acid.
  - e. formation of polar covalent bonds.
8. The hydrogen bond between two water molecules arises because water is
  - a. polar.
  - b. nonpolar.
  - c. a liquid.
  - d. small.
  - e. hydrophobic.
9. When table salt ( $\text{NaCl}$ ) is added to water,
  - a. a covalent bond is broken.
  - b. an acidic solution is formed.
  - c. the  $\text{Na}^+$  and  $\text{Cl}^-$  ions are separated.
  - d. the  $\text{Na}^+$  ions are attracted to the hydrogen atoms of water.
  - e. water molecules surround the  $\text{Na}^+$  (but not  $\text{Cl}^-$ ) ions.
10. The three most abundant elements in a human skin cell are
  - a. calcium, carbon, and oxygen.
  - b. carbon, hydrogen, and oxygen.
  - c. carbon, hydrogen, and sodium.
  - d. carbon, nitrogen, and potassium.
  - e. nitrogen, hydrogen, and argon.

## FOR DISCUSSION

1. Using the information in the periodic table (Figure 2.2), draw a Bohr model (see Figures 2.5 and 2.7) of silicon dioxide, showing electrons shared in covalent bonds.
2. Compare a covalent bond between two hydrogen atoms with a hydrogen bond between a hydrogen and an oxygen atom, with regard to the electrons involved, the role of polarity, and the strength of the bond.
3. Write an equation describing the combustion of glucose ( $\text{C}_6\text{H}_{12}\text{O}_6$ ) to produce carbon dioxide and water.
4. The pH of the human stomach is about 2.0, while the pH of the small intestine is about 10.0. What are the hydrogen ion concentrations  $[\text{H}^+]$  inside these two organs?

## ADDITIONAL INVESTIGATION

Would you expect the elemental composition of Earth's crust to be the same as that of the human body? How could you find out?



# 3

# Proteins, Carbohydrates, and Lipids

## Molecular fossils

**A**bout 68 million years ago, a *Tyrannosaurus rex*, the fearsome dinosaur of movie stardom, died in what is now Wyoming in the United States. Over time, the giant carcass became buried 60 feet below the surface of what geologists call the Hell Creek Formation. In 2003, a thigh bone from the long-dead beast was found by the famous dinosaur hunter/biologist, John Horner from the Museum of the Rockies. Mary Schweitzer, a molecular paleontologist, was visiting Horner's Montana lab from North Carolina State University. She cut into the bone and found that it contained the remnants of soft tissues (such as bone marrow). This discovery was remark-

able, because up until then scientists had thought that after about a million years, all the soft tissues in bone were replaced with minerals.

Back on the east coast, Lewis Cantley, a biochemist at Harvard University, read about Schweitzer's find in a newspaper and saw the possibility for a unique opportunity: for the first time, a scientist would be able to isolate and study the complex molecules of soft tissues from an extinct organism. He asked Schweitzer to send him a sample, and when he and his colleagues analyzed the dinosaur material, they found fragments of protein molecules.

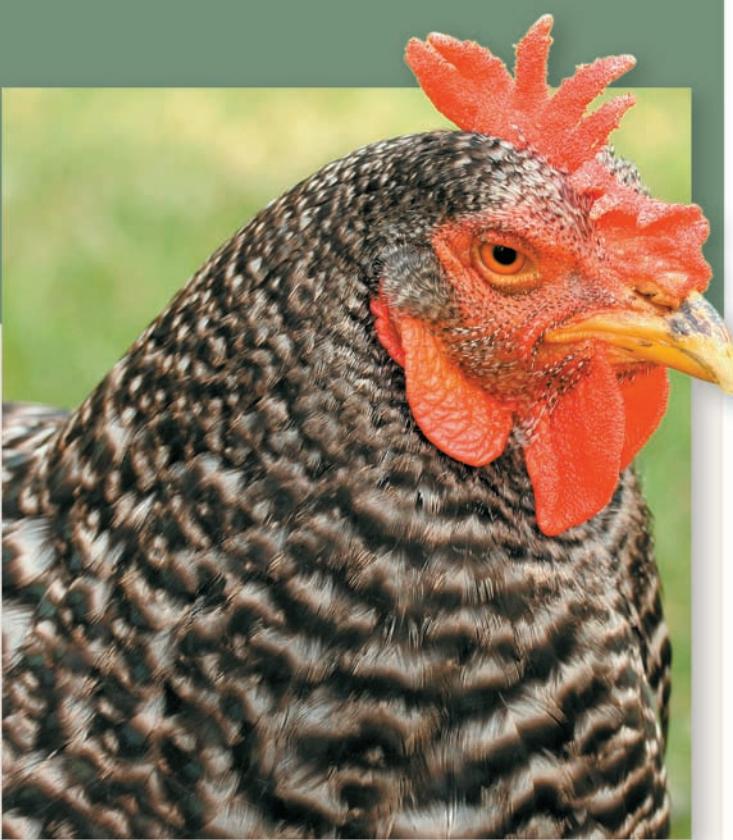
Protein molecules are composed of long chains of individual molecules called amino acids. The protein frag-

ments extracted from the *T. rex* bone were identified as collagen, a substance found in many modern animals. Moreover, the identity and specific order of the amino acids in the dinosaur collagen fragments closely matched that of collagen from chickens, and the dinosaur collagen folded into shapes very similar to those of bird collagen. This similarity to birds is not surprising, because, based on other evidence, scientists believe that birds are evolutionarily closely related to dinosaurs. Cantley's molecular analysis further confirmed this belief.

Proteins are one of the four major kinds of large molecules that characterize living systems. These *macromolecules*, which also include *carbohydrates*, *lipids*, and *nucleic acids*, differ in several significant ways from the small molecules and ions described in Chapter 2. First—no surprise—they are larger; the molecular weights of some



**Molecular Clues** A thigh bone from a *Tyrannosaurus rex* that died 68 million years ago contained fragments of the protein collagen.



**Molecular Evolution** The sequence of amino acids in collagen dictates the shape the protein folds into. Collagen's amino acid sequence is similar in *T. rex* and in chickens, indicating that the two species share a common evolutionary ancestor.

nucleic acids reach billions of daltons. Second, these molecules all contain carbon atoms, and so belong to a group of what are known as *organic* chemicals. Third, the atoms of individual macromolecules are held together mostly by covalent bonds, which gives them important structural stability and distinctive three-dimensional geometries. These distinctive shapes are the basis of many of the functions of macromolecules, particularly the proteins.

Finally, carbohydrates, proteins, lipids, and nucleic acids are all unique to the living world. None of these molecular classes occurs in inanimate nature. You aren't likely to find protein in a rock—but if you do, you can be sure it came from a living organism.

**IN THIS CHAPTER** we will describe the chemical and biological properties of proteins, carbohydrates, and lipids. We will identify the components that make up these larger molecules, describe their assembly and geometries, as well as the roles they play in living organisms.

## CHAPTER OUTLINE

- 3.1 What Kinds of Molecules Characterize Living Things?**
- 3.2 What Are the Chemical Structures and Functions of Proteins?**
- 3.3 What Are the Chemical Structures and Functions of Carbohydrates?**
- 3.4 What Are the Chemical Structures and Functions of Lipids?**

### 3.1 What Kinds of Molecules Characterize Living Things?

Four kinds of molecules are characteristic of living things: proteins, carbohydrates, lipids, and nucleic acids. With the exception of the lipids, these *biological molecules* are **polymers** (*poly*, “many”; *mer*, “unit”) constructed by the covalent bonding of smaller molecules called **monomers**. The monomers that make up each kind of biological molecule have similar chemical structures:

- *Proteins* are formed from different combinations of 20 *amino acids*, all of which share chemical similarities.
- *Carbohydrates* can form giant molecules by linking together chemically similar sugar monomers (*monosaccharides*) to form polysaccharides.
- *Nucleic acids* are formed from four kinds of nucleotide monomers linked together in long chains.
- *Lipids* also form large structures from a limited set of smaller molecules, but in this case noncovalent forces maintain the interactions between the lipid monomers.

Polymers with molecular weights exceeding 1,000 grams per mole are considered to be **macromolecules**. The proteins, carbohydrates, and nucleic acids of living systems certainly fall into this category. Although large lipid structures are not polymers in the strictest sense, it is convenient to treat them as a special type of macromolecule (see Section 3.4).

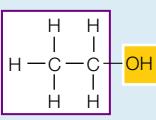
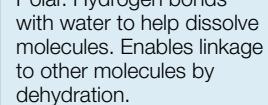
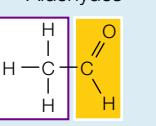
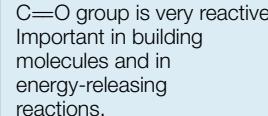
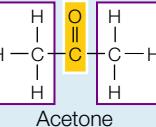
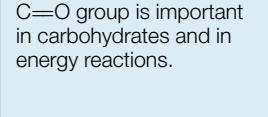
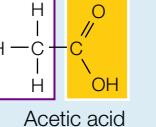
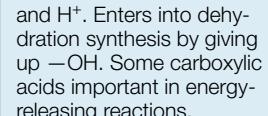
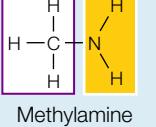
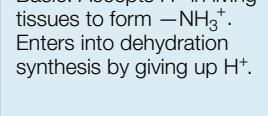
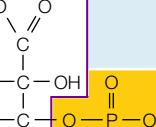
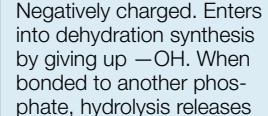
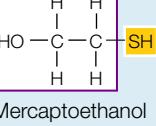
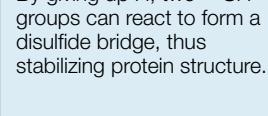
How the macromolecules function and interact with other molecules depends on the properties of certain chemical groups in their monomers, the *functional groups*.

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**GO TO** Animated Tutorial 3.1 • Macromolecules

**Functional groups give specific properties to biological molecules**

Certain small groups of atoms, called **functional groups**, are consistently found together in very different biological molecules. You will encounter several functional groups repeatedly in your study of biology (Figure 3.1). Each functional group has specific chemical properties and, when it is attached to a larger molecule, it confers those properties on the larger molecule. One of these properties is polarity. Looking at the structures in Figure 3.1, can you determine which functional groups are the most

Functional group	Class of compounds and an example	Properties
Hydroxyl	Alcohols  Ethanol 	Polar. Hydrogen bonds with water to help dissolve molecules. Enables linkage to other molecules by dehydration.
Aldehyde	Aldehydes  Acetaldehyde 	C=O group is very reactive. Important in building molecules and in energy-releasing reactions.
Keto	Ketones  Acetone 	C=O group is important in carbohydrates and in energy reactions.
Carboxyl	Carboxylic acids  Acetic acid 	Acidic. Ionizes in living tissues to form $\text{COO}^-$ and $\text{H}^+$ . Enters into dehydration synthesis by giving up $\text{OH}$ . Some carboxylic acids important in energy-releasing reactions.
Amino	Amines  Methylamine 	Basic. Accepts $\text{H}^+$ in living tissues to form $\text{NH}_3^+$ . Enters into dehydration synthesis by giving up $\text{H}^+$ .
Phosphate	Organic phosphates  3-Phosphoglycerate 	Negatively charged. Enters into dehydration synthesis by giving up $\text{OH}$ . When bonded to another phosphate, hydrolysis releases much energy.
Sulfhydryl	Thiols  Mercaptoethanol 	By giving up H, two $\text{SH}$ groups can react to form a disulfide bridge, thus stabilizing protein structure.

polar? (Hint: Look for C—O, N—H, and P—O bonds.) The consistent chemical behavior of functional groups helps us understand the properties of the molecules that contain them.

Because macromolecules are so large, they contain many different functional groups (see Figure 3.1). A single large protein may contain hydrophobic, polar, and charged functional groups, each of which gives different specific properties to local sites on the macromolecule. As we will see, sometimes these

### 3.1 Some Functional Groups Important to Living Systems

Highlighted here are the seven functional groups most commonly found in biologically important molecules. “R” is a variable chemical grouping.

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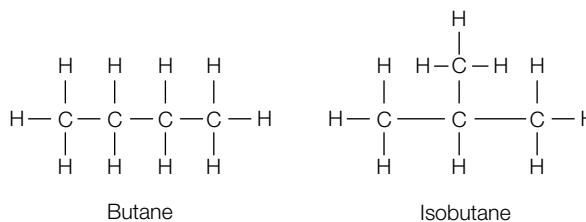
GO TO Web Activity 3.1 • Functional Groups

different groups interact on the same macromolecule. These diverse groups and their properties help determine the shapes of macromolecules as well as how they interact with other macromolecules and with smaller molecules.

### Isomers have different arrangements of the same atoms

**Isomers** are molecules that have the same chemical formula—the same kinds and numbers of atoms—but the atoms are arranged differently. (The prefix *iso-*, meaning “same,” is encountered in many biological terms.) Of the different kinds of isomers, we will consider two: structural isomers and optical isomers.

**Structural isomers** differ in how their atoms are joined together. Consider two simple molecules, each composed of four carbon and ten hydrogen atoms bonded covalently, both with the formula  $\text{C}_4\text{H}_{10}$ . These atoms can be linked in two different ways, resulting in different molecules:

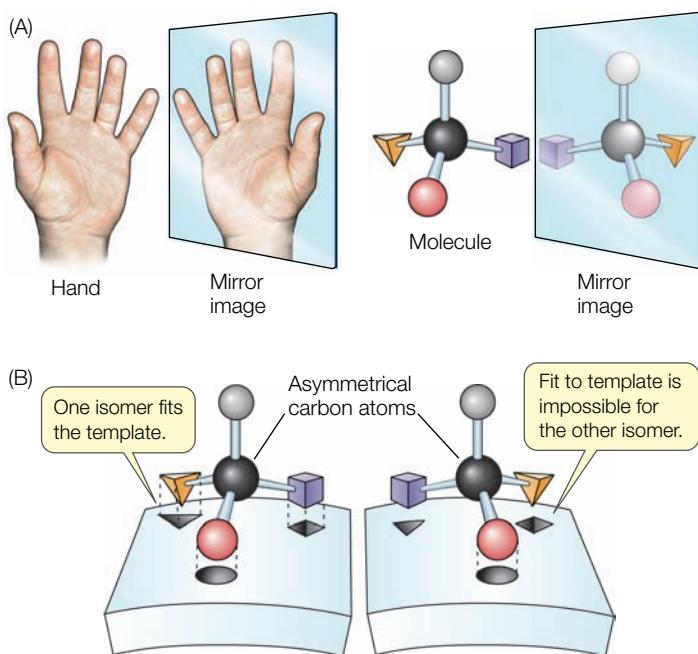


The different bonding relationships in butane and isobutane are distinguished by their structural formulas, and the two molecules have different chemical properties.

**Optical isomers** occur when a carbon atom has four different atoms or groups of atoms attached to it. This pattern allows two different ways of making the attachments, each the mirror image of the other (Figure 3.2). Such a carbon atom is called an *asymmetrical carbon*, and the two resulting molecules are optical isomers of each other. You can envision your right and left hands as optical isomers. Just as a glove is specific for a particular hand, some biochemical molecules that can interact with one optical isomer of a carbon compound are unable to “fit” the other.

### The structures of macromolecules reflect their functions

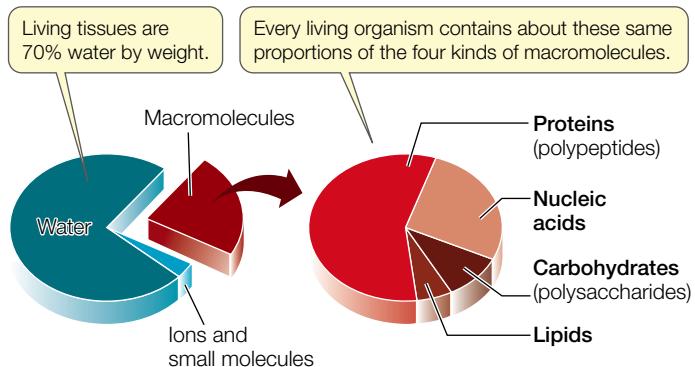
The four kinds of biological macromolecules are present in roughly the same proportions in all living organisms (Figure 3.3). Furthermore, a protein that has a certain function in an apple tree probably has a similar function in a human being because its chemistry is the same wherever it is found. Such *biochemical unity* reflects the evolution of all life from a common ancestor, by descent with modification. An important advantage of biochemical unity is that some organisms can acquire



**3.2 Optical Isomers** (A) Optical isomers are mirror images of each other. (B) Molecular optical isomers result when four different atoms or groups are attached to a single carbon atom. If a template (representing a larger biological molecule in a living system) is laid out to match the groups on one carbon atom, the groups on that carbon's optical isomer cannot be rotated to fit the same template. This is a source of specificity in biological structure and biochemical transformations.

needed raw materials by eating other organisms. When you eat an apple, the molecules you take in include carbohydrates, lipids, and proteins that can be broken down and rebuilt into the varieties of those molecules needed by humans.

Each type of macromolecule performs some combination of functions, such as energy storage, structural support, protection, catalysis (speeding up a chemical reaction), transport, defense, regulation, movement, and information storage. These roles are not necessarily exclusive; for example, both carbohydrates and proteins can play structural roles, supporting and protecting tissues and organs. However, only the nucleic acids specialize in



**3.3 Substances Found in Living Tissues** The substances shown here make up the nonmineral components of living tissues (bone would be an example of a mineral component).

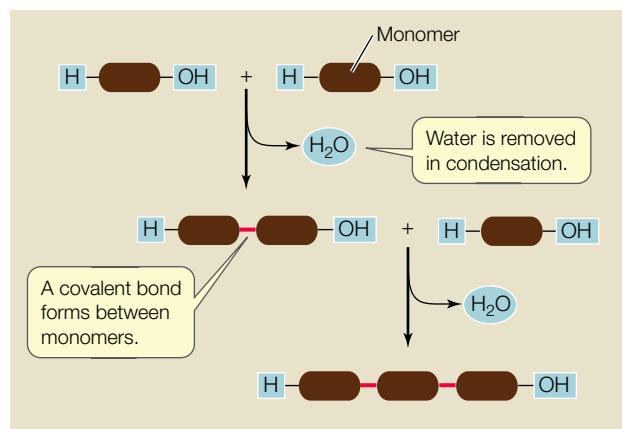
information storage and transmission. These macromolecules function as hereditary material, carrying the traits of both species and individuals from generation to generation.

The functions of macromolecules are directly related to their three-dimensional shapes and to the sequences and chemical properties of their monomers. Some macromolecules fold into compact spherical forms with surface features that make them water-soluble and capable of intimate interaction with other molecules. Some proteins and carbohydrates form long, fibrous systems (such as those found in hair) that provide strength and rigidity to cells and tissues. The long, thin assemblies of proteins such as those in muscles can contract, resulting in movement.

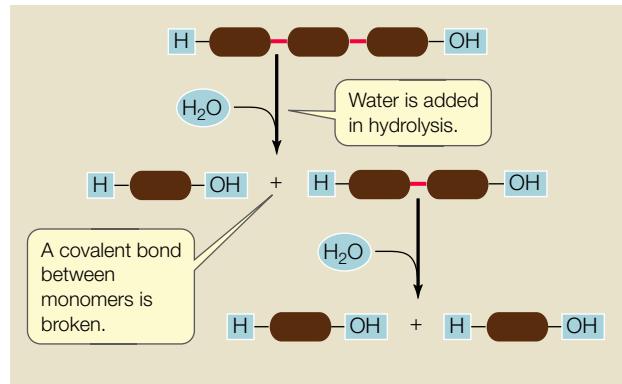
### Most macromolecules are formed by condensation and broken down by hydrolysis

Polymers are constructed from monomers by a series of reactions called **condensation reactions** (sometimes called *dehydration* reactions; both terms refer to the loss of water). Condensation reactions result in covalent bonds between monomers. A molecule of water is released with each covalent bond formed (Figure 3.4A). The condensation reactions that produce the different kinds of polymers differ in detail, but in

#### (A) Condensation



#### (B) Hydrolysis



**3.4 Condensation and Hydrolysis of Polymers** (A) Condensation reactions link monomers into polymers and produce water. (B) Hydrolysis reactions break polymers into individual monomers and consume water.

all cases, polymers form only if water molecules are removed and energy is added to the system. In living systems, specific energy-rich molecules supply the necessary energy.

The reverse of a condensation reaction is a **hydrolysis reaction** (*hydro*, “water”; *lysis*, “break”). Hydrolysis reactions result in the breakdown of polymers into their component monomers. Water reacts with the covalent bonds that link the polymer together. For each covalent bond that is broken, a water molecule splits into two ions ( $H^+$  and  $OH^-$ ), which each become part of one of the products (Figure 3.4B). The linkages between monomers can thus be formed and broken inside living tissues.

### 3.1 RECAP

The four kinds of large molecules that distinguish living tissues are proteins, lipids, carbohydrates, and nucleic acids. These biological molecules carry out a wide range of life-sustaining functions. Most of them are polymers, made up of linked monomeric subunits. Very large polymers are called macromolecules.

- How do functional groups affect the structure and function of macromolecules? (Keep this question in mind as you read the rest of this chapter.) See pp. 39–40 and Figure 3.1
- Why is biochemical unity, as seen in the proportions of the four types of macromolecules present in all organisms, important for life? See p. 40 and Figure 3.3
- How do monomers link up to make polymers and how do they break down into monomers again? See pp. 41–42 and Figure 3.4

The four types of macromolecules can be seen as the building blocks of life. The unique properties of the nucleic acids will be covered in Chapter 4. The remainder of this chapter describes the structures and functions of the proteins, carbohydrates, and lipids.

## 3.2 What Are the Chemical Structures and Functions of Proteins?

While all of the kinds of large molecules are essential to the function of organisms, few have such diverse roles as the proteins. In virtually every chapter of this book, you will be studying examples of their extensive functions:

- Enzymes* are catalytic proteins that speed up biochemical reactions.
- Defensive proteins* such as antibodies recognize and respond to non-self substances that invade the organism from the environment.
- Hormonal and regulatory proteins* such as insulin control physiological processes.
- Receptor proteins* receive and respond to molecular signals from inside and outside the organism.

- Storage proteins* store chemical building blocks—amino acids—for later use.
- Structural proteins* such as collagen provide physical stability and movement.
- Transport proteins* such as hemoglobin carry substances within the organism.
- Genetic regulatory proteins* regulate when, how, and to what extent a gene is expressed.

Among the functions of macromolecules listed earlier, only two—energy storage and information storage—are not usually performed by proteins.

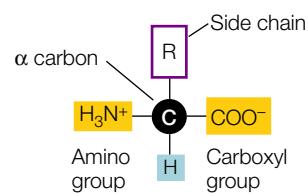
All **proteins** are polymers made up of different proportions and sequences of 20 amino acids. Proteins range in size from small ones such as insulin, which has a molecular weight of 5,733 daltons and 51 amino acids, to huge molecules such as the muscle protein titin, with a molecular weight of 2,993,451 daltons and 26,926 amino acids. All proteins consist of one or more *polypeptide chains*—unbranched (linear) polymer of covalently linked amino acids. The *composition* of a protein refers to the relative amounts of the different amino acids present in its polypeptide chains. Variation in the *sequence* of the amino acids in polypeptide chains is the source of the diversity in protein structure and function, because each chain folds into specific three-dimensional shape that is defined by the precise sequence of the amino acids present in the chain.

Many proteins are made up of more than one polypeptide chain. For example, the oxygen-carrying protein hemoglobin has four chains that are folded separately and come together to make up the functional protein. Proteins can also associate with one another, forming multi-protein complexes that carry out intricate tasks such as DNA synthesis.

To understand the many functions of proteins, we must first explore protein structure. We begin by examining the properties of amino acids and how they link together to form polypeptide chains. Then we will describe how a linear chain of amino acids is consistently folded into a specific, compact, three-dimensional shape. Finally, we will see how this three-dimensional structure provides a definitive physical and chemical environment that influences how other molecules can interact with the protein.

### Amino acids are the building blocks of proteins

The amino acids have both a carboxyl functional group and an amino functional group (see Figure 3.1) attached to the same carbon atom, called the  $\alpha$  (alpha) carbon. Also attached to the  $\alpha$  carbon atom are a hydrogen atom and a **side chain**, or **R group**, designated by the letter R.



The  $\alpha$  carbon is asymmetrical because it is bonded to four different atoms or groups of atoms. Therefore, amino acids exist

in two isomeric forms, called D-amino acids and L-amino acids. D and L are abbreviations of the Latin terms for right (*dextro*) and left (*levo*). Only L-amino acids are commonly found in proteins in most organisms, and their presence is an important chemical “signature” of life.

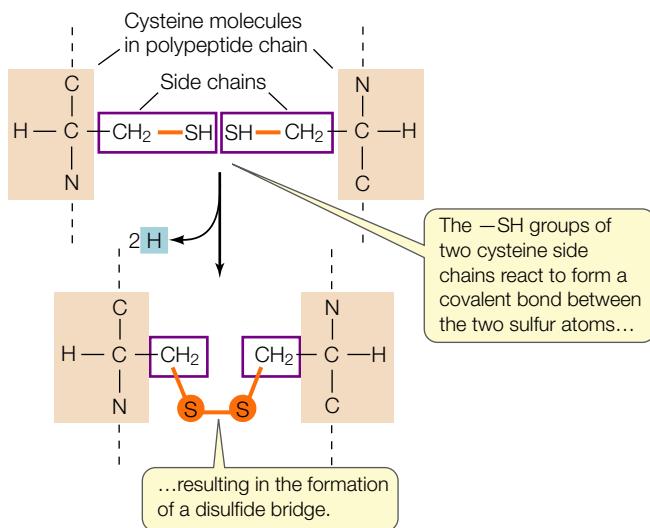
At the pH values commonly found in cells, both the carboxyl and amino groups of amino acids are ionized: the carboxyl group has lost a hydrogen ion, and the amino group has gained one. Thus *amino acids are simultaneously acids and bases*.

The side chains of amino acids contain functional groups that are important in determining the three-dimensional structure and thus the function of the protein. As **Table 3.1** shows, the 20 amino acids found in living organisms are grouped and distinguished by their side chains:

- The five amino acids that have electrically charged side chains (+1, -1) attract water (are hydrophilic) and attract oppositely charged ions of all sorts.
- The five amino acids that have polar side chains ( $\delta^+$ ,  $\delta^-$ ) tend to form hydrogen bonds with water and with other polar or charged substances. These amino acids are also hydrophilic.
- Seven amino acids have side chains that are nonpolar hydrocarbons or very slightly modified hydrocarbons. In the watery environment of the cell, these hydrophobic side chains may cluster together in the interior of the protein. These amino acids are hydrophobic.

**TABLE 3.1**  
**The Twenty Amino Acids**

<p>Amino acids have both three-letter and single-letter abbreviations.</p>	
<p><b>A. Amino acids with electrically charged hydrophilic side chains</b></p>	
<p>Positive <math>+</math></p>	<p>Negative <math>-</math></p>
<p>Arginine (Arg; R)</p>	<p>Histidine (His; H)</p>
<p>Lysine (Lys; K)</p>	<p>Aspartic acid (Asp; D)</p>
<p>Glutamic acid (Glu; E)</p>	
<p>The general structure of all amino acids is the same... ...but each has a different side chain.</p>	
<p><b>B. Amino acids with polar but uncharged side chains (hydrophilic)</b></p>	
<p>Serine (Ser; S)</p>	<p>Threonine (Thr; T)</p>
<p>Asparagine (Asn; N)</p>	<p>Glutamine (Gln; Q)</p>
<p>Tyrosine (Tyr; Y)</p>	
<p><b>C. Special cases</b></p>	
<p>Cysteine (Cys; C)</p>	<p>Glycine (Gly; G)</p>
<p>Proline (Pro; P)</p>	
<p><b>D. Amino acids with nonpolar hydrophobic side chains</b></p>	
<p>Alanine (Ala; A)</p>	<p>Isoleucine (Ile; I)</p>
<p>Leucine (Leu; L)</p>	<p>Methionine (Met; M)</p>
<p>Phenylalanine (Phe; F)</p>	<p>Tryptophan (Trp; W)</p>
<p>Valine (Val; V)</p>	



**3.5 A Disulfide Bridge** Two cysteine molecules in a polypeptide chain can form a disulfide bridge ( $-S-S-$ ) by oxidation (removal of H atoms).

Three amino acids—cysteine, glycine, and proline—are special cases, although the side chains of the latter two are generally hydrophobic.

- The *cysteine* side chain, which has a terminal —SH group, can react with another cysteine side chain in an oxidation reaction to form a covalent bond called a **disulfide bridge**, or *disulfide bond* ( $-S-S-$ ) (Figure 3.5). Disulfide bridges help determine how a polypeptide chain folds.
- The *glycine* side chain consists of a single hydrogen atom and is small enough to fit into tight corners in the interior of a protein molecule, where a larger side chain could not fit.
- Proline* possesses a modified amino group that lacks a hydrogen and instead forms a covalent bond with the hydrocarbon side chain, resulting in a ring structure. This limits both its hydrogen-bonding ability and its ability to rotate about the  $\alpha$  carbon. Thus proline is often found where a protein bends or loops.

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**GO TO** Web Activity 3.2 • Features of Amino Acids

### Peptide linkages form the backbone of a protein

When amino acids polymerize, the carboxyl and amino groups attached to the  $\alpha$  carbon are the reactive groups. The carboxyl group of one amino acid reacts with the amino group of another, undergoing a condensation reaction that forms a **peptide linkage** (also called a *peptide bond*). Figure 3.6 gives a simplified description of this reaction.

Just as a sentence begins with a capital letter and ends with a period, polypeptide chains have a beginning and an end. The “capital letter” marking the beginning of a polypeptide is the amino group of the first amino acid added to the chain and is known as the *N terminus*. The “period” is the carboxyl group of the last amino acid added; this is the *C terminus*.

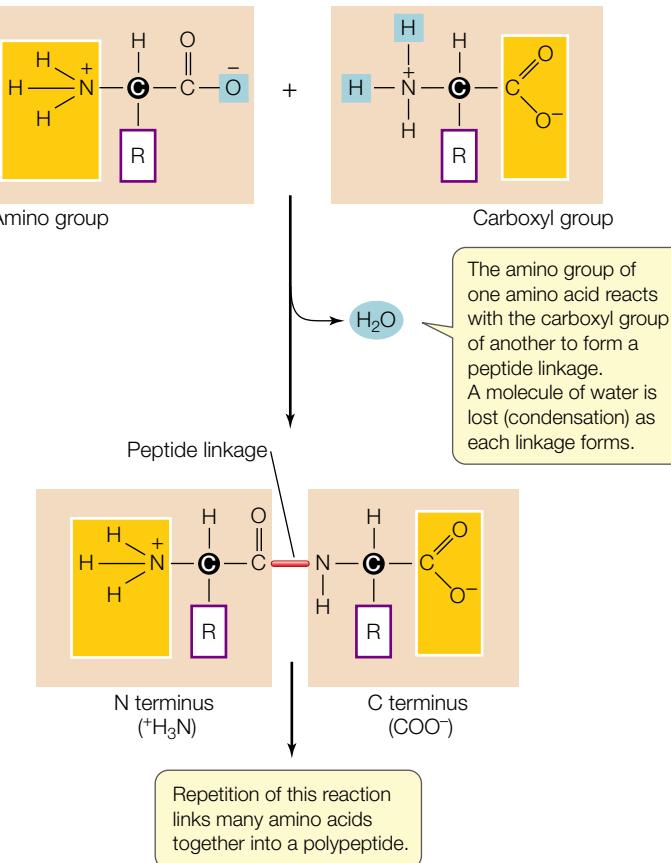
Two characteristics of the peptide bond are especially important in the three-dimensional structure of proteins:

- In the C—N linkage, the adjacent  $\alpha$  carbons ( $\alpha$ C—C—N— $\alpha$ C) are not free to rotate fully, which limits the folding of the polypeptide chain.
- The oxygen bound to the carbon (C=O) in the carboxyl group carries a slight negative charge ( $\delta^-$ ), whereas the hydrogen bound to the nitrogen (N—H) in the amino group is slightly positive ( $\delta^+$ ). This asymmetry of charge favors hydrogen bonding within the protein molecule itself and with other molecules, contributing to both the structure and the function of many proteins.

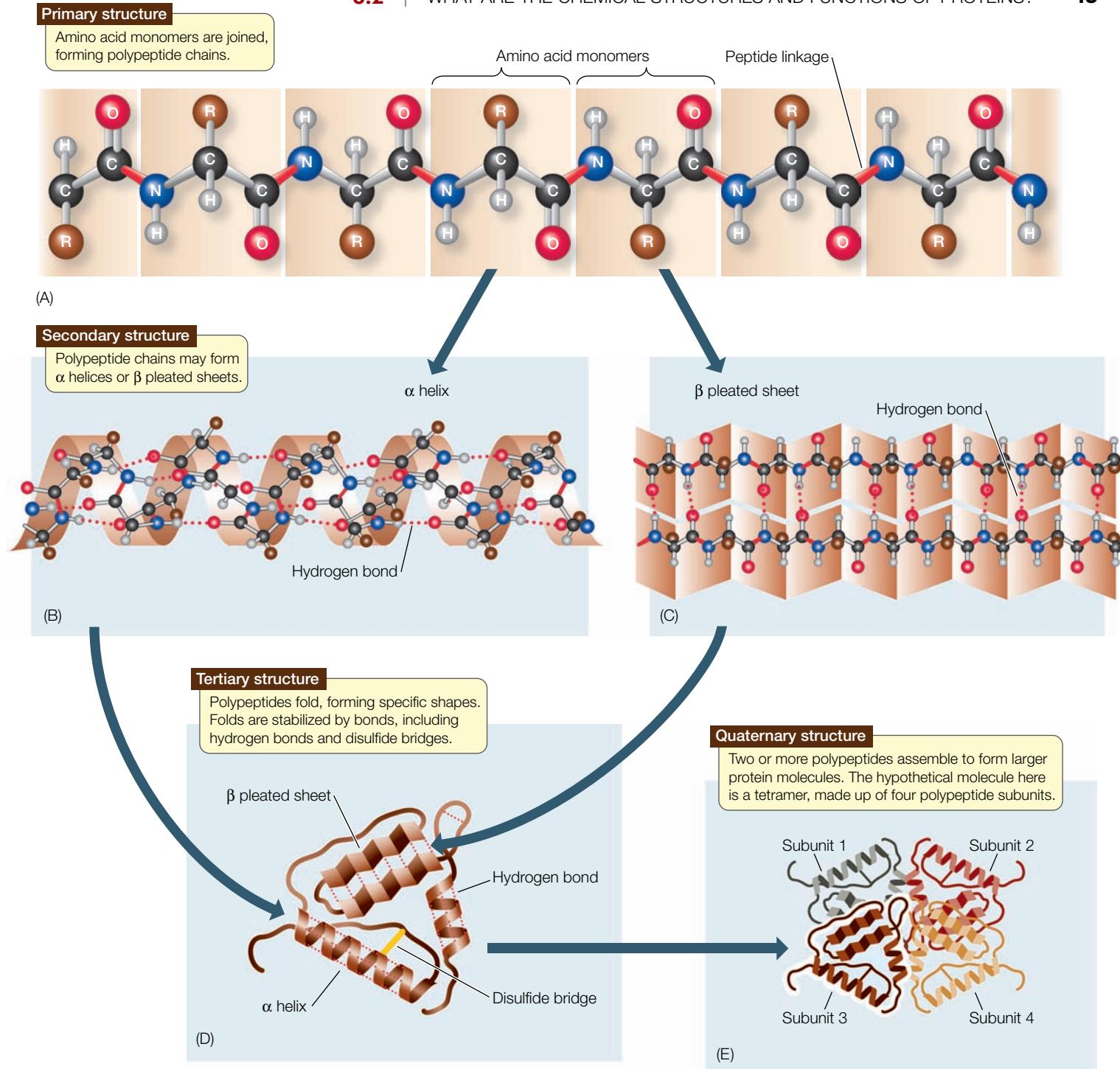
Before we explore the significance of these characteristics of the peptide linkage, however, we will describe the significance of the sequence of amino acids in determining a protein’s structure.

### The primary structure of a protein is its amino acid sequence

There are four levels of protein structure: primary, secondary, tertiary, and quaternary. We will consider each of these in turn over the next few pages. The precise sequence of amino acids in a polypeptide chain held together by peptide linkages constitutes the **primary structure** of a protein (Figure 3.7A). The peptide backbone of the polypeptide chain consists of the repeating sequence —N—C—C— made up of the N atom from the



**3.6 Formation of Peptide Linkages** In living things, the reaction leading to a peptide linkage (also called a peptide bond) has many intermediate steps, but the reactants and products are the same as those shown in this simplified diagram.



**3.7 The Four Levels of Protein Structure** Secondary, tertiary, and quaternary structure all arise from the primary structure of the protein.

amino group, the  $\alpha$  carbon atom, and the C atom from the carboxyl group of each amino acid.

Scientists have determined the primary structure of many proteins. The single-letter abbreviations for amino acids (see Table 3.1) are used to record the amino acid sequence of a protein. Here, for example, are the first 20 amino acids (out of a total of 124) in the protein ribonuclease from a cow:

KETAAAKFERQHMDSTSAA

The theoretical number of different proteins is enormous. Since there are 20 different amino acids, there could be  $20 \times 20 = 400$  distinct dipeptides (two linked amino acids), and  $20 \times 20 \times 20 =$

8,000 different tripeptides (three linked amino acids). Imagine this process of multiplying by 20 extended to a protein made up of 100 amino acids (which would be considered a small protein). There could be  $20^{100}$  (that's approximately  $10^{130}$ ) such small proteins, each with its own distinctive primary structure. How large is the number  $20^{100}$ ? Physicists tell us that there aren't that many electrons in the entire universe.

At the higher levels of protein structure (secondary, tertiary and quaternary), local coiling and folding of the polypeptide

chain(s) give the molecule its final functional shape. All of these levels, however, derive from the protein's primary structure—that is, the precise location of specific amino acids in the polypeptide chain. The properties associated with a precise sequence of amino acids determine how the protein can twist and fold, thus adopting a specific stable structure that distinguishes it from every other protein.

Primary structure is established by covalent bonds. The next level of protein structure makes use of weaker hydrogen bonds.

### The secondary structure of a protein requires hydrogen bonding

A protein's **secondary structure** consists of regular, repeated spatial patterns in different regions of a polypeptide chain. There are two basic types of secondary structure, both determined by hydrogen bonding between the amino acids that make up the primary structure, the  $\alpha$  helix and the  $\beta$  pleated sheet.

**THE  $\alpha$  HELIX** The  $\alpha$  (**alpha**) **helix** is a right-handed coil that turns in the same direction as a standard wood screw (Figure 3.7B). The R groups extend outward from the peptide backbone of the helix. The coiling results from hydrogen bonds that form between the  $\delta^+$  hydrogen of the N—H of one amino acid and the  $\delta^-$  oxygen of the C=O of another. When this pattern of hydrogen bonding is established repeatedly over a segment of the protein, it stabilizes the coil.

**THE  $\beta$  PLEATED SHEET** A  $\beta$  (**beta**) **pleated sheet** is formed from two or more polypeptide chains that are almost completely extended and aligned. The sheet is stabilized by hydrogen bonds between the N—H groups on one chain and the C=O groups on the other (Figure 3.7C). A  $\beta$  pleated sheet may form between separate polypeptide chains, as in spider silk, or be-

tween different regions of a single polypeptide chain that is bent back on itself. Many proteins contain regions of both  $\alpha$  helix and  $\beta$  pleated sheet in the same polypeptide chain.

### The tertiary structure of a protein is formed by bending and folding

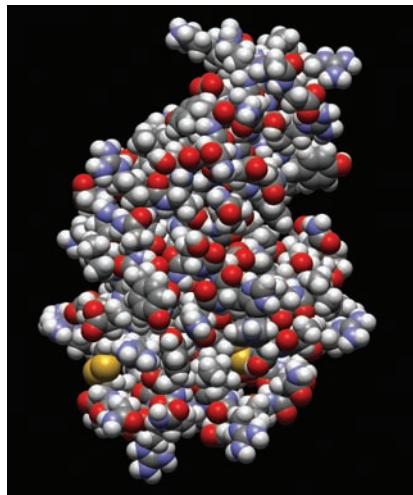
In many proteins, the polypeptide chain is bent at specific sites and then folded back and forth, resulting in the **tertiary structure** of the protein (Figure 3.7D). Although  $\alpha$  helices and  $\beta$  pleated sheets contribute to the tertiary structure, usually only portions of the macromolecule have these secondary structures, and large regions consist of tertiary structure unique to a particular protein. Tertiary structure results in a macromolecule's definitive three-dimensional shape, often including a buried interior as well as a surface that is exposed to the environment.

The protein's exposed outer surfaces present functional groups capable of interacting with other molecules in the cell. These molecules might be other proteins (as happens in quaternary structure, as we will see below) or smaller chemical reactants (as in enzymes; see Section 7.4).

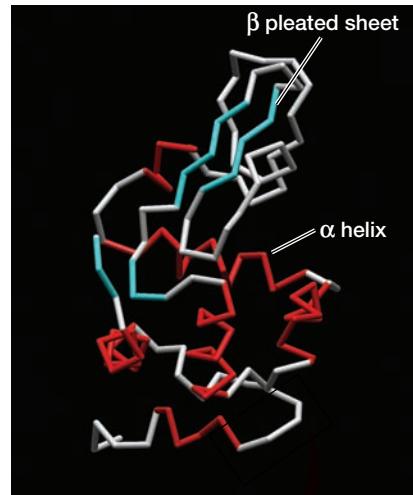
While hydrogen bonding between the N—H and C=O groups within and between chains is responsible for secondary structure, the interactions between R groups—the amino acid side chains—determine tertiary structure. We described the various strong and weak interactions between atoms in Section 2.2. Many of these interactions are involved in determining and maintaining tertiary structure.

**3.8 Three Representations of Lysozyme** Different molecular representations of a protein emphasize different aspects of its tertiary structure: surface features, sites of bends and folds, sites where alpha or beta structure predominate. These three representations of lysozyme are similarly oriented.

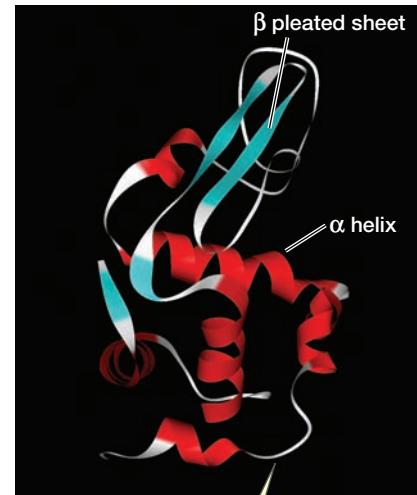
(A) Space-filling model



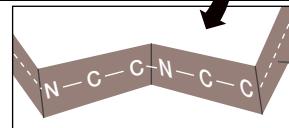
(B) Stick model



(C) Ribbon model



A realistic depiction of lysozyme shows dense packing of its atoms.



The "backbone" of lysozyme consists of repeating N—C—C units of amino acids.

- Covalent *disulfide bridges* can form between specific cysteine side chains (see Figure 3.5), holding a folded polypeptide in place.
- *Hydrogen bonds* between side chains also stabilize folds in proteins.
- *Hydrophobic* side chains can aggregate together in the interior of the protein, away from water, folding the polypeptide in the process.
- *van der Waals forces* can stabilize the close interactions between hydrophobic side chains.
- *Ionic bonds* can form between positively and negatively charged side chains, forming *salt bridges* between amino acids. Ionic bonds can also be buried deep within a protein, away from water.

A complete description of a protein's tertiary structure would specify the location of every atom in the molecule in three-dimensional space relative to all the other atoms. Such a description is available for the protein lysozyme (**Figure 3.8**).

The different ways of depicting the molecule have their uses. The space-filling model might be used to study how other molecules interact with specific sites and R groups on a protein's surface. The stick model emphasizes the sites where bends occur in order to make the folds of the polypeptide chain. The ribbon model, perhaps the most widely used, shows the different types of secondary structure and how they fold into the tertiary structure.

Remember that both secondary and tertiary structure derive from primary structure. If a protein is heated slowly, the heat energy will disrupt only the weak interactions, causing the secondary and tertiary structure to break down. The protein is then said to be **denatured**. But the protein can return to its normal tertiary structure when it cools, demonstrating that all the information needed to specify the unique shape of a protein is contained in its primary structure. This was first shown (using chemicals instead of heat to denature the protein) by biochemist Christian Anfinsen for the protein ribonuclease (**Figure 3.9**).

### The quaternary structure of a protein consists of subunits

Many functional proteins contain two or more polypeptide chains, called *subunits*, each of them folded into its own unique tertiary structure. The protein's **quaternary structure** results from the ways in which these subunits bind together and interact (**Figure 3.7E**).

The models of hemoglobin in **Figure 3.10** illustrate quaternary structure. Hydrophobic interactions, van der Waals forces, hydrogen bonds, and ionic bonds all help hold the four subunits together to form a hemoglobin molecule. However, the weak nature of these forces permits small changes in the quaternary structure to aid the

## INVESTIGATING LIFE

### 3.9 Primary Structure Specifies Tertiary Structure

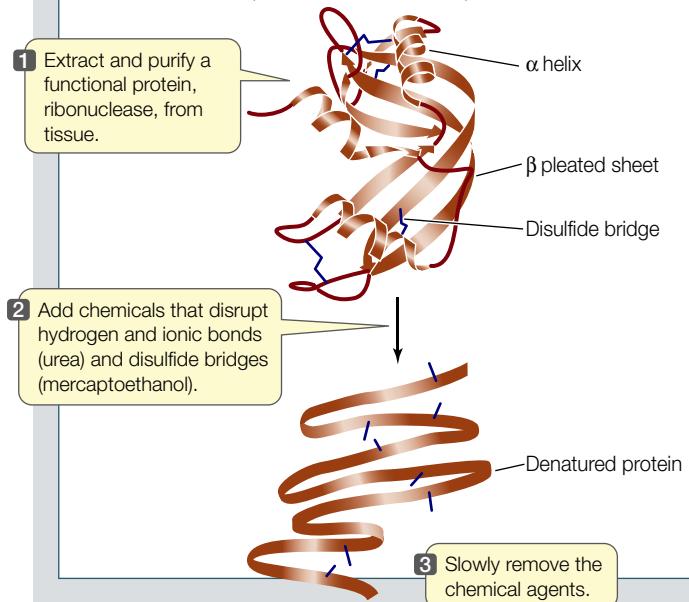
Using the protein ribonuclease, Christian Anfinsen showed that proteins spontaneously fold into a functionally correct three-dimensional configuration. As long as the primary structure is not disrupted, the information for correct folding under the right conditions is retained.

#### HYPOTHESIS

Under controlled conditions that simulate normal cellular environment in the laboratory, the primary structure of a denatured protein can reestablish the protein's three-dimensional structure.

#### METHOD

Chemically denature functional ribonuclease, disrupting disulfide bridges and other intramolecular interactions that maintain the protein's shape, so that only primary structure (i.e., the amino acid sequence) remains. Once denaturation is complete, remove the disruptive chemicals.



#### RESULTS

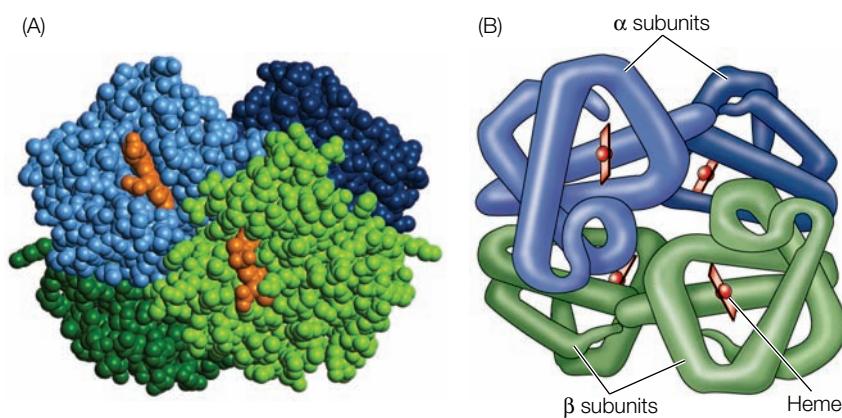
When the disruptive agents are removed, three-dimensional structure is restored and the protein once again is functional.



#### CONCLUSION

In normal cellular conditions, the primary structure of a protein specifies how it folds into a functional, three-dimensional structure.

**3.10 Quaternary Structure of a Protein** Hemoglobin consists of four folded polypeptide subunits that assemble themselves into the quaternary structure shown here. In these two graphic representations, each type of subunit is a different color. The heme groups contain iron and are the oxygen-carrying sites.



protein's function—which is to carry oxygen in red blood cells. As hemoglobin binds one  $O_2$  molecule, the four subunits shift their relative positions slightly, changing the quaternary structure. Ionic bonds are broken, exposing buried side chains that enhance the binding of additional  $O_2$  molecules. The quaternary structure changes again when hemoglobin releases its  $O_2$  molecules to the cells of the body.

### Shape and surface chemistry contribute to protein function

The shape and structure of a protein allow specific sites on its exposed surface to bind noncovalently to another molecule, which may be large or small. The binding is said to be specific because only certain compatible chemical groups will bind to one another. The specificity of protein binding depends on two general properties of the protein: its shape, and the chemistry of its exposed surface groups.

- **Shape.** When a small molecule collides with and binds to a much larger protein, it is like a baseball being caught by a catcher's mitt: the mitt has a shape that binds to the ball and fits around it. Just as a hockey puck or a ping-pong ball does not fit a baseball catcher's mitt, a given molecule will not bind to a protein unless there is a general "fit" between their two three-dimensional shapes.
- **Chemistry.** The exposed amino acid R groups on the surface of a protein permit chemical interactions with other substances (Figure 3.11). Three types of interactions may be involved: ionic, hydrophobic, and hydrogen bonding. Many important functions of proteins involve interactions between exposed-surface R groups and other molecules.

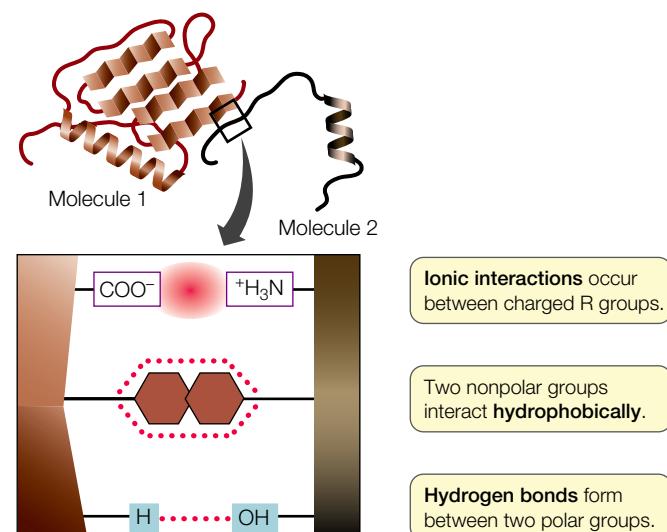
### Environmental conditions affect protein structure

Because it is determined by weak forces, the three-dimensional structure of proteins is influenced by environmental conditions. Conditions that would not break covalent bonds can disrupt the

weaker, noncovalent interactions that determine secondary and tertiary structure. Such alterations may affect a protein's shape and thus its function. Various conditions can alter the weak, noncovalent interactions:

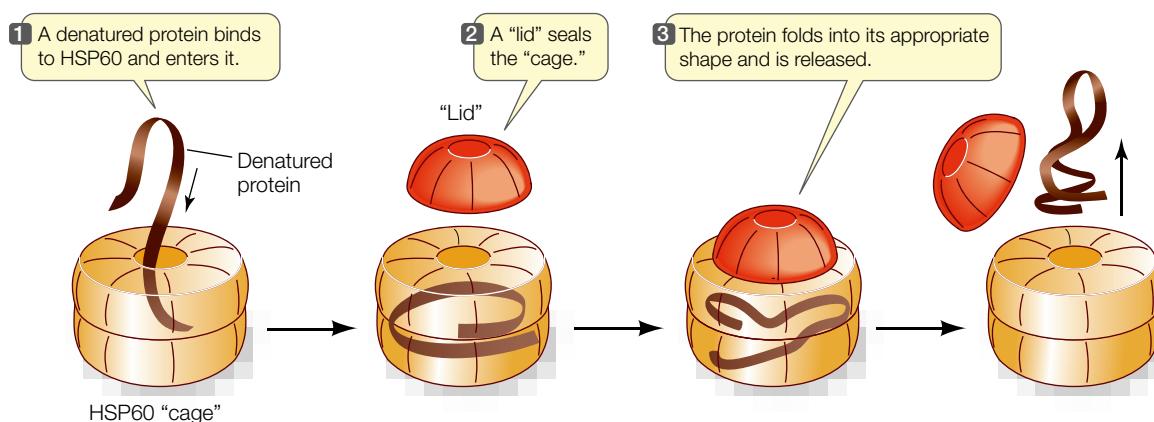
- *Increases in temperature* cause more rapid molecular movements and thus can break hydrogen bonds and hydrophobic interactions.
- *Alterations in pH* can change the pattern of ionization of exposed carboxyl and amino groups in the R groups of amino acids, thus disrupting the pattern of ionic attractions and repulsions.
- *High concentrations of polar substances* such as urea can disrupt the hydrogen bonding that is crucial to protein structure. This was used in the experiment on reversible protein denaturation shown in Figure 3.9.
- *Nonpolar substances* may also disrupt normal protein structure in cases where hydrophobic groups are essential to maintain the structure.

Denaturation can be irreversible when amino acids that were buried in the interior of the protein become exposed at the surface, and vice versa, causing a new structure to form or different molecules to bind to the protein. Boiling an egg denatures its proteins and is, as you know, not reversible.



### 3.11 Noncovalent Interactions Between Proteins and Other Molecules

Noncovalent interactions allow a protein (brown) to bind tightly to another molecule (green) with specific properties. Noncovalent interactions also allow regions within the same protein to interact with one another.



### 3.12 Chaperones Protect Proteins from Inappropriate Binding

Chaperone proteins surround new or denatured proteins and prevent them from binding to the wrong substance. Heat shock proteins such as HSP60, whose actions are illustrated here, are one class of chaperone proteins.

#### Molecular chaperones help shape proteins

Because of their specific shapes and the exposure of chemical groups on their surfaces, proteins can bind specific substances. Within a living cell, a polypeptide chain is sometimes in danger of binding the wrong substance. Two important examples of such a situation are:

- Following denaturation: Inappropriate environmental conditions in a cell, such as elevated temperature, can cause the denatured protein to re-fold incorrectly.
- Just after a protein is made: When a protein has not yet folded completely, it can present a surface that binds the wrong molecule.

In these cases, change may be irreversible. Eukaryotic cells have a special class of proteins that act to counteract threats to three-dimensional structure. Proteins in this class, called **chaperones**, act as molecular caretakers for other proteins. Like the chaperones at a high school dance, they prevent inappropriate interactions and enhance the appropriate ones.

Molecular chaperones were discovered by accident in 1962, when the temperature of an incubator holding fruit flies was accidentally turned up. Italian geneticist Ferruccio Ritossa noticed that this "heat shock" did not kill the flies. Instead, there was enhanced synthesis of a set of proteins that were later described as chaperones. They bound to many target proteins in the fruit fly cells and kept them from being denatured, and in some cases facilitated the correct refolding of proteins.

The general class of stress-induced chaperone proteins is called the **heat shock proteins (HSPs)**, after this discovery. HSPs are made by most eukaryotic cells, and many enhance protein folding in addition to their protective role during periods of stress. As an example, HSP60 forms a cage that sucks a protein in, causes it to fold into the correct shape, and then releases it (Figure 3.12). Tumors make abundant HSPs, possibly to stabilize proteins important in the cancer process, and so HSP-inhibiting drugs are being designed. In some clinical situations, treatment with these inhibitors results in the inappropriate folding of tumor-cell proteins, causing the tumors to stop growing and even disappear.

### 3.2 RECAP

Proteins are polymers of amino acids. The sequence of amino acids in a protein determines its primary structure. Secondary, tertiary, and quaternary structures arise through interactions between the amino acids. A protein's three-dimensional shape and exposed chemical groups establish binding specificity for other substances.

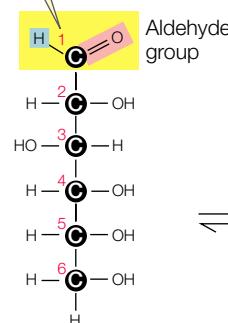
- What are the attributes of an amino acid's R group that would make it hydrophobic? Hydrophilic? See pp. 42–43 and Table 3.1
- Sketch and explain how two amino acids link together to form a peptide linkage. See p. 44 and Figure 3.6
- What are the four levels of protein structure and how are they all ultimately determined by the protein's primary structure (i.e., its amino acid sequence)? See pp. 44–48 and Figure 3.7
- How do environmental factors such as temperature and pH affect the weak interactions that give a protein its specific shape and function? See p. 48

The seemingly infinite number of protein configurations made possible by the biochemical properties of the 20 amino acids has driven the evolution of life's diversity. The linkage configurations of sugar monomers (monosaccharides) drives the structure of the next group of macromolecules, the carbohydrates that provide energy for life.

### 3.3 What Are the Chemical Structures and Functions of Carbohydrates?

**Carbohydrates** are a large group of molecules that all have a similar atomic composition but differ greatly in size, chemical properties, and biological functions. Carbohydrates have the general formula  $C_n(H_2O)_n$ , which makes them appear as hydrates of carbon (association between water molecules and carbon in the ratio  $C_1H_2O_1$ ), hence their name. When their molecular structures are examined, the linked carbon atoms are seen to be bonded with hydrogen atoms ( $-H$ ) and hydroxyl groups

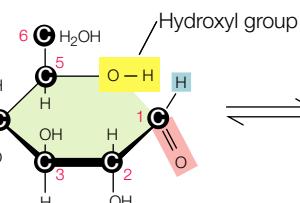
The numbers in red indicate the standard convention for numbering the carbons.



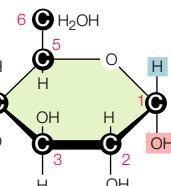
Straight-chain form

The straight-chain form of glucose has an aldehyde group at carbon 1.

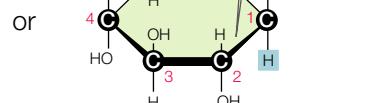
**3.13 From One Form of Glucose to the Other** All glucose molecules have the formula  $C_6H_{12}O_6$ , but their structures vary. When dissolved in water, the  $\alpha$  and  $\beta$  “ring” forms of glucose interconvert. The convention used here for numbering the carbon atoms is standard in biochemistry.



Intermediate form

 $\alpha$ -D-glucose

The dark line indicates that the edge of the molecule extends toward you; the thin line extends back away from you.

 $\beta$ -D-glucose

Depending on the orientation of the aldehyde group when the ring closes, either of two molecules— $\alpha$ -D-glucose or  $\beta$ -D-glucose—forms.

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GO TO Web Activity 3.3 • Forms of Glucose

( $-\text{OH}$ ), the components of water. Carbohydrates have three major biochemical roles:

- They are a source of stored energy that can be released in a form usable by organisms.
- They are used to transport stored energy within complex organisms.
- They serve as *carbon skeletons* that can be rearranged to form new molecules.

Some carbohydrates are relatively small, with molecular weights of less than 100 Da. Others are true macromolecules, with molecular weights in the hundreds of thousands.

There are four categories of biologically important carbohydrates:

- **Monosaccharides** (*mono*, “one”; *saccharide*, “sugar”), such as glucose, ribose, and fructose, are *simple sugars*. They are the monomers from which the larger carbohydrates are constructed.
- **Disaccharides** (*di*, “two”) consist of two monosaccharides linked together by covalent bonds. The most familiar is sucrose, which is made up of covalently bonded glucose and fructose molecules.
- **Oligosaccharides** (*oligo*, “several”) are made up of several (3–20) monosaccharides.
- **Polysaccharides** (*poly*, “many”), such as starch, glycogen, and cellulose, are polymers made up of hundreds or thousands of monosaccharides.

### Monosaccharides are simple sugars

All living cells contain the monosaccharide **glucose**; it is the familiar “blood sugar,” used to transport energy in humans. Cells use glucose as an energy source, breaking it down through a series of reactions that release stored energy and produce water and carbon dioxide; this is a cellular form of the combustion reaction described in Chapter 2.

Glucose exists in straight chains and in ring forms. The ring forms predominate in virtually all biological circumstances because they are more stable under physiological conditions. There are two versions of glucose ring, called  $\alpha$ - and  $\beta$ -glucose, which differ only in the orientation of the  $-\text{H}$  and  $-\text{OH}$  attached to carbon 1 (Figure 3.13). The  $\alpha$  and  $\beta$  forms interconvert and exist in equilibrium when dissolved in water.

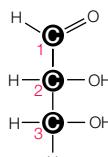
Different monosaccharides contain different numbers of carbons. Some monosaccharides are structural isomers, with the same kinds and numbers of atoms, but in different arrangements (Figure 3.14). Such seemingly small structural changes can significantly alter properties. Most of the monosaccharides in living systems belong to the D (right-handed) series of isomers.

**Pentoses** (*pente*, “five”) are five-carbon sugars. Two pentoses are of particular biological importance: the backbones of the nucleic acids RNA and DNA contain ribose and deoxyribose, respectively (see Section 4.1). These two pentoses are not isomers of each other; rather, one oxygen atom is missing from carbon 2 in deoxyribose (*de-*, “absent”). The absence of this oxygen atom is an important distinction between RNA and DNA.

The **hexoses** (*hex*, “six”), a group of structural isomers, all have the formula  $C_6H_{12}O_6$ . Included among the hexoses are glucose, fructose (so named because it was first found in fruits), mannose, and galactose.

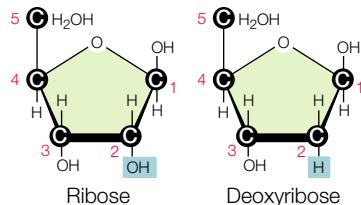
### Glycosidic linkages bond monosaccharides

The disaccharides, oligosaccharides, and polysaccharides are all constructed from monosaccharides that are covalently bonded together by condensation reactions that form **glycosidic linkages**. A single glycosidic linkage between two monosaccharides forms a disaccharide. For example, sucrose—common table sugar in the human diet and a major disaccharide in plants—is a disaccharide formed from a glucose and a fructose molecule.

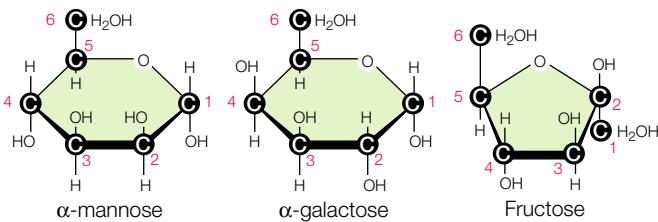
**Three-carbon sugar**

Glyceraldehyde is the smallest monosaccharide and exists only as the straight-chain form.

Glyceraldehyde

**Five-carbon sugars (pentoses)**

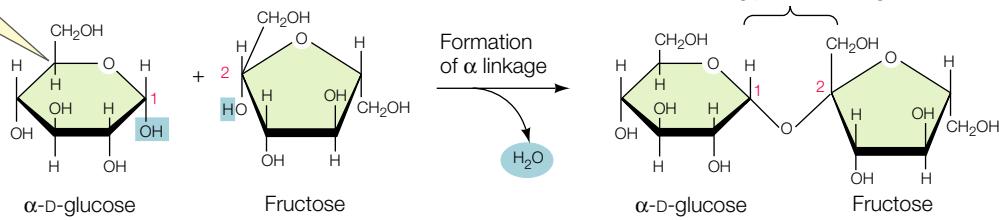
Ribose and deoxyribose each have five carbons, but very different chemical properties and biological roles.

**Six-carbon sugars (hexoses)**

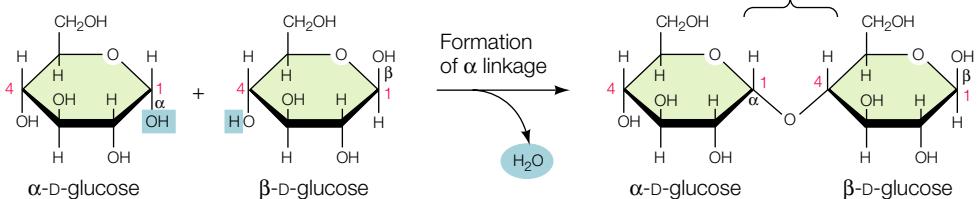
These hexoses are structural isomers. All have the formula  $C_6H_{12}O_6$ , but each has distinct biochemical properties.

The presence of a carbon atom (C) at a junction such as this is implied.

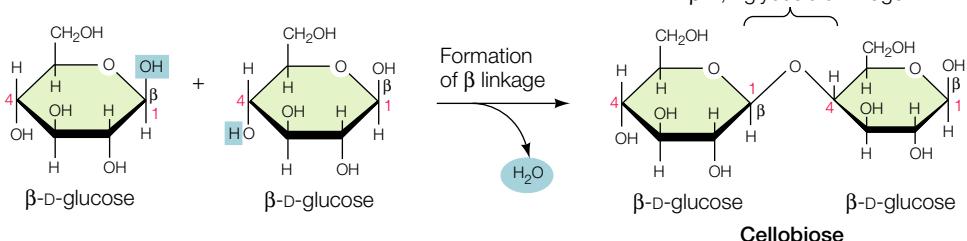
In sucrose, glucose and fructose are linked by an  $\alpha$ -1,2 glycosidic linkage.



Maltose is produced when an  $\alpha$ -1,4 glycosidic linkage forms between two glucose molecules. The hydroxyl group on carbon 1 of one D-glucose in the  $\alpha$  (down) position reacts with the hydroxyl group on carbon 4 of the other glucose.



In cellobiose, two glucoses are linked by a  $\beta$ -1,4 glycosidic linkage.



The disaccharides maltose and cellobiose are made from two glucose molecules (Figure 3.15). Maltose and cellobiose are structural isomers, both having the formula  $C_{12}H_{22}O_{11}$ . However, they have different chemical properties and are recognized by different enzymes in biological tissues. For example, maltose can be hydrolyzed into its monosaccharides in the human body, whereas cellobiose cannot.

Oligosaccharides contain several monosaccharides bound by glycosidic linkages at various sites. Many oligosaccharides have additional functional groups, which give them special properties. Oligosaccharides are often covalently bonded to proteins and lipids on the outer cell surface, where they serve as recognition signals. The different human blood groups (for example, the ABO blood types) get their specificity from oligosaccharide chains.

**3.15 Disaccharides Form by Glycosidic Linkages** Glycosidic linkages between two monosaccharides can create many different disaccharides. Which disaccharide is formed depends on which monosaccharides are linked; on the site of linkage (i.e., which carbon atoms are involved); and on the form ( $\alpha$  or  $\beta$ ) of the linkage.

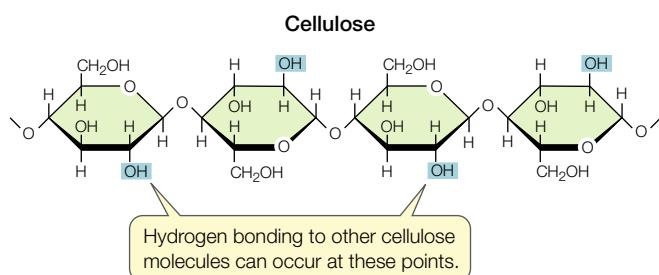
### Polysaccharides store energy and provide structural materials

Polysaccharides are large (sometimes gigantic) polymers of monosaccharides connected by glycosidic linkages (Figure 3.16). In contrast to proteins, polysaccharides are not necessarily linear chains of monomers. Each monomer unit has several sites that may be capable of forming glycosidic linkages, and thus branched molecules are possible.

**STARCH** Starches comprise a family of giant molecules of broadly similar structure. While all starches are polysaccharides of glucose with  $\alpha$ -glycosidic linkages ( $\alpha$ -1,4 and  $\alpha$ -1,6 glycosidic

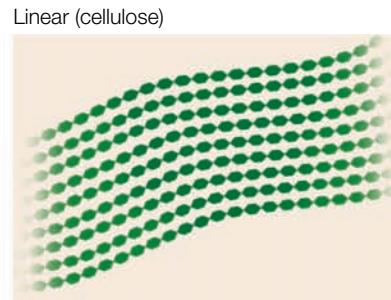
bonds; Figure 3.16A), the different starches can be distinguished by the amount of branching that occurs at carbons 1 and 6 (Figure 3.16B). Starch is the principal energy storage compound of plants. Some plant starches, such as amylose, are unbranched; others are moderately branched (amylopectin, for example). Starch readily binds water. When that water is removed, however, hydrogen bonds tend to form between the unbranched polysaccharide chains, which then aggregate, as in the large starch grains observed in the storage material of plant seeds (see Figure 3.16C).

#### (A) Molecular structure

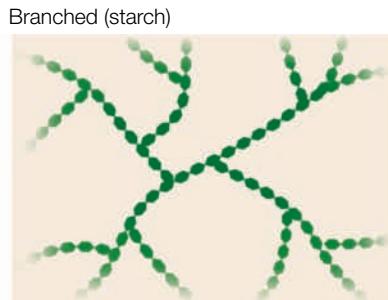


Cellulose is an unbranched polymer of glucose with  $\beta$ -1,4 glycosidic linkages that are chemically very stable.

#### (B) Macromolecular structure

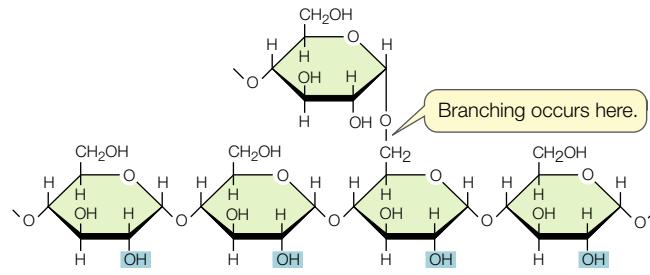


Parallel cellulose molecules form hydrogen bonds, resulting in thin fibrils.



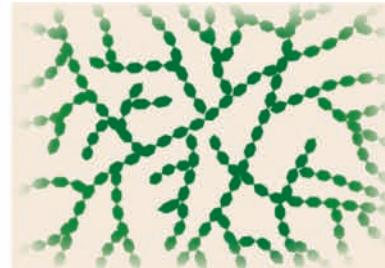
Branching limits the number of hydrogen bonds that can form in starch molecules, making starch less compact than cellulose.

#### Starch and glycogen



Glycogen and starch are polymers of glucose with  $\alpha$ -1,4 glycosidic linkages.  $\alpha$ -1,6 glycosidic linkages produce branching at carbon 6.

#### Highly branched (glycogen)

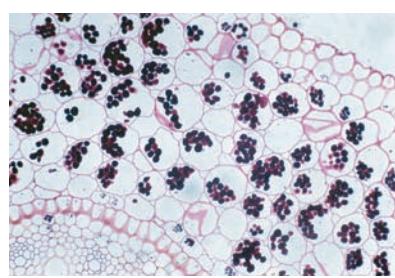


The high amount of branching in glycogen makes its solid deposits more compact than starch.

#### (C) Polysaccharides in cells



Layers of cellulose fibrils, as seen in this scanning electron micrograph, give plant cell walls great strength.



Within these plant cells, starch deposits (dyed purple in this micrograph) have a granular shape.



The pink-stained granules in this electron micrograph are glycogen deposits in the human liver.

#### 3.16 Representative Polysaccharides

Cellulose, starch, and glycogen have different levels of branching and compaction of the polysaccharides.

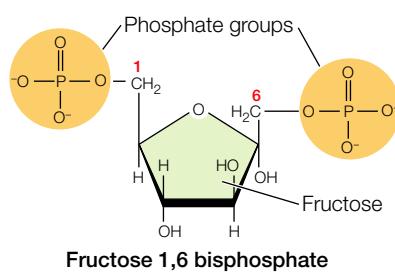
**GLYCOGEN** Glycogen is a water-insoluble, highly branched polymer of glucose. It stores glucose in liver and muscle, serving as an energy storage compound for animals as starch does for plants. Both glycogen and starch are readily hydrolyzed into glucose monomers, which in turn can be broken down to liberate their stored energy.

But if it is glucose that is needed for fuel, why store it in the form of glycogen? The reason is that 1,000 glucose molecules would exert 1,000 times the *osmotic pressure* of a single glycogen molecule, causing water to enter the cells (see Section 6.3). If it were not for polysaccharides, many organisms would expend a lot of energy expelling excess water from their cells.

**CELLULOSE** As the predominant component of plant cell walls, cellulose is by far the most abundant organic compound on Earth. Like starch and glycogen, cellulose is a polysaccharide of glucose, but its individual monosaccharides are connected by  $\beta$ - rather than by  $\alpha$ -glycosidic linkages. Starch is easily degraded by the actions of chemicals or enzymes. Cellulose, however, is chemically more stable because of its  $\beta$ -glycosidic linkages. Thus, whereas starch is easily broken down to supply glucose for energy-producing reactions, cellulose is an excellent structural material that can withstand harsh environmental conditions without substantial change.

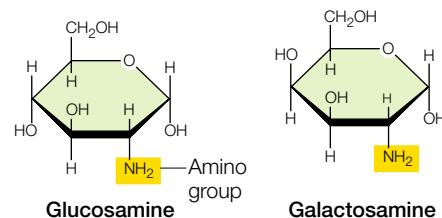
(A) Sugar phosphate

Fructose 1,6 bisphosphate is involved in the reactions that liberate energy from glucose. (The numbers in its name refer to the carbon sites of phosphate bonding; *bis*- indicates that two phosphates are present.)



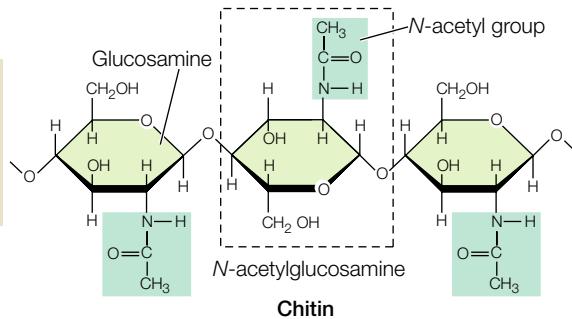
**(B) Amino sugars**

The monosaccharides glucosamine and galactosamine are amino sugars with an amino group in place of a hydroxyl group



**(C) Chitin**

Chitin is a polymer of *N*-acetylglucosamine; *N*-acetyl groups provide additional sites for hydrogen bonding between the polymers.



**Chemically modified carbohydrates contain additional functional groups**

Some carbohydrates are chemically modified by the addition of functional groups, such as phosphate and amino groups (**Figure 3.17**). For example, carbon 6 in glucose may be oxidized from  $-\text{CH}_2\text{OH}$  to a carboxyl group ( $-\text{COOH}$ ), producing glucuronic acid. Or a phosphate group may be added to one or more of the  $-\text{OH}$  sites. Some of the resulting *sugar phosphates*, such as fructose 1,6-bisphosphate, are important intermediates in cellular energy reactions, which will be discussed in Chapter 9.

When an amino group is substituted for an —OH group, *amino sugars*, such as glucosamine and galactosamine, are produced. These compounds are important in the extracellular matrix (see Section 5.4), where they form parts of glycoproteins, which are molecules involved in keeping tissues together. Galactosamine is a major component of cartilage, the material that forms caps on the ends of bones and stiffens the ears and nose. A derivative of glucosamine is present in the polymer *chitin*, the principal structural polysaccharide in the external skeletons of insects and many crustaceans (e.g., crabs and lobsters) and a component of the cell walls of fungi. Because these organisms are among the most abundant eukaryotes on Earth, chitin rivals cellulose as one of the most abundant substances in the living world.

**3.17 Chemically Modified Carbohydrates** Added functional groups can modify the form and properties of a carbohydrate.

Galactosamine is an important component of cartilage, a connective tissue in vertebrates.



The external skeletons of insects are made up of chitin.



### 3.3 RECAP

Carbohydrates are composed of carbon, hydrogen, and oxygen in the general ratio of 1:2:1. They provide energy and structure to cells and are precursors of numerous important biological molecules. Monosaccharide monomers can be connected by glycosidic linkages to form disaccharides, oligosaccharides, and polysaccharides.

- Draw the chemical structure of a disaccharide formed by two monosaccharides. **See Figure 3.15**
- What qualities of the polysaccharides starch and glycogen make them useful for energy storage? **See pp. 52–53 and Figure 3.16**
- From looking at the cellulose molecules in Figure 3.16A, can you see where a large number of hydrogen bonds are present in the linear structure of cellulose shown in Figure 3.16B? Why is this structure so strong?

We have seen how amino acid monomers form protein polymers and how sugar monomers form the polymers of carbohydrates. Now we will look at the lipids, which are unique among the four classes of large biological molecules in that they are not, strictly speaking, polymers.

### 3.4 What Are the Chemical Structures and Functions of Lipids?

**Lipids**—colloquially called *fats*—are hydrocarbons that are insoluble in water because of their many nonpolar covalent bonds. As we saw in Section 2.2, nonpolar hydrocarbon molecules are hydrophobic and preferentially aggregate among themselves, away from water (which is polar). When nonpolar hydrocarbons are sufficiently close together, weak but additive van der Waals forces hold them together. The huge macromolecular aggregations that can form are not polymers in a strict chemical sense, because the individual lipid molecules are not covalently bonded. With this understanding, it is still useful to consider aggregations of individual lipids as a different sort of polymer.

There are several different types of lipids, and they play a number of roles in living organisms:

- Fats and oils store energy.
- Phospholipids play important structural roles in cell membranes.
- Carotenoids and chlorophylls help plants capture light energy.
- Steroids and modified fatty acids play regulatory roles as hormones and vitamins.

- Fat in animal bodies serves as thermal insulation.
- A lipid coating around nerves provides electrical insulation.
- Oil or wax on the surfaces of skin, fur, and feathers repels water.

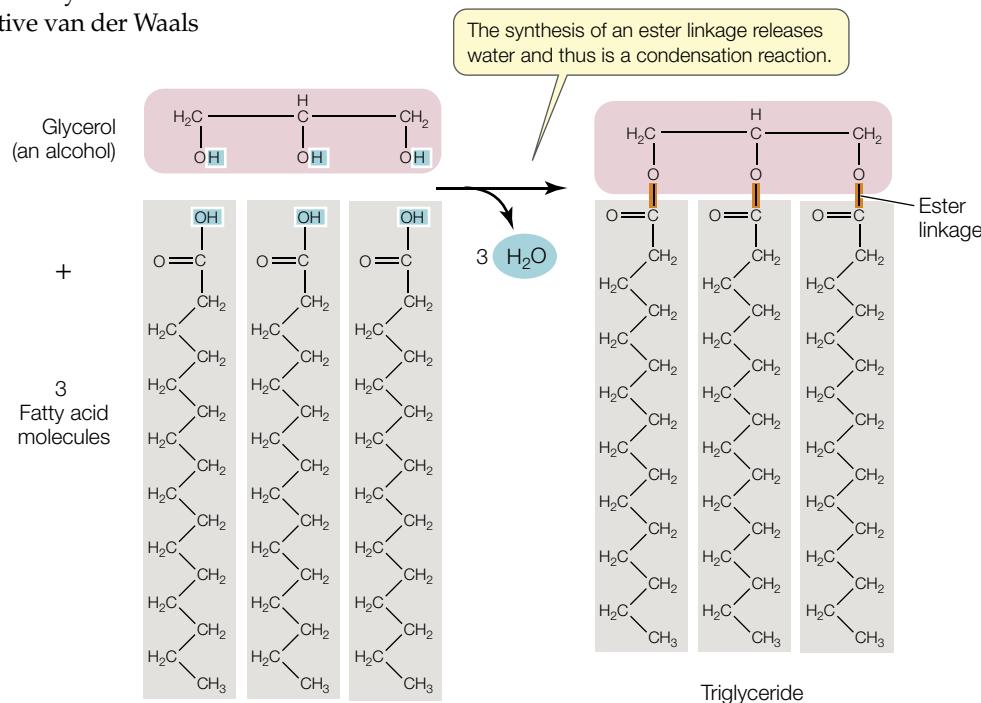
#### Fats and oils are hydrophobic

Chemically, fats and oils are *triglycerides*, also known as *simple lipids*. Triglycerides that are solid at room temperature (around 20°C) are called **fats**; those that are liquid at room temperature are called **oils**. Triglycerides are composed of two types of building blocks: *fatty acids* and *glycerol*. **Glycerol** is a small molecule with three hydroxyl ( $-\text{OH}$ ) groups (thus it is an alcohol). A **fatty acid** is made up of a long nonpolar hydrocarbon chain and a polar carboxyl group ( $-\text{COOH}$ ). These chains are very hydrophobic, with their abundant C—H and C—C bonds, which have low electronegativity and are nonpolar (see Section 2.2).

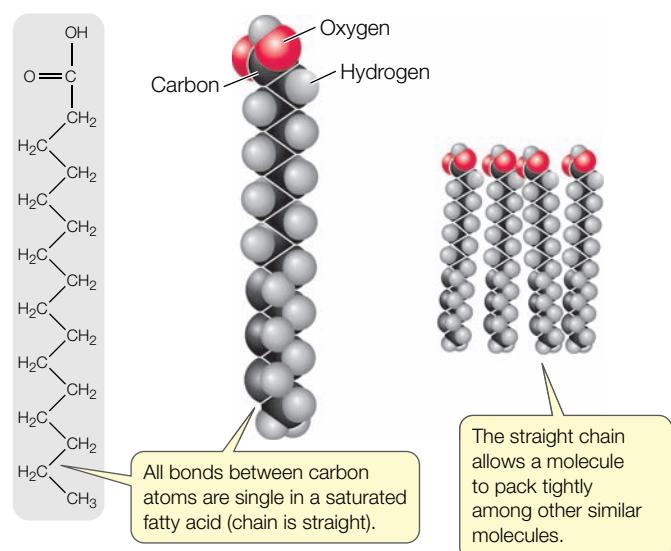
A **triglyceride** contains three fatty acid molecules and one molecule of glycerol. Synthesis of a triglyceride involves three condensation (dehydration) reactions. In each reaction, the carboxyl group of a fatty acid bonds with a hydroxyl group of glycerol, resulting in a covalent bond called an **ester linkage** and the release of a water molecule (Figure 3.18). The three fatty acids in a triglyceride molecule need not all have the same hydrocarbon chain length or structure; some may be saturated fatty acids, while others may be unsaturated:

- In **saturated fatty acids**, all the bonds between the carbon atoms in the hydrocarbon chain are single bonds—there are no double bonds. That is, all the bonds are saturated with

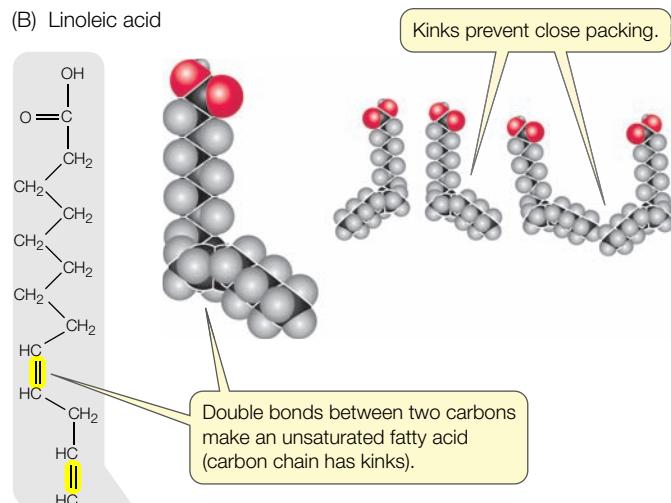
**3.18 Synthesis of a Triglyceride** In living things, the reaction that forms a triglyceride is more complex, but the end result is the same as shown here.



(A) Palmitic acid



(B) Linoleic acid



**3.19 Saturated and Unsaturated Fatty Acids** (A) The straight hydrocarbon chain of a saturated fatty acid allows the molecule to pack tightly with other, similar molecules. (B) In unsaturated fatty acids, kinks in the chain prevent close packing. The color convention in the models shown here (gray, H; red, O; black, C) is commonly used.

hydrogen atoms (**Figure 3.19A**). These fatty acid molecules are relatively rigid and straight, and they pack together tightly, like pencils in a box.

- In **unsaturated fatty acids**, the hydrocarbon chain contains one or more double bonds. Linoleic acid is an example of a *polyunsaturated* fatty acid that has two double bonds near the middle of the hydrocarbon chain, which causes kinks in the molecule (**Figure 3.19B**). Such kinks prevent the unsaturated fat molecules from packing together tightly.

The kinks in fatty acid molecules are important in determining the fluidity and melting point of a lipid. The triglycerides

of animal fats tend to have many long-chain saturated fatty acids, packed tightly together; these fats are usually solids at room temperature and have a high melting point. The triglycerides of plants, such as corn oil, tend to have short or unsaturated fatty acids. Because of their kinks, these fatty acids pack together poorly and have a low melting point, and these triglycerides are usually liquids at room temperature.

Fats are excellent storehouses for chemical energy. As you will see in Chapter 9, when the C—H bond is broken, it releases significant energy that an organism can use for its own purposes, such as movement or building up complex molecules. On a per weight basis, broken-down fats yield more than twice as much energy as do degraded carbohydrates.

### Phospholipids form biological membranes

We have mentioned the hydrophobic nature of the many C—C and C—H bonds in fatty acids. But what about the carboxyl functional group at the end of the molecule? When it ionizes and forms  $\text{COO}^-$ , it is strongly hydrophilic. So a fatty acid is a molecule with a hydrophilic end and a long hydrophobic tail. It has two opposing chemical properties; the technical term for this is **amphipathic**. This explains what happens when oil (fatty acid) and water mix: the fatty acids orient themselves so that their polar ends face outward (i.e., toward the water) and their nonpolar tails face inward (away from water). Although no covalent bonds link individual lipids in large aggregations, such stable aggregations form readily in aqueous conditions. So these large lipid structures can be considered a different kind of macromolecule.

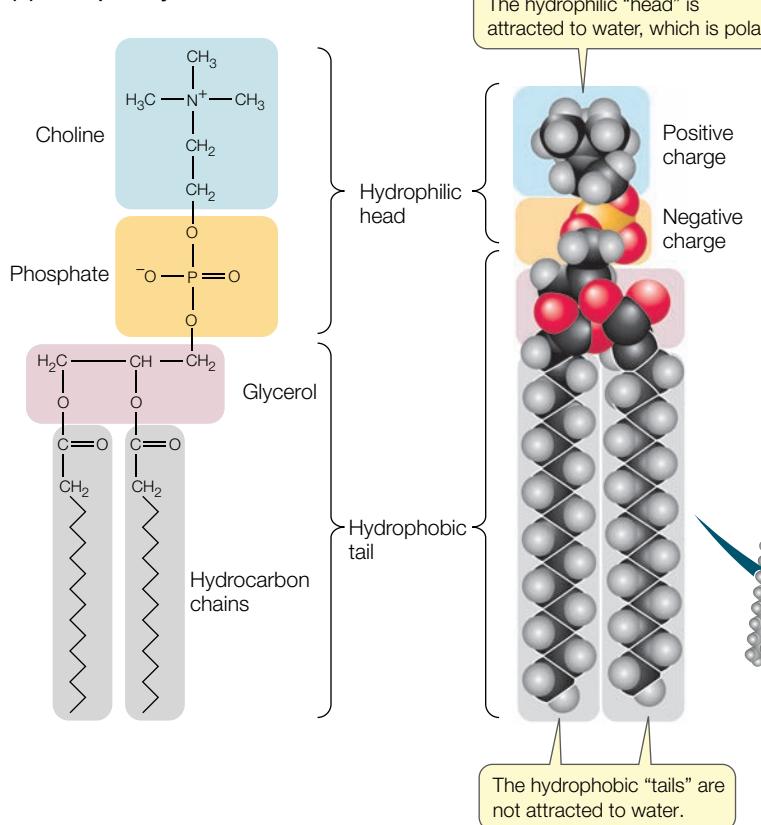
Like triglycerides, **phospholipids** contain fatty acids bound to glycerol by ester linkages. In phospholipids, however, any one of several phosphate-containing compounds replaces one of the fatty acids, giving these molecules amphipathic properties—that is properties of both water soluble and water insoluble molecules (**Figure 3.20A**). The phosphate functional group has a negative electric charge, so this portion of the molecule is hydrophilic, attracting polar water molecules. But the two fatty acids are hydrophobic, so they tend to avoid water and aggregate together or with other hydrophobic substances.

In an aqueous environment, phospholipids line up in such a way that the nonpolar, hydrophobic “tails” pack tightly together and the phosphate-containing “heads” face outward, where they interact with water. The phospholipids thus form a **bilayer**: a sheet two molecules thick, with water excluded from the core (**Figure 3.20B**). Biological membranes have this kind of **phospholipid bilayer** structure, and we will devote Chapter 6 to their biological functions.

### Lipids have roles in energy conversion, regulation, and protection

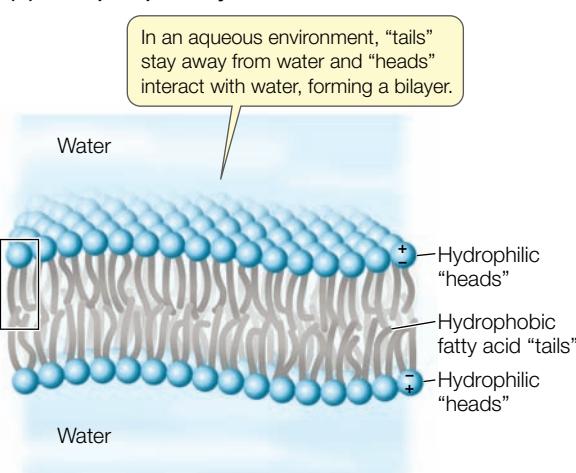
In the previous section, we focused on lipids involved in energy storage and cell structure, whose molecular structures are variations on the glycerol-fatty acid structure. However, there are other nonpolar and amphipathic lipids that are not based on this structure.

## (A) Phosphatidylcholine

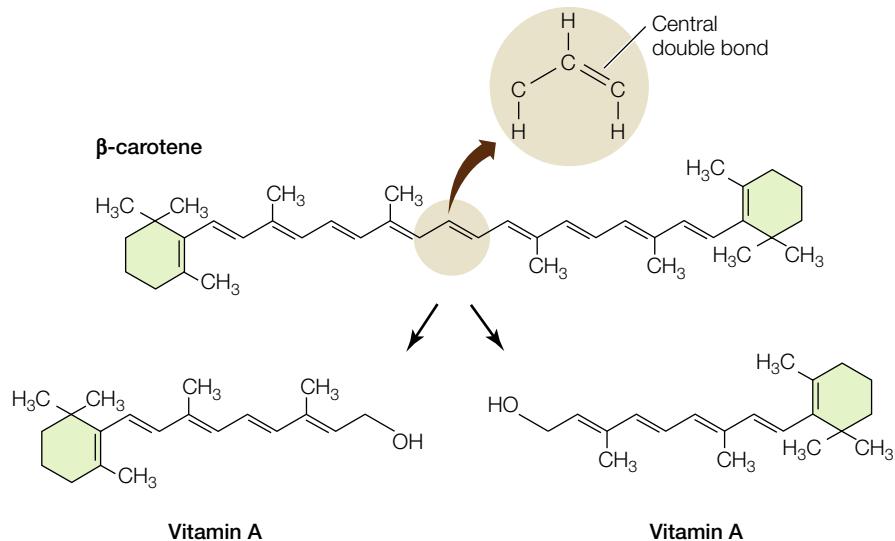


**3.20 Phospholipids** (A) Phosphatidylcholine (lecithin) demonstrates the structure of a phospholipid molecule. In other phospholipids, the amino acid serine, the sugar alcohol inositol, or other compounds replace choline. (B) In an aqueous environment, hydrophobic interactions bring the “tails” of phospholipids together in the interior of a bilayer. The hydrophilic “heads” face outward on both sides of the bilayer, where they interact with the surrounding water molecules.

## (B) Phospholipid bilayer



**CAROTENOIDS** The carotenoids are a family of light-absorbing pigments found in plants and animals. Beta-carotene ( $\beta$ -carotene) is one of the pigments that traps light energy in leaves during photosynthesis. In humans, a molecule of  $\beta$ -carotene can be broken down into two vitamin A molecules (Figure 3.21), from which we make the pigment *cis*-retinal, which is required for vision. Carotenoids are responsible for the colors of carrots, tomatoes, pumpkins, egg yolks, and butter.

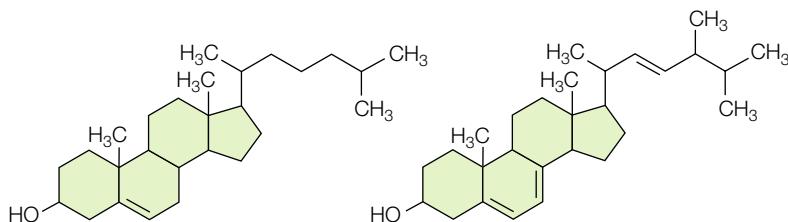


**STEROIDS** The steroids are a family of organic compounds whose multiple rings share carbons (Figure 3.22). The steroid cholesterol is an important constituent of membranes. Other steroids function as hormones, chemical signals that carry messages from one part of the body to another (see Chapter 41). Cholesterol is synthesized in the liver and is the starting material for making testosterone and other steroid hormones, such as estrogen.

**VITAMINS** Vitamins are small molecules that are not synthesized by the human body and so must be acquired from the diet (see

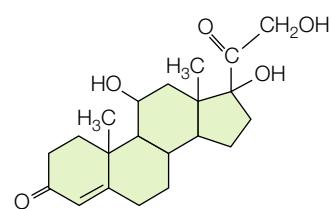
Chapter 50). For example, vitamin A is formed from the  $\beta$ -carotene found in green and yellow vegetables (see Figure 3.21). In humans, a deficiency of vitamin A leads to dry skin, eyes, and internal body surfaces, retarded growth and development, and night blindness, which is a diagnostic symptom for the deficiency. Vitamins D, E, and K are also lipids.

**3.21  $\beta$ -Carotene is the Source of Vitamin A** The carotenoid  $\beta$ -carotene is symmetrical around its central double bond. When that bond is broken, two molecules of vitamin A are formed. The structural formula presented here is standard chemical shorthand for large organic molecules with many carbon atoms; it is simplified by omitting the C (indicating a carbon atom) at the intersections representing covalent bonds. The presence of hydrogen atoms (H) to fill all the available bonding sites on each C is assumed.

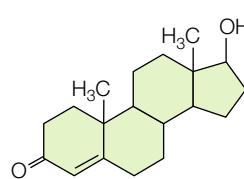


**Cholesterol** is a constituent of membranes and is the source of steroid hormones.

**Vitamin D<sub>2</sub>** can be produced in the skin by the action of light on a cholesterol derivative.

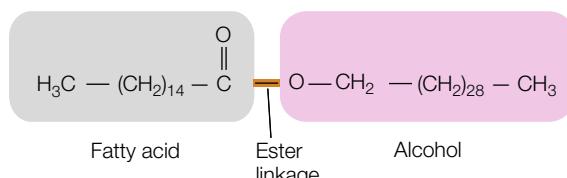


**Cortisol** is a hormone secreted by the adrenal glands.



**Testosterone** is a male sex hormone.

**WAXES** The sheen on human hair is more than cosmetic. Glands in the skin secrete a waxy coating that repels water and keeps the hair pliable. Birds that live near water have a similar waxy coating on their feathers. The shiny leaves of plants such as holly, familiar during winter holidays, also have a waxy coating. Finally, bees make their honeycombs out of wax. All waxes have the same basic structure: they are formed by an ester linkage between a saturated, long-chain fatty acid and a saturated, long-chain alcohol. The result is a very long molecule, with 40–60 CH<sub>2</sub> groups. For example, here is the structure of beeswax:



This highly nonpolar structure accounts for the impermeability of wax to water.

**3.22 All Steroids Have the Same Ring Structure** The steroids shown here, all important in vertebrates, are composed of carbon and hydrogen and are highly hydrophobic. However, small chemical variations, such as the presence or absence of a hydroxyl group, can produce enormous functional differences among these molecules.

## 3.4 RECAP

Lipids include both nonpolar and amphipathic molecules that are largely composed of carbon and hydrogen. They are important in energy storage, light absorption, regulation and biological structures. Cell membranes contain phospholipids, which are composed of hydrophobic fatty acids linked to glycerol and a hydrophilic phosphate group.

- Draw the molecular structures of fatty acids and glycerol and show how they are linked to form a triglyceride. **See p. 54 and Figure 3.18**
- What is the difference between fats and oils? **See p. 54**
- How does the polar nature of phospholipids result in their forming a bilayer? **See p. 55 and Figure 3.20**
- Why are steroids and some vitamins classified as lipids? **See p. 56**

All the types of molecules we have discussed in this chapter are found only in living organisms, but a final class of biological macromolecules has special importance to the living world. The function of the nucleic acids is nothing less than the transmission of life's "blueprint" to each new organism. This chapter showed the wonderful biochemical unity of life, a unity that implies all life has a common origin. Essential to this origin were the monomeric nucleotides and their polymers, nucleic acids. In the next chapter, we turn to the related topics of nucleic acids and the origin of life.

## CHAPTER SUMMARY

### 3.1 What Kinds of Molecules Characterize Living Things?

#### SEE ANIMATED TUTORIAL 3.1

- Macromolecules** are **polymers** constructed by the formation of covalent bonds between smaller molecules called **monomers**. Macromolecules in living organisms include polysaccharides, proteins, and nucleic acids. Large lipid structures may also be considered macromolecules.
- Functional groups** are small groups of atoms that are consistently found together in a variety of different macromolecules. Functional groups have particular chemical properties that they

confer on any larger molecule of which they are a part. **Review Figure 3.1, WEB ACTIVITY 3.1**

- Structural and optical **isomers** have the same kinds and numbers of atoms, but differ in their structures and properties. **Review Figure 3.2**
- The many functions of macromolecules are directly related to their three-dimensional shapes, which in turn result from the sequences and chemical properties of their monomers.
- Monomers are joined by **condensation reactions**, which release a molecule of water for each bond formed. **Hydrolysis reactions** use water to break polymers into monomers. **Review Figure 3.4**

### 3.2 What Are the Chemical Structures and Functions of Proteins?

- The functions of proteins include support, protection, catalysis, transport, defense, regulation, and movement.
- Amino acids** are the monomers from which proteins are constructed. Four groups are attached to a central carbon atom: a hydrogen atom, an amino group, a carboxyl group, and a variable R group. The particular properties of each amino acids depend on its **side chain**, or **R group**, which may be charged, polar, or hydrophobic. **Review Table 3.1, WEB ACTIVITY 3.2**
- Peptide linkages**, also called peptide bonds, covalently link amino acids into polypeptide chains. These bonds form by condensation reactions between the carboxyl and amino groups. **Review Figure 3.6**
- The **primary structure** of a protein is the sequence of amino acids in the chain. This chain is folded into a **secondary structure**, which in different parts of the protein may form an  **$\alpha$  helix** or a  **$\beta$  pleated sheet**. **Review Figure 3.7A–C**
- Disulfide bridges** and noncovalent interactions between amino acids cause polypeptide chains to fold into three-dimensional **tertiary structures** and allow multiple chains to interact in a **quaternary structure**. **Review Figure 3.7D,E**
- Heat, alterations in pH, or certain chemicals can all result in protein **denaturation**, which involves the loss of tertiary and/or secondary structure as well as biological function. **Review Figure 3.9**
- The specific shape and structure of a protein allows it to bind noncovalently to other molecules. **Review Figure 3.11**
- Chaperone proteins** enhance correct protein folding and prevent binding to inappropriate ligands. **Review Figure 3.12**

### 3.3 What Are the Chemical Structures and Functions of Carbohydrates?

- Carbohydrates** contain carbon bonded to hydrogen and oxygen atoms in a ratio of 1:2:1, or  $(\text{CH}_2\text{O})_n$ .

- Monosaccharides** are the monomers that make up carbohydrates. **Hexoses** such as **glucose** are six-carbon monosaccharides; **pentoses** have five carbons. **Review Figure 3.14, WEB ACTIVITY 3.3**
- Glycosidic linkages**, which have either an  $\alpha$  or a  $\beta$  orientation in space, covalently link monosaccharides into larger units such as **disaccharides**, **oligosaccharides**, and **polysaccharides**. **Review Figure 3.15**
- Starch** stores energy in plants. Starch and **glycogen** are formed by  $\alpha$ -glycosidic linkages between glucose monomers and are distinguished by the amount of branching they exhibit. They can be easily broken down to release stored energy. **Review Figure 3.16**
- Cellulose** is a very stable glucose polymer and is the principal structural component of plant cell walls.

### 3.4 What Are the Chemical Structures and Functions of Lipids?

- Fats and oils are **triglycerides**, composed of three fatty acids covalently bonded to a molecule of glycerol by ester linkages. **Review Figure 3.18**
- Saturated** fatty acids have a hydrocarbon chain with no double bonds. The hydrocarbon chains of **unsaturated** fatty acids have one or more double bonds that bend the chain, making close packing less possible. **Review Figure 3.19**
- Phospholipids** have a hydrophobic hydrocarbon “tail” and a hydrophilic phosphate “head”; that is, they are **amphipathic**. In water, the interactions of the tails and heads of phospholipids generate a **phospholipid bilayer**. The heads are directed outward, where they interact with the surrounding water. The tails are packed together in the interior of the bilayer, away from water. **Review Figure 3.20**
- Other lipids include vitamins A and D, steroids and plant pigments such as carotenoids.

### SELF-QUIZ

- The most abundant molecule in the cell is
  - a carbohydrate.
  - a lipid.
  - a nucleic acid.
  - a protein.
  - water.
- All lipids are
  - triglycerides.
  - polar.
  - hydrophilic.
  - polymers of fatty acids.
  - more soluble in nonpolar solvents than in water.
- All carbohydrates
  - are polymers.
  - are simple sugars.
  - consist of one or more simple sugars.
  - are found in biological membranes.
  - are more soluble in nonpolar solvents than in water.
- Which of the following is *not* a carbohydrate?
  - Glucose
  - Starch
  - Cellulose
  - Hemoglobin
  - Deoxyribose
- All proteins
  - are enzymes.
  - consist of one or more polypeptide chains.
  - are amino acids.
  - have quaternary structures.
  - are more soluble in nonpolar solvents than in water.
- Which of the following statements about the primary structure of a protein is *not* true?
  - It may be branched.
  - It is held together by covalent bonds.
  - It is unique to that protein.
  - It determines the tertiary structure of the protein.
  - It is the sequence of amino acids in the protein.

7. The amino acid leucine
  - a. is found in all proteins.
  - b. cannot form peptide linkages.
  - c. has a hydrophobic side chain.
  - d. has a hydrophilic side chain.
  - e. is identical to the amino acid lysine.
8. The quaternary structure of a protein
  - a. consists of four subunits—hence the name quaternary.
  - b. is unrelated to the function of the protein.
  - c. may be either alpha or beta.
  - d. depends on covalent bonding among the subunits.
  - e. depends on the primary structures of the subunits.
9. The amphipathic nature of phospholipids is
  - a. determined by the fatty acid composition.
  - b. important in membrane structure.
  - c. polar but not nonpolar.
  - d. shown only if the lipid is in a nonpolar solvent.
  - e. important in energy storage by lipids.
10. Which of the following statements about condensation reactions is *not* true?
  - a. Protein synthesis results from them.
  - b. Polysaccharide synthesis results from them.
  - c. They involve covalent bonds.
  - d. They consume water as a reactant.
  - e. Different condensation reactions produce different kinds of macromolecules.

## FOR DISCUSSION

1. Suppose that, in a given protein, one lysine is replaced by aspartic acid (see Table 3.1). Does this change occur in the primary structure or in the secondary structure? How might it result in a change in tertiary structure? In quaternary structure?
2. If there are 20 different amino acids commonly found in proteins, how many different dipeptides are there? How many different tripeptides?

## ADDITIONAL INVESTIGATION

Human hair is composed of a protein, keratin. At the hair salon, two techniques are used to modify the three-dimensional shape of hair. Styling involves heat, and a perm involves cleaving and

reforming disulfide bonds. How would you investigate these phenomena in terms of protein structure?

## WORKING WITH DATA (GO TO [yourBioPortal.com](http://yourBioPortal.com))

**Primary Structure Specifies Tertiary Structure** In this hands-on exercise based on Figure 3.9, you will learn about the methods used to disrupt the chemical interactions that determine

the tertiary structure of proteins. You will examine the original data that led Anfinsen to conclude that denaturation of ribonuclease is reversible.

# 4

# Nucleic Acids and the Origin of Life

## Looking for life

The trip had lasted a long and anxious ten months when, in the summer of 1976, the first of two visitors from Earth landed on a plain on the Martian surface. A second spacecraft arrived in September. The task of these robotic laboratories, part of NASA's Viking project, was to search for life.

On Earth, life has existed for several billion years and has spread over most of the planet's surface. Determining life's origins is difficult, however, because (with few exceptions) simple organisms leave no fossils. On Mars, scientists thought, things might be different. A primitive form of life might exist there now, or might have left chemical signatures that remain in place, untouched by other organisms.

The two Viking spacecraft that landed on Mars in 1976 analyzed soil samples for the small molecules of life, in-

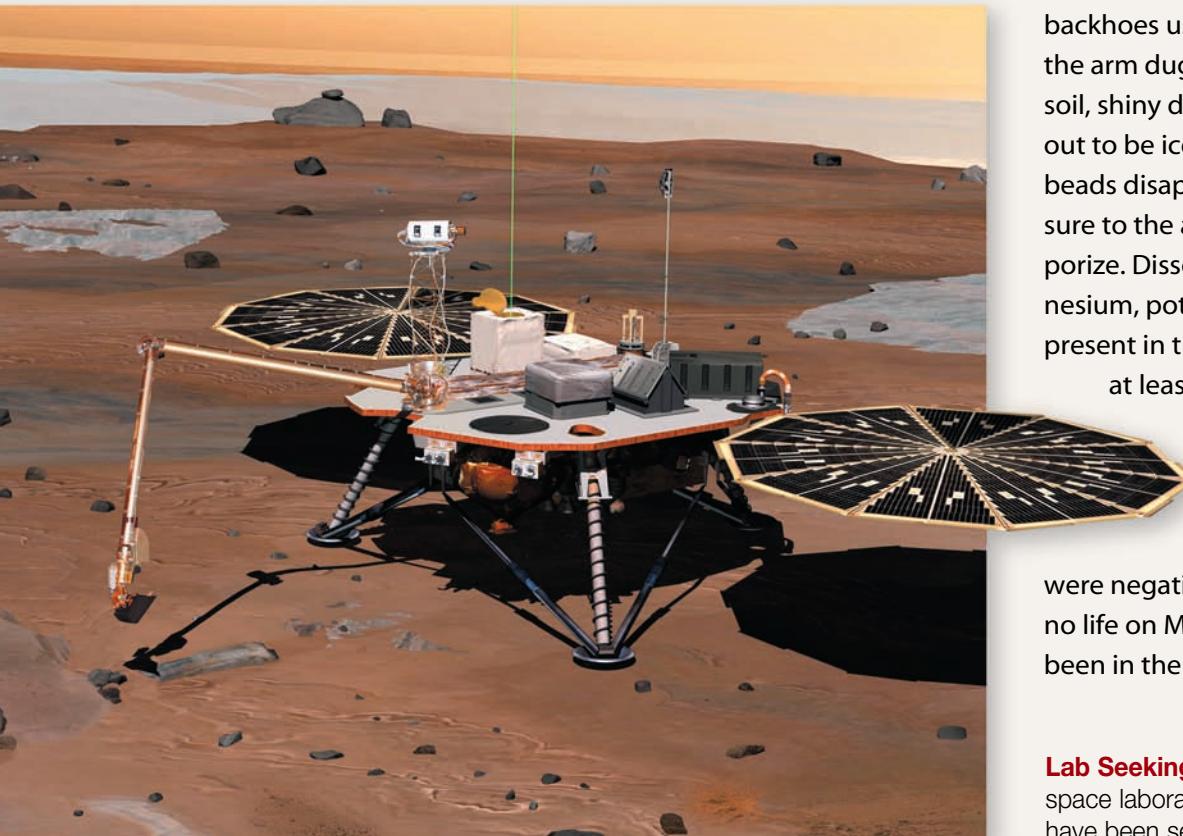
cluding simple sugars and amino acids. None were found. The robotic laboratories immersed soil samples in an aqueous solution of sugars, amino acids, and minerals. Living organisms take in and break down such substances from their environment, releasing gases such as CO<sub>2</sub>. A small amount of CO<sub>2</sub> was detected in one experiment, but, frustratingly, no gases were released in further experiments.

The results from the Viking landers remain controversial. Why did that one experiment detect a sign of life? The 1976 robotic landers are still on Mars but have long since stopped working. In 2008, more probes were sent from Earth, carrying more sophisticated instruments. One of them, the Phoenix lander, is in a northern region of Mars, at a latitude corresponding to that of Alaska on

Earth. Phoenix has a robotic arm like the backhoes used in a construction site. When the arm dug a small trench into the Martian soil, shiny dice-sized beads of what turned out to be ice were exposed, although the beads disappeared in a few days as exposure to the atmosphere caused them to vaporize. Dissolved ions such as sodium, magnesium, potassium and chloride were all present in the frozen water, indicating that

at least those requirements for life are present on Mars. Once again, the soil was analyzed for traces of current or past organisms; once again, the results were negative. But even if there probably is no life on Mars today, there might have been in the past.

**Lab Seeking Life** Landers such as the robotic space laboratory Phoenix, shown here on Earth, have been sent to look for traces of life on Mars.





**Ice on Mars** The Phoenix landing site (blue dot) is near the Martian north pole, where chemical traces of life might be preserved in the hypercold environment. When the lander scooped up a patch of soil for analysis, it also took photos that revealed ice crystals just below the surface of the Red Planet.

As we saw in Chapter 2, water is a key requirement for life. Remote measurements from orbiting spacecraft and chemical measurements using special telescopes have shown that water is present on Mars and, indeed, on some of the moons of other planets in our solar system.

Scientists are using their knowledge of the small and large molecules that are present in living organisms to search for the chemical signatures of life on other planets. Chapters 2 and 3 described molecules that are important for biological structure and function. In Chapter 4, we turn to certain molecules involved in the origin and perpetuation of life itself.

**IN THIS CHAPTER** we first describe the structure of nucleic acids, the informational macromolecules needed for the perpetuation of life. We then turn to biologists' speculations on the origin of life and describe early experimental evidence that life on Earth today comes from pre-existing life. We present some ideas on the formation of the building blocks of life, including the monomers and polymers that characterize biological systems. Finally, we describe some proposals for the origin of cells.

## CHAPTER OUTLINE

- 4.1** What Are the Chemical Structures and Functions of Nucleic Acids?
- 4.2** How and Where Did the Small Molecules of Life Originate?
- 4.3** How Did the Large Molecules of Life Originate?
- 4.4** How Did the First Cells Originate?

### 4.1 What Are the Chemical Structures and Functions of Nucleic Acids?

From medicine to evolution, from agriculture to forensics, the properties of nucleic acids impact our lives every day. It is with nucleic acids that the concept of “information” entered the biological vocabulary. Nucleic acids are uniquely capable of coding for and transmitting biological information.

The **nucleic acids** are polymers specialized for the storage, transmission between generations, and use of genetic information. There are two types of nucleic acids: **DNA** (*deoxyribonucleic acid*) and **RNA** (*ribonucleic acid*). DNA is a macromolecule that encodes hereditary information and passes it from generation to generation. Through an RNA intermediate, the information encoded in DNA is used to specify the amino acid sequences of proteins. Information flows from DNA to DNA during reproduction. In the non-reproductive activities of the cell, information flows from DNA to RNA to proteins. It is the proteins that ultimately carry out life’s functions.

#### Nucleotides are the building blocks of nucleic acids

Nucleic acids are composed of monomers called **nucleotides**, each of which consists of a pentose sugar, a phosphate group, and a nitrogen-containing **base**. (Molecules consisting of a pentose sugar and a nitrogenous base—but no phosphate group—are called *nucleosides*.) The bases of the nucleic acids take one of two chemical forms: a six-membered single-ring structure called a **pyrimidine**, or a fused double-ring structure called a **purine** (Figure 4.1). In DNA, the pentose sugar is **deoxyribose**, which differs from the **ribose** found in RNA by the absence of one oxygen atom (see Figure 3.14).

In both RNA and DNA, the backbone of the macromolecule consists of a chain of alternating pentose sugars and phosphate groups (sugar–phosphate–sugar–phosphate). The bases are attached to the sugars and project from the polynucleotide chain (Figure 4.2). The nucleotides are joined by **phosphodiester linkages** between the sugar of one nucleotide and the phosphate of the next (*diester* refers to the two covalent bonds formed by —OH groups reacting with acidic phosphate groups). The phosphate groups link carbon 3 in one pentose sugar to carbon 5 in the adjacent sugar.

Most RNA molecules consist of only one polynucleotide chain. DNA, however, is usually double-stranded; its two polynucleotide chains are held together by hydrogen bonding between their nitrogenous bases. The two strands of DNA run in opposite directions. You can see what this means by drawing an arrow through a phosphate group from carbon 5 to

**4.1 Nucleotides Have Three Components** Nucleotide monomers are the building blocks of DNA and RNA polymers.

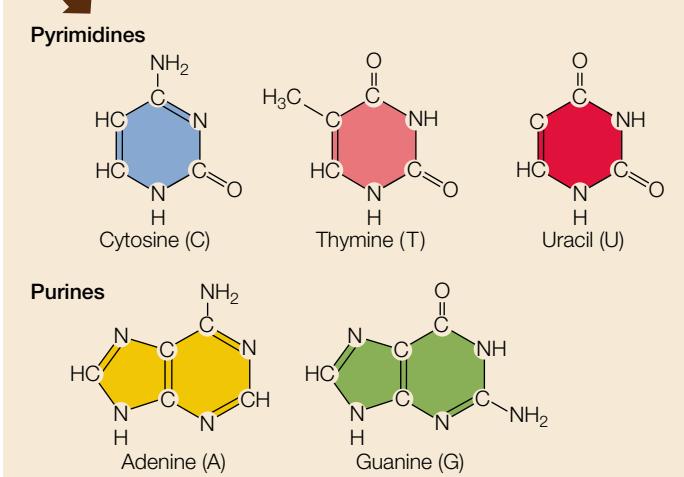
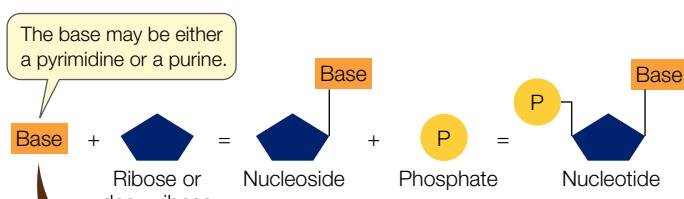
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GO TO Web Activity 4.1 • Nucleic Acid Building Blocks

carbon 3 in the next ribose. If you do this for both strands of the DNA in Figure 4.2, the arrows will point in opposite directions. This *antiparallel* orientation allows the strands to fit together in three-dimensional space.

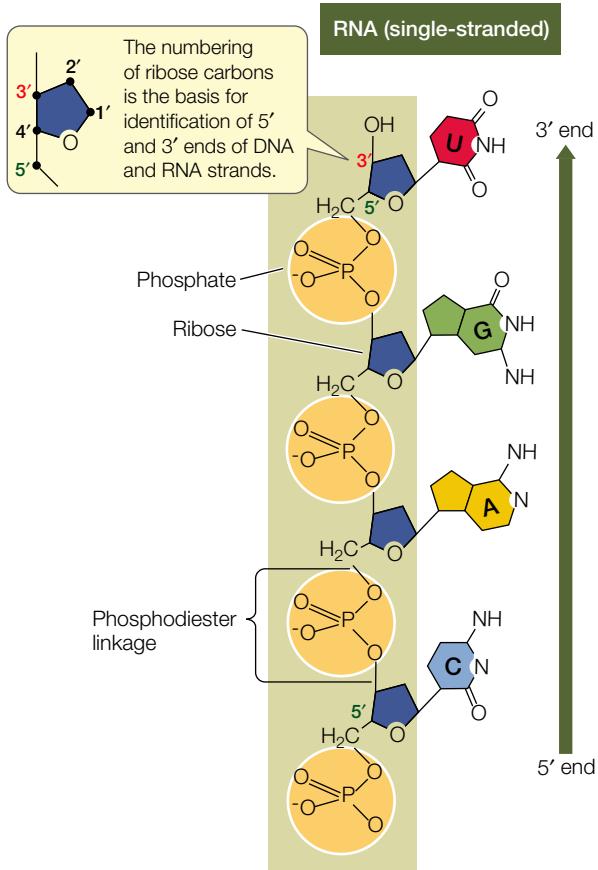
### Base pairing occurs in both DNA and RNA

Only four nitrogenous bases—and thus only four nucleotides—are found in DNA. The DNA bases and their abbreviations are **adenine (A)**, **cytosine (C)**, **guanine (G)**, and **thymine (T)**. Adenine and guanine are purines; thymine and cytosine are pyrimidines. RNA is also made up of four different monomers, but its nucleotides differ from those of DNA. In RNA the nucleotides are termed *ribonucleotides* (the ones in DNA are *deoxyribonucleotides*). They contain ribose rather than deoxyribose, and in-

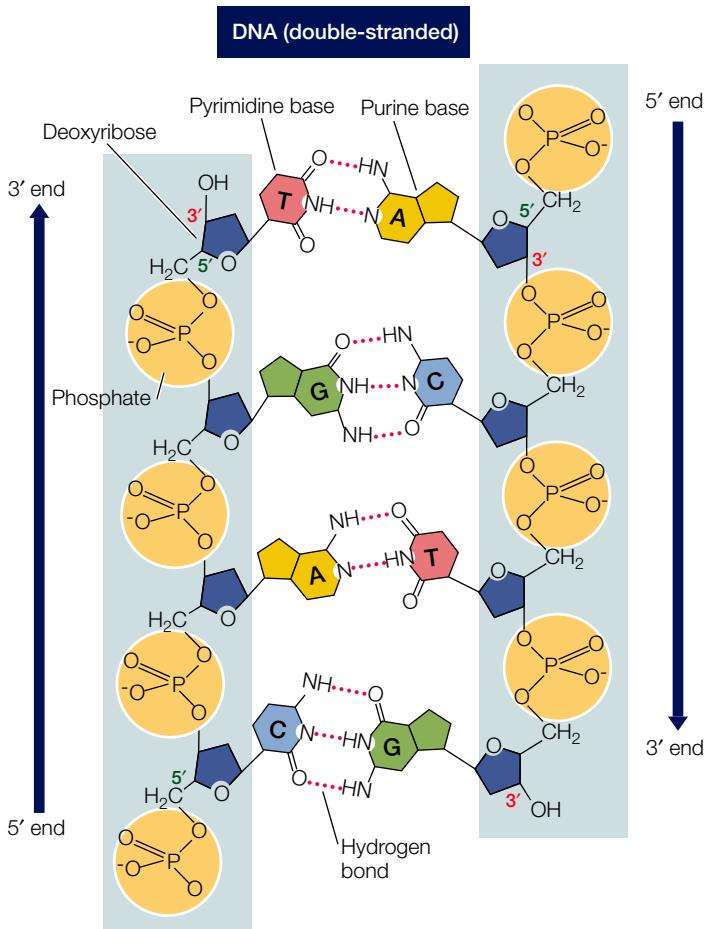


### 4.2 Distinguishing Characteristics of DNA and RNA Polymers

RNA is usually a single strand. DNA usually consists of two strands running in opposite directions (antiparallel).



In RNA, the bases are attached to ribose. The bases in RNA are the purines adenine (A) and guanine (G) and the pyrimidines cytosine (C) and uracil (U).



In DNA, the bases are attached to deoxyribose, and the base thymine (T) is found instead of uracil. Hydrogen bonds between purines and pyrimidines hold the two strands of DNA together.

**TABLE 4.1**  
**Distinguishing RNA from DNA**

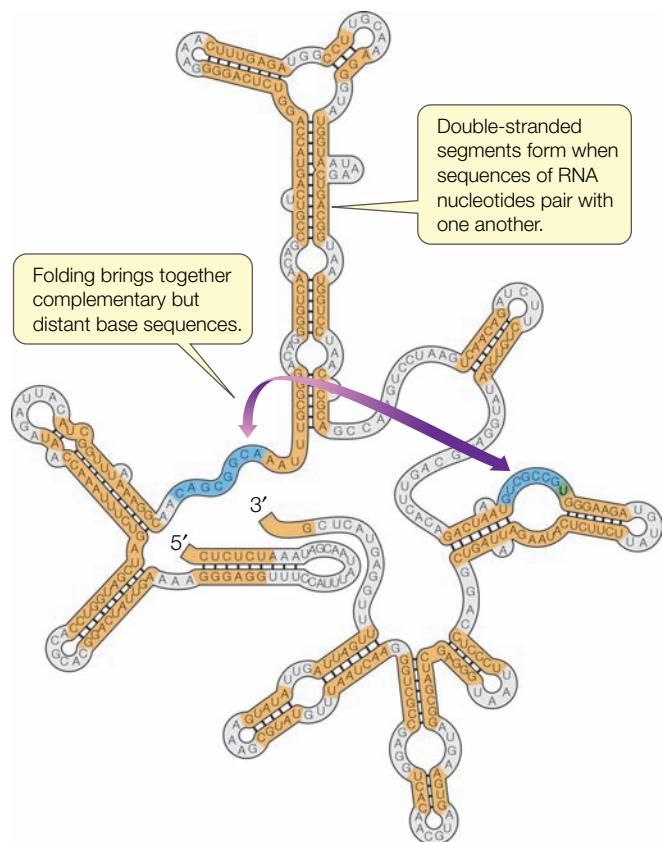
NUCLEIC ACID	SUGAR	BASES	STRANDS
RNA	Ribose	Adenine	Single
		Cytosine	
		Guanine	
		Uracil	
DNA	Deoxyribose	Adenine	Double
		Cytosine	
		Guanine	
		Thymine	

stead of the base thymine, RNA uses the base **uracil (U)**. The other three bases are the same in RNA and DNA (**Table 4.1**).

The key to understanding the structure and function of nucleic acids is the principle of **complementary base pairing**. In double-stranded DNA, adenine and thymine always pair (A-T), and cytosine and guanine always pair (C-G).

Three factors make base pairing complementary:

- The sites for hydrogen bonding on each base
- The geometry of the sugar–phosphate backbone, which brings complementary bases near each other



**4.3 Hydrogen Bonding in RNA** When a single-stranded RNA folds on itself, hydrogen bonds between complementary sequences can stabilize it into a three-dimensional shape with complicated surface characteristics.

- The molecular sizes of the paired bases; the pairing of a larger purine with a smaller pyrimidine ensures stability and uniformity in the double-stranded molecule of DNA

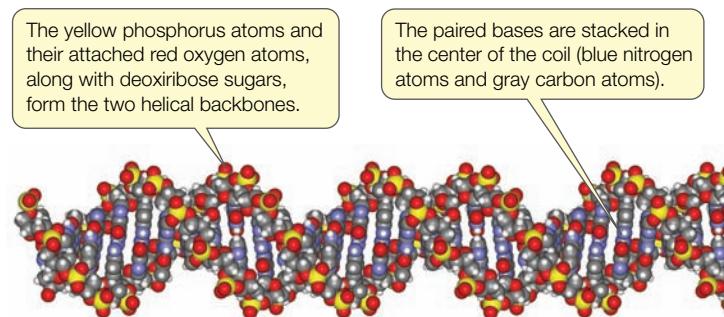
Although RNA is generally single-stranded, complementary hydrogen bonding between ribonucleotides plays important roles in determining the three-dimensional shapes of some types of RNA molecules, since portions of the single-stranded RNA can fold back and pair with each other (**Figure 4.3**). Complementary base pairing can also take place between ribonucleotides and deoxyribonucleotides. In RNA, guanine and cytosine pair (G-C), as in DNA, but adenine pairs with uracil (A-U). Adenine in an RNA strand can pair either with uracil (in another RNA strand) or with thymine (in a DNA strand).

The three-dimensional physical appearance of DNA is strikingly uniform. The segment shown in **Figure 4.4** could be from any DNA molecule. The variations in DNA—the different sequences of bases—are strictly internal. Through hydrogen bonding, the two complementary polynucleotide strands pair and twist to form a **double helix**. When compared with the complex and varied tertiary structures of proteins, this uniformity is surprising. But this structural contrast makes sense in terms of the functions of these two classes of macromolecules. As we describe in Section 3.2, the different and unique shapes of proteins permit these macromolecules to recognize specific “target” molecules. The area on the surface of a protein that interacts with the target molecule must match the shape of at least part of the target molecule. In other words, structural diversity in the target molecules requires corresponding diversity in the structures of the proteins themselves. Structural diversity is necessary in DNA as well. However, the diversity of DNA is found in its base sequence rather than in the physical shape of the molecule. Different DNA base sequences encode specific information.

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GO TO Web Activity 4.2 • DNA Structure

### DNA carries information and is expressed through RNA

DNA is a purely *informational* molecule. The information is encoded in the sequence of bases carried in its strands—the infor-



**4.4 The Double Helix of DNA** The backbones of the two strands in a DNA molecule are coiled in a double helix that is held together by hydrogen bonds between the purines and pyrimidines in the interior of the structure. In this model, the small white atoms represent hydrogen.

**4.5 DNA Stores Information** The DNA macromolecule stores information that can either be copied (replicated) or transcribed into RNA. RNA can then be translated into protein.

mation encoded in the sequence TCAGCA is different from the information in the sequence CCAGCA. DNA has two functions in terms of information. Taken together, they comprise the *central dogma of molecular biology* (Figure 4.5).

- DNA can reproduce itself exactly. This is called *DNA replication*. It is done by polymerization on a template.
- DNA can copy its information into RNA, in a process called *transcription*. The nucleotide sequence in RNA can specify a sequence of amino acids in a polypeptide. This is called *translation*.

While the details of these important processes are described in later chapters, it is important to realize two things at this point:

1. *DNA replication and transcription depend on the base pairing properties of nucleic acids.* The hydrogen-bonded base pairs are A-T and G-C in DNA and A-U and G-C in RNA (see Figure 4.2). Consider this double-stranded DNA region:

```
T CAGCA
      AGTCGT
```

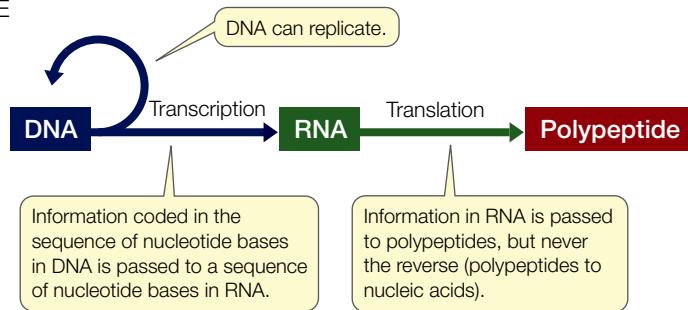
Transcription of the lower strand will result in a single strand of RNA with the sequence UCAGCA. Can you figure out what the top strand would produce?

2. *DNA replication usually involves the entire DNA molecule, but only relatively small sections of the DNA are transcribed into RNA molecules.* Since DNA holds essential information, it must be replicated completely so that each new cell or new organism receives a complete set of DNA from its parent. The complete set of DNA in a living organism is called its **genome**. However, not all of the information in the genome is needed at all times (Figure 4.6A).

The sequences of DNA that encode specific proteins are transcribed into RNA and are called **genes** (Figure 4.6B). In humans, the genes that encode the subunits of the protein hemoglobin (see Figure 3.10) are expressed only in the precursors of red blood cells. The genetic information in each globin gene is transcribed into RNA and then translated into a globin polypeptide. In other tissues, such as the muscles, the genes that encode the globin subunits are not transcribed, but others are—for example, the genes for the myosin proteins that are the major component of muscle fibers (see Section 48.1).

### The DNA base sequence reveals evolutionary relationships

Because DNA carries hereditary information from one generation to the next, a theoretical series of DNA molecules, with changes in base sequences, stretches back through the lineage of every organism to the beginning of biological evolution on Earth, about 4 billion years ago. Therefore, closely related living species should have more similar base sequences than species that are more distantly related. The details of how scientists use this information are covered in Chapter 24.

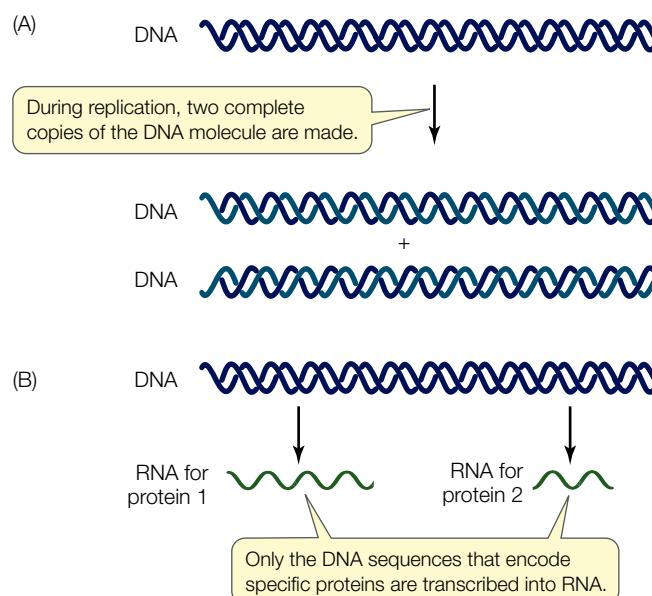


The elucidation and examination of DNA base sequences has confirmed many of the evolutionary relationships that were inferred from more traditional comparisons of body structures, biochemistry, and physiology. Many studies of anatomy, physiology, and behavior have concluded that the closest living relative of humans (*Homo sapiens*) is the chimpanzee (genus *Pan*). In fact, the chimpanzee genome shares more than 98 percent of its DNA base sequence with the human genome. Increasingly, scientists turn to DNA analyses to elucidate evolutionary relationships when other comparisons are not possible or are not conclusive. For example, DNA studies revealed a close relationship between starlings and mockingbirds that was not expected on the basis of their anatomy or behavior.

### Nucleotides have other important roles

Nucleotides are more than just the building blocks of nucleic acids. As we will describe in later chapters, there are several nucleotides with other functions:

- ATP (adenosine triphosphate) acts as an energy transducer in many biochemical reactions (see Section 8.2).



**4.6 DNA Replication and Transcription** DNA is usually completely replicated (A) but only partially transcribed (B). RNA transcripts encode the genes for specific proteins. Transcription of the many different proteins is activated at different times and, in multicellular organisms, in different cells of the body.

- GTP (guanosine triphosphate) serves as an energy source, especially in protein synthesis. It also plays a role in the transfer of information from the environment to cells (see Section 7.2).
- cAMP (cyclic adenosine monophosphate) is a special nucleotide in which an additional bond forms between the sugar and phosphate group. It is essential in many processes, including the actions of hormones and the transmission of information by the nervous system (see Section 7.3).

## 4.1 RECAP

The nucleic acids DNA and RNA are polymers made up of nucleotide monomers. The sequence of nucleotides in DNA carries the information that is used by RNA to specify primary protein structure. The genetic information in DNA is passed from generation to generation and can be used to understand evolutionary relationships.

- List the key differences between DNA and RNA. Between purines and pyrimidines. **See p. 61, Table 4.1, and Figure 4.1**
- How do purines and pyrimidines pair up in complementary base pairing? **See pp. 62–63 and Figure 4.2**
- What are the differences between DNA replication and transcription? **See pp. 63–64 and Figures 4.5 and 4.6**
- How can DNA molecules be very diverse, even though they appear to be structurally similar? **See p. 64**

We have seen that the nucleic acids RNA and DNA carry the blueprint of life, and that the inheritance of these macromolecules reaches back to the beginning of evolutionary time. But when, where, and how did nucleic acids arise on Earth? How did the building blocks of life such as amino acids and sugars originally arise?

## 4.2 How and Where Did the Small Molecules of Life Originate?

Chapter 2 points out that living things are composed of the same atomic elements as the inanimate universe—the 92 naturally occurring elements of the periodic table (see Figure 2.2). But the arrangements of these atoms into molecules are unique in biological systems. You will not find biological molecules in inanimate matter unless they came from a once-living organism.

It is impossible to know for certain how life on Earth began. But one thing is sure: life (or at least life as we know it) is not constantly being re-started. That is, *spontaneous generation* of life from inanimate nature is not happening before our eyes. Now and for many millenia past, all life has come from life that existed before. But people, including scientists, did not always believe this.

### Experiments disproved spontaneous generation of life

The idea that life could have originated from nonliving matter is common in many cultures and religions. During the European Renaissance (from about 1450 to 1700, a period that witnessed the birth of modern science), most people thought that at least some forms of life arose repeatedly and directly from inanimate or decaying matter by *spontaneous generation*. Many thought that mice arose from sweaty clothes placed in dim light; that frogs sprang directly from moist soil; and that rotting meat produced flies. Scientists such as the Italian physician and poet Francesco Redi, however, doubted these assumptions. Redi proposed that flies arose not by some mysterious transformation of decaying meat, but from other flies that laid their eggs on the meat. In 1668, Redi performed a scientific experiment—a relatively new concept at the time—to test his hypothesis. He set out several jars containing chunks of meat.

- One jar contained meat exposed to both air and flies.
- A second jar was covered with a fine cloth so that the meat was exposed to air, but not to flies.
- The third jar was sealed so the meat was exposed to neither air nor flies.

As he had hypothesized, Redi found maggots, which then hatched into flies, only in the first jar. This finding demonstrated that maggots could occur only where flies were present. The idea that a complex organism like a fly could appear *de novo* from a nonliving substance in the meat, or from “something in the air,” was laid to rest. Well, perhaps not quite to rest.

In the 1660s, newly developed microscopes revealed a vast new biological world. Under microscopic observation, virtually every environment on Earth was found to be teeming with tiny organisms. Some scientists believed these organisms arose spontaneously from their rich chemical environment, by the action of a “life force.” But experiments by the great French scientist Louis Pasteur showed that microorganisms can arise only from other microorganisms, and that an environment without life remains lifeless (**Figure 4.7**).

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**GO TO** Animated Tutorial 4.1 • Pasteur's Experiment

Pasteur’s and Redi’s experiments showed that living organisms cannot arise from nonliving materials *under the conditions that existed on Earth during their lifetimes*. But their experiments did not prove that spontaneous generation never occurred. Eons ago, conditions on Earth and in the atmosphere above it were vastly different. Indeed, conditions similar to those found on primitive Earth may have existed, or may exist now, on other bodies in our solar system and elsewhere. This has led scientists to ask whether life has originated on other bodies in space, as it did on Earth.

### Life began in water

As we emphasize in Chapter 2 and in the opening story of this chapter, the presence of water on a planet or moon is a necessary prerequisite for life as we know it. Astronomers believe our solar system began forming about 4.6 billion years ago, when a

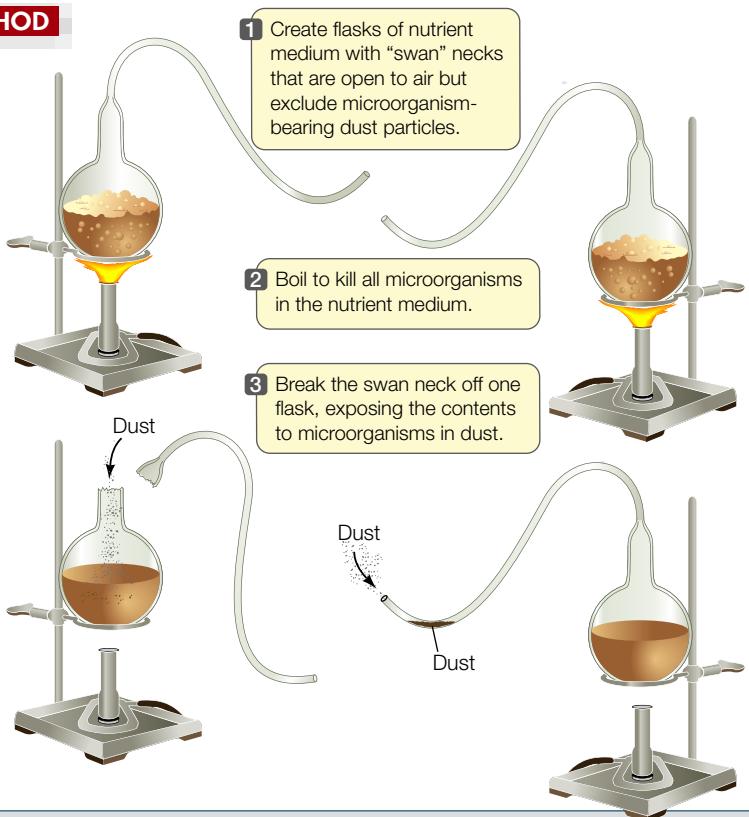
# INVESTIGATING LIFE

## 4.7 Disproving the Spontaneous Generation of Life

Previous experiments disproving spontaneous generation were called into question in regard to microorganisms, whose abundance and diversity were appreciated but whose living processes were not understood. Louis Pasteur's classic experiments disproved the spontaneous generation of microorganisms.

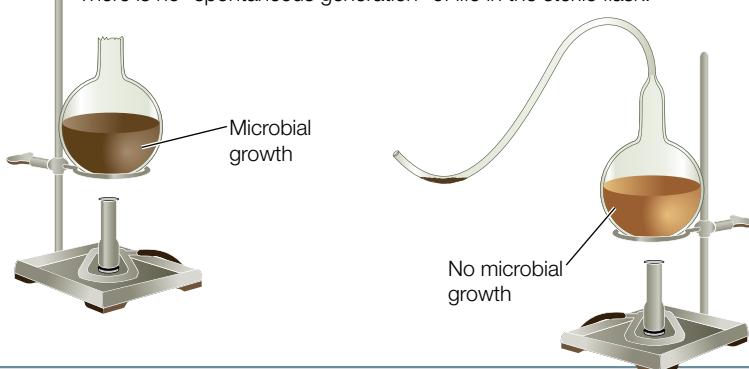
**HYPOTHESIS** Microorganisms come only from other microorganisms and cannot arise by spontaneous generation.

### METHOD



### RESULTS

Microbial life grows only in the flasks exposed to microorganisms. There is no "spontaneous generation" of life in the sterile flask.



**CONCLUSION** All life comes from pre-existing life. An environment without life remains lifeless.

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star exploded and collapsed to form the sun and 500 or so bodies, called planetesimals. These planetesimals collided with one another to form the inner planets, including Earth and Mars. The first chemical signatures indicating the presence of life on Earth appear to be about 4 billion years old. So it took 600 million years, during a geological time frame called the Hadean, for the chemical conditions on Earth to become just right for life. Key among those conditions was the presence of water.

Ancient Earth probably had a lot of water high in its atmosphere. But the new planet was hot, and the water remained in vapor form and dissipated into space. As Earth cooled, it became possible for water to condense on the planet's surface—but where did that water come from? One current view is that comets (loose agglomerations of dust and ice that have orbited the sun since the planets formed) struck Earth and Mars repeatedly, bringing to those planets not only water but other chemical components of life, such as nitrogen.

As the planets cooled and chemicals from their crusts dissolved in the water, simple chemical reactions would have taken place. Some of these reactions might have led to life, but impacts by large comets and rocky meteorites released enough energy to heat the developing oceans almost to boiling, thus destroying any early life. On Earth, these large impacts eventually subsided, and some time around 3.8 to 4 billion years ago life gained a foothold. There has been life on Earth ever since. Because Mars and some other celestial bodies have a similar geological history, the possibility exists that life exists or has existed on them. This possibility was an impetus for sending the Viking and Phoenix landers to Mars.

Several models have been proposed to explain the origin of life on Earth. The next sections discuss two alternative theories: that life came from outside of Earth, or that life arose on Earth through chemical evolution.

### Life may have come from outside Earth

In 1969, a remarkable event led to the discovery that a meteorite from space carried molecules that were characteristic of life on Earth. On September 28 of that year, fragments of a meteorite fell around the town of Murchison, Australia. Using gloves to avoid Earth-derived contamination, scientists immediately shaved off tiny pieces of the rock, put them in



**4.8 The Murchison Meteorite** Pieces from a fragment of the meteorite that landed in Australia in 1969 were put into test tubes with water. Soluble molecules present in the rock, including amino acids, nucleotide bases, and sugars, dissolved in the water. Plastic gloves and sterile instruments were used to reduce the possibility of contamination with substances from Earth.

test tubes and extracted them in water (**Figure 4.8**). They found a number of the molecules that are unique to life, including purines, pyrimidines, sugars, and ten amino acids.

Were these molecules truly brought from space as part of the meteorite, or did they get there after the rock landed on Earth? There were a number of reasons to believe the molecules were not Earthly contaminants:

- The scientists took great care to avoid contamination. They used gloves and sterile instruments, took pieces from below the rock's surface, and did their work very soon after it landed (hopefully before Earth organisms could contaminate the samples).
- Amino acids found in living organisms on Earth are left-handed (see Figure 3.2). The amino acids in the meteorite were a mixture of right- and left-handed forms, with a slight preponderance of the left-handed. Thus the amino acids in the meteorite were not likely to have come from a living organism on Earth.
- In the story that opens Chapter 2, we describe how the ratio of isotopes in a living organism reflects that isotope ratio in the environment where the organism lives. The isotope ratios for carbon and hydrogen in the sugars from the meteorite were different from the ratios of those elements found on Earth.

In 1984, another informative meteorite, this one the size of a softball, was found in Antarctica. We know that the meteorite, ALH 84001, came from Mars because the composition of the gases trapped within the rock was identical to the composition found in the Martian atmosphere, which is quite different from Earth's atmosphere. Radioactive dating and mineral analyses determined that ALH 84001 was 4.5 billion years old and was blasted off the Martian surface 16 million years ago. It landed on Earth fairly recently, about 13,000 years ago.

Scientists found water trapped below the Martian meteorite's surface. This discovery was not surprising, given that surface observations had already shown that water was once abundant on Mars (see the chapter-opening story). Because water is essential for life, scientists wondered whether the meteorite might contain other signs of life as well. Their analysis revealed two substances related to living systems. First, simple carbon-containing molecules called polycyclic aromatic hydrocarbons were present in small but unmistakable amounts; these substances can be formed by living organisms. Second, crystals of magnetite, an iron oxide mineral made by many living organisms on Earth, were found in the interior of the rock.

ALH 84001 and the Murchison meteorite are not the only visitors from outer space that have been shown to contain chemical signatures of life. While the presence of such molecules in rocks may suggest that those rocks once harbored life, it does not prove that there were living organisms in the rocks when they landed on Earth. Most scientists find it hard to believe that an organism could survive thousands of years of traveling through space in a meteorite, followed by intense heat as the meteorite passed through Earth's atmosphere. But there is some evidence that the heat inside some meteorites may not have been severe. When weakly magnetized rock is heated, it reorients its magnetic field to align with the magnetic field around it. In the case of ALH 84001, this would have been Earth's powerful magnetic field, which would have affected the meteorite as it approached our planet.

Careful measurements indicate that, while reorientation did occur at the surface of the rock, it did not occur on the inside. The scientists who took these measurements, Benjamin Weiss and Joseph Kirschvink at the California Institute of Technology, concluded that the inside of ALH 84001 was never heated over 40°C as it entered Earth's atmosphere. This suggests that a long interplanetary trip by living organisms could be possible.

### Prebiotic synthesis experiments model the early Earth

It is clear that other bodies in the solar system have, or once had, water and other simple molecules. Possibly, a meteorite was the source of the simple molecules that were the original building blocks for life on Earth. But a second theory for the origin of life on Earth, **chemical evolution**, holds that conditions on primitive Earth led to the formation of these simple molecules (prebiotic synthesis), and these molecules led to the formation of life forms. Scientists have sought to reconstruct those primitive conditions, both physically (hot or cold) and chemically (by re-creating the combinations and proportions of elements that may have been present).

**HOT CHEMISTRY** The amounts of trace metals such as molybdenum and rhenium in sediments under oceans and lakes is directly proportional to the amount of oxygen gas (O<sub>2</sub>) present in and above the water. Measurements of dated sedimentary cores indicate that none of these rare metals was present prior to 2.5 billion years ago. This and other lines of evidence suggest that there was little oxygen gas in Earth's early atmosphere. Oxygen gas is thought to have accumulated about 2.5 billion years ago

as the by-product of photosynthesis by single-celled life forms; today 21 percent of our atmosphere is O<sub>2</sub>.

In the 1950s, Stanley Miller and Harold Urey at the University of Chicago set up an experimental “atmosphere” containing the gases thought to have been present in Earth’s early atmosphere: hydrogen gas, ammonia, methane gas, and water vapor. They passed an electric spark through these gases, to simulate lightning as a source of energy to drive chemical reactions. Then, they cooled the system so the gases would condense and collect in a watery solution, or “ocean” (Figure 4.9). After a few days of continuous operation, the system contained numerous complex molecules, including amino acids, purines, and pyrimidines—some of the building blocks of life.

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**GO TO** Animated Tutorial 4.2 • Synthesis of Prebiotic Molecules

The results of this experiment were profoundly important in giving weight to speculations about the chemical origin of life on Earth and elsewhere in the universe. Decades of experimental work and critical evaluation followed. The experiments showed that, under the conditions used by Miller and Urey, many small molecular building blocks of life could be formed:

- All five bases that are present in DNA and RNA (i.e., A, T, C, G and U)
- 17 of the 20 amino acids used in protein synthesis
- 3- to 6-carbon sugars

However, the 5-carbon sugar ribose was not produced in these experiments.

In science, an experiment and its results must be repeated, reinterpreted, and refined as more knowledge accumulates. The results of the Miller–Urey experiments have undergone several such refinements.

The amino acids in living things are always L-isomers (see Figure 3.2 and p. 43). But a mixture of D- and L-isomers appeared in the amino acids formed in the Miller–Urey experiments. Recent experiments show that natural processes could have selected the L-amino acids from the mixture. Some minerals, especially calcite-based rocks, have unique crystal structures that selectively bind to D- or L-amino acids, separating the two. Such rocks were abundant on early Earth. This suggests that while both kinds of amino acid structures were made, binding to certain rocks may have eliminated the D- amino

acids. (Interestingly, some meteorites, such as the Murchison meteorite, also have this selectivity.)

Ideas about Earth’s original atmosphere have changed since Miller and Urey did their experiments. There is abundant evidence indicating that major volcanic eruptions occurred 4 bil-

## INVESTIGATING LIFE

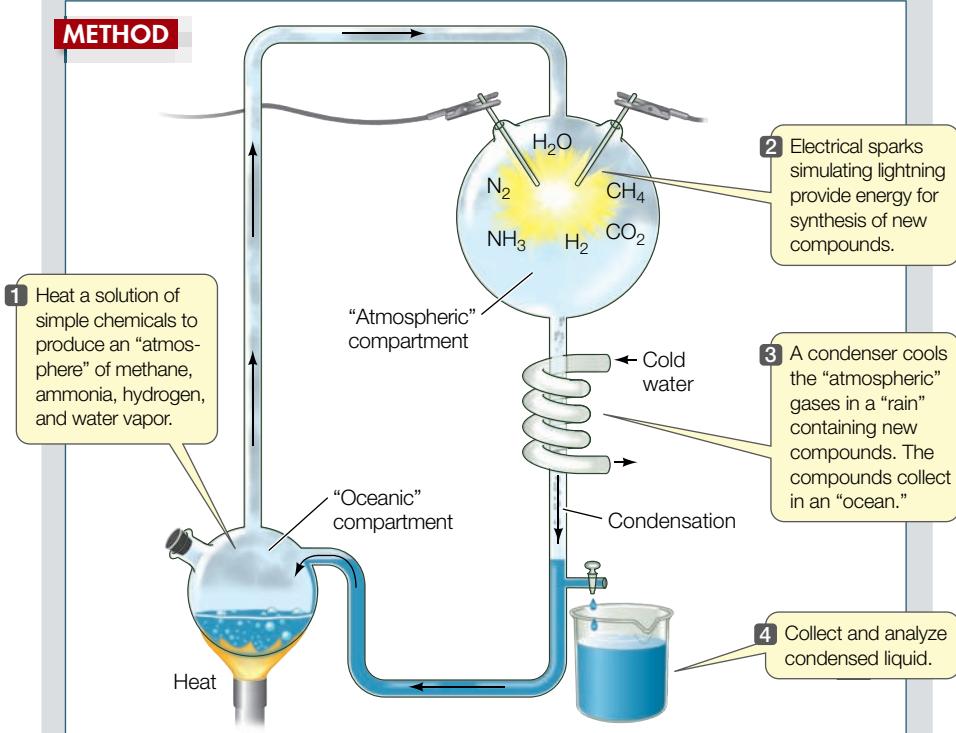
### 4.9 Miller and Urey Synthesized Prebiotic Molecules in an Experimental Atmosphere

With an increased understanding of the atmospheric conditions that existed on primitive Earth, the researchers devised an experiment to see if these conditions could lead to the formation of organic molecules.

#### HYPOTHESIS

Organic chemical compounds can be generated under conditions similar to those that existed in the atmosphere of primitive Earth.

#### METHOD



#### RESULTS



Reactions in the condensed liquid eventually formed organic chemical compounds, including purines, pyrimidines, and amino acids.

#### CONCLUSION

The chemical building blocks of life could have been generated in the probable atmosphere of early Earth.

**FURTHER INVESTIGATION:** What result would you predict if O<sub>2</sub> were present in the “atmosphere” in this experiment?

Go to [yourBioPortal.com](http://yourBioPortal.com) for original citations, discussions, and relevant links for all INVESTIGATING LIFE figures.

lion years ago, which would have released carbon dioxide ( $\text{CO}_2$ ), nitrogen ( $\text{N}_2$ ), hydrogen sulfide ( $\text{H}_2\text{S}$ ), and sulfur dioxide ( $\text{SO}_2$ ) into the atmosphere. Experiments using these gases in addition to the ones in the original experiment have produced more diverse molecules, including:

- Vitamin B<sub>6</sub>, pantothenic acid (a component of coenzyme A), and nicotinamide (part of NAD, which is involved in energy metabolism).
- Carboxylic acids such as succinic and lactic acids (also involved in energy metabolism) and fatty acids.
- Ribose, a key component of RNA, which can be formed from formaldehyde gas ( $\text{HCHO}$ ), evidence of which has been found in space.

**COLD CHEMISTRY** Stanley Miller also performed a long-term experiment in which the electric spark was not used. In 1972, he filled test tubes with ammonia gas, water vapor and cyanide ( $\text{HCN}$ ), another molecule that is thought to have formed on primitive Earth. After checking that there were no contaminating substances or organisms that might confound the results, he sealed the tubes and cooled them to  $-100^\circ\text{C}$ , the temperature of the ice that covers Europa, one of Jupiter's moons. Opening the tubes 25 years later, he found amino acids and nucleotide bases. Apparently, pockets of liquid water within the ice had allowed high concentrations of the starting materials to accumulate, thereby speeding up chemical reactions. The important conclusion is that the cold water within ice on ancient Earth, and other celestial bodies such as Mars, Europa, and Enceladus (one of Saturn's moons; satellite photos have revealed geysers of liquid water coming from its interior) may have provided environments for the prebiotic synthesis of molecules required for the subsequent formation of simple living systems.

## 4.2 RECAP

Life does not arise repeatedly through spontaneous generation, but comes from pre-existing life. Water is an essential ingredient for the emergence of life. Meteorites that have landed on Earth provide some evidence for an extraterrestrial origin of life. Prebiotic chemical synthesis experiments provide support for the idea that life's simple molecules formed in the primitive Earth environment.

- Explain how Redi's and Pasteur's experiments disproved spontaneous generation. **See p. 65 and Figure 4.7**
- What is the evidence that life on Earth came from other bodies in the solar system? **See pp. 66–67**
- What is the significance of the Miller–Urey experiment, what did it find, and what were its limitations? **See p. 68 and Figure 4.9**

Chemistry experiments using conditions modeling the ancient Earth's environment suggest an origin for the monomers (such as amino acids) that make up the polymers (such as proteins)

that characterize life. How did these polymers develop on the ancient Earth?

## 4.3 How Did the Large Molecules of Life Originate?

The Miller–Urey experiment and other experiments that followed it provide a plausible scenario for the formation of the building blocks of life under conditions that prevailed on primitive Earth. The next step in forming and supporting a general theory on the origin of life on Earth would be an explanation of the formation of polymers from these monomers.

### Chemical evolution may have led to polymerization

Scientists have used a number of model systems to try to simulate conditions under which polymers might have been made. Each of these systems is based on several observations and speculations:

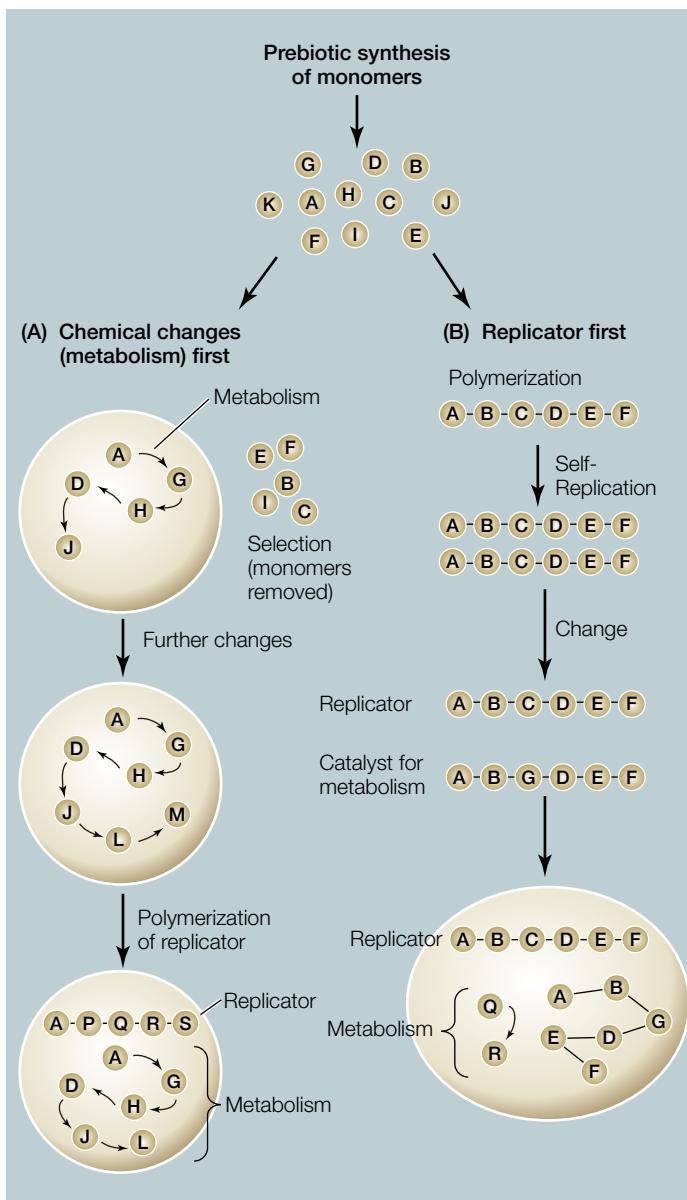
- *Solid mineral surfaces*, such as powder-like clays, have large surface areas. Scientists speculate that the silicates within clay may have been catalytic (speeded up the reactions) in the formation of early carbon-based molecules.
- *Hydrothermal vents* deep in the ocean, where hot water emerges from beneath Earth's crust, lack oxygen gas and contain metals such as iron and nickel. In laboratory experiments, these metals have been shown to catalyze the polymerization of amino acids to polypeptides in the absence of oxygen.
- *Hot pools* at the edges of oceans may, through evaporation, have concentrated monomers to the point where polymerization was favored (the "primordial soup" hypothesis).

In whatever ways the earliest stages of chemical evolution occurred, they resulted in the emergence of monomers and polymers that have probably remained unchanged in their general structure and function for several billion years.

### There are two theories for the emergence of nucleic acids, proteins, and complex chemistry

Earlier in this chapter, we described the key roles of nucleic acids as informational molecules that are passed on from one generation to the next. We also described how DNA is transcribed to RNA, which can then be translated into protein (see Figure 4.5). Chapter 3 describes the roles of proteins as catalysts, speeding up biochemical transformations (see Section 3.2). In existing life forms, nucleic acids and proteins require one another in order to perpetuate life. For the origin of life, this results in a chicken-or-egg problem. Which came first, the genetic material (nucleic acids) or proteins? Two ideas have emerged. One suggests that sequential catalytic changes (primitive metabolism) came first. The other suggests that replication by nucleic acids preceded metabolism (Figure 4.10).

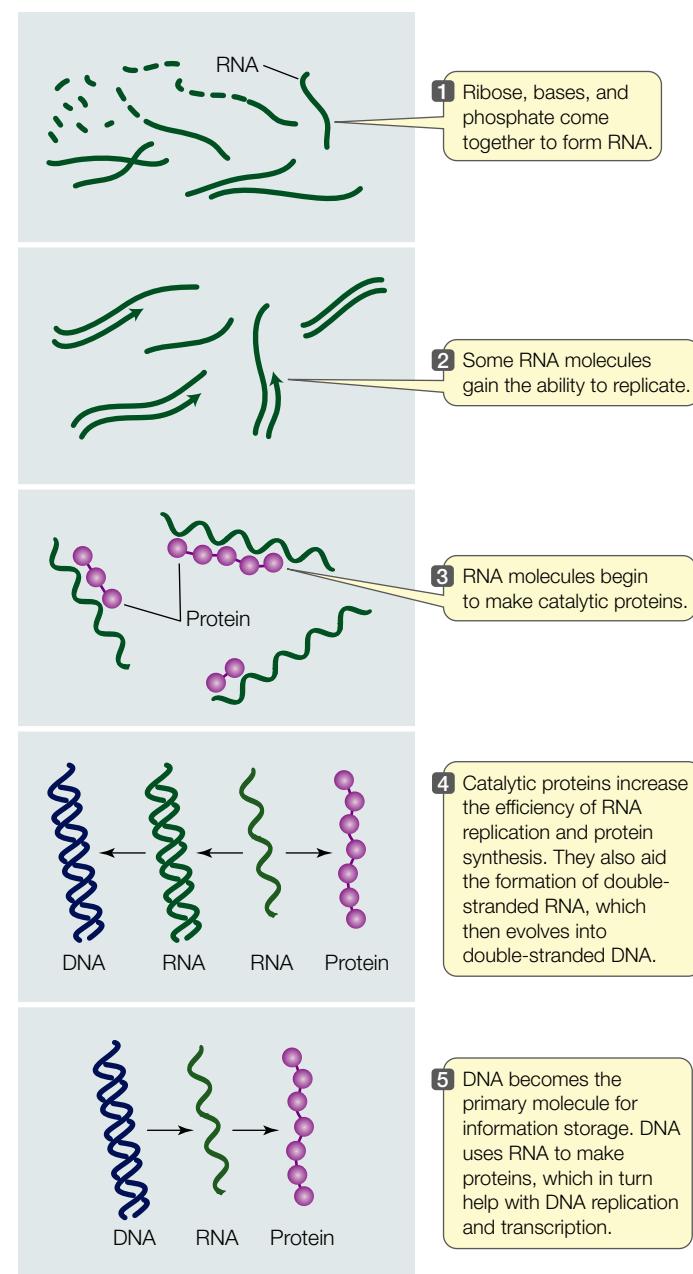
**CHEMICAL CHANGES (METABOLISM) FIRST** In this model, life began in tiny droplets, or compartments, that concentrated and sepa-



**4.10 Two Pathways to Life** Biologists have proposed two ways in which simple monomers could have become self-replicating systems capable of biological functions. (A) The chemical changes (metabolism) first pathway. (B) The replicator first pathway.

rated their contents from the external environment. Within such a chemically rich environment, some substances could occasionally and randomly undergo chemical changes. Proponents of this model speculate that those compartments where the changes were effective for survival in the environment might even have been selected for growth and some primitive form of reproduction. Could catalysis, the speeding up of reactions essential for life, occur in such an environment? The German scientist Günter Wächtershäuser proposed that catalysis and reproduction could have occurred without proteins on a mineral called pyrite (iron disulfide), which has been found at hydrothermal vents and which could serve as a source of energy for polymerization reactions. Over time, nucleic acids and eventually proteins might have formed in the concentrated droplets. Then, in some of these proteins, the ability to catalyze biochemical reactions—including the replication of nucleic acids—could have evolved.

**REPLICATOR FIRST** In this model, the genetic material—nucleic acids—came first. The nucleotide building blocks made by prebiotic chemistry came together to form polymers. Some of these polymers might have had the right shape to be catalytic so that they could reproduce themselves and catalyze other chemical transformations. Such transformations might have included the synthesis of proteins, just as RNA is translated into proteins in living organisms today (see Figure 4.5). Along the way, those molecules that were best adapted to the environment would survive and reproduce. Eventually they would have become incorporated into living cells.



**4.11 The “RNA World” Hypothesis** In a world before DNA, this view postulates that RNA alone was both the blueprint for protein synthesis and a catalyst for its own replication. Eventually, the more compact information storage molecules of DNA could have evolved from RNA.

**4.12 An Early Catalyst for Life?** In the laboratory, a ribozyme (a folded RNA molecule) can catalyze the polymerization of several short RNA strands into a longer molecule. Such a process could be a precursor for the copying of nucleic acids, which is essential for their replication and for gene expression.

There are two major problems with the replicator first model:

- Nucleic acid polymers have not been observed in prebiotic chemistry simulations.
- DNA, the genetic material in almost all current organisms, is not self-catalytic.

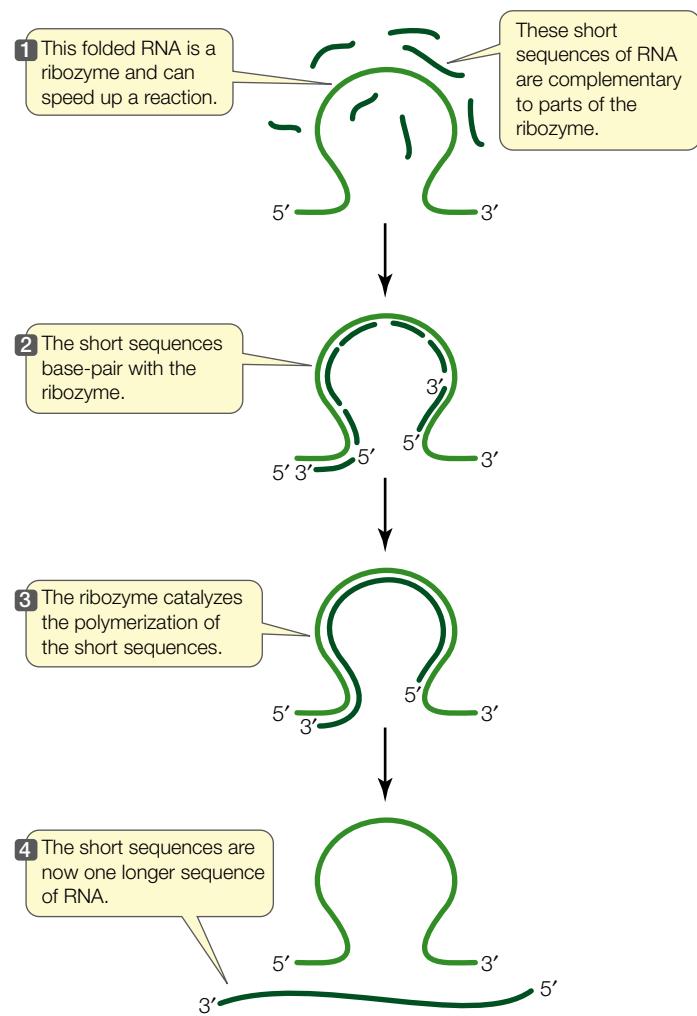
The first problem remains, but the second has a plausible solution: RNA can be a catalyst and can catalyze its own synthesis.

### RNA may have been the first biological catalyst

The three-dimensional structure of a folded RNA molecule presents a unique surface to the external environment (see Figure 4.3). The surfaces of RNA molecules can be every bit as specific as those of proteins. Just as the shapes of proteins allow them to function as catalysts, speeding up reactions that would ordinarily take place too slowly to be biologically useful, the three-dimensional shapes and other chemical properties of certain RNA molecules allow them to function as catalysts. Catalytic RNAs, called **ribozymes**, can catalyze reactions on their own nucleotides as well as in other cellular substances. Although in retrospect it is not too surprising, the discovery of catalytic RNAs was a major shock to a community of biologists who were convinced that all biological catalysts were proteins (enzymes). It took almost a decade for the work of the scientists involved, Thomas Cech and Sidney Altman, to be fully accepted by other scientists. Later, they were awarded the Nobel Prize.

Given that RNA can be both informational (in its nucleotide sequence) and catalytic (due to its ability to form unique three-dimensional shapes), it has been hypothesized that early life consisted of an “RNA world”—a world before DNA. It is thought that when RNA was first made, it could have acted as a catalyst for its own replication as well as for the synthesis of proteins. DNA could eventually have evolved from RNA (Figure 4.11). Some laboratory evidence supports this scenario:

- When certain short RNA sequences are added to a mixture of nucleotides, RNA polymers can be formed at a rate 7 million times greater than the formation of polymers without the added RNA. This added RNA is not a template, but a catalyst.
- In the test tube, a ribozyme can catalyze the assembly of short RNAs into a longer molecule (Figure 4.12). This may be how nucleic acid replication evolved.
- In living organisms today, the formation of peptide linkages (see Figure 3.6) is catalyzed by ribozymes.
- In certain viruses called retroviruses, there is an enzyme called reverse transcriptase that catalyzes the synthesis of DNA from RNA.



### 4.3 RECAP

The emergence of the chemical reactions characteristic of life (metabolism), and the polymerization of monomers to polymers, may have occurred on the surfaces of hydrothermal vents. One theory proposes that metabolism came before polymerization; another suggests that the reverse occurred. RNA may have been the first genetic material and catalyst.

- What are the two theories for the emergence of metabolism and polymers? See pp. 69–71 and Figure 4.10
- How does RNA self-replicate? See p. 71 and Figure 4.12

The discovery of mechanisms for the formation of small and large molecules is essential to answering questions about the origin of life on Earth. But we also need to understand how organized systems formed that include these molecules and display the characteristic properties of life, such as reproduction, energy processing, and responsiveness to the environment. These properties are present in cells, and we now turn to ideas on their origin.

## 4.4 How Did the First Cells Originate?

As you have seen from many of the theories for the origin of life, the evolution of biochemistry occurred under localized conditions. That is, the chemical reactions of metabolism, polymerization, and replication could not occur in a dilute aqueous environment. There had to be a compartment of some sort that brought together and concentrated the compounds involved in these events. Biologists have proposed that initially this compartment may have simply been a tiny droplet of water on the surface of a rock. But another major event in the origin of life was necessary.

Life as we know it is separated from the environment within structurally defined units called **cells**. The internal contents of a cell are separated from the nonbiological environment by a special barrier—a **membrane**. The membrane is not just a barrier; it regulates what goes into and out of the cell, as we describe in Chapter 6. This role of the surface membrane is very important because it permits the interior of the cell to maintain a chemical composition that is different from its external environment. How did the first cells with membranes come into existence?

### Experiments describe the origin of cells

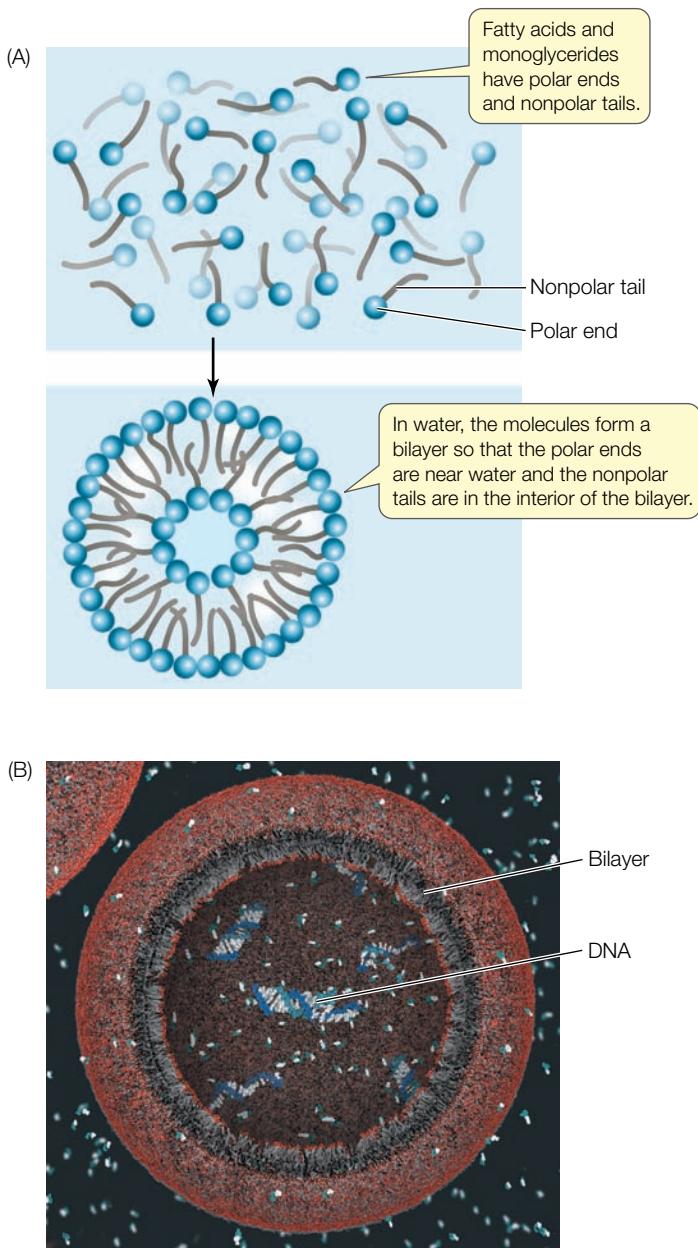
Jack Szostak and his colleagues at Harvard University built a laboratory model that gives insights into the origin of cells. To do this, they first put fatty acids (which can be made in prebiotic experiments) into water. Recall from Chapter 3 that fatty acids are *amphipathic*: they have a hydrophilic polar end and a long, nonpolar tail that is hydrophobic (see Figure 3.20). When placed in water, fatty acids will arrange themselves in a round “huddle” much like a football team: the hydrophilic ends point outward to interact with the aqueous environment and the fatty acid tails point inward, away from the water molecules.

What if some water becomes trapped in the interior of this “huddle”? Now the layer of hydrophobic fatty acid tails is in water, which is an unstable situation. To stabilize this, a second layer of fatty acids forms. This *lipid bilayer* has the polar ends of the fatty acids facing both outward and inward, because they are attracted to the polar water molecules present on each side of the double layer. The nonpolar tails form the interior of the bilayer (Figure 4.13). These prebiotic, water-filled structures, defined by a lipid bilayer membrane, very much resemble living cells. Scientists refer to these compartments as **protocells**. Examining their properties revealed that

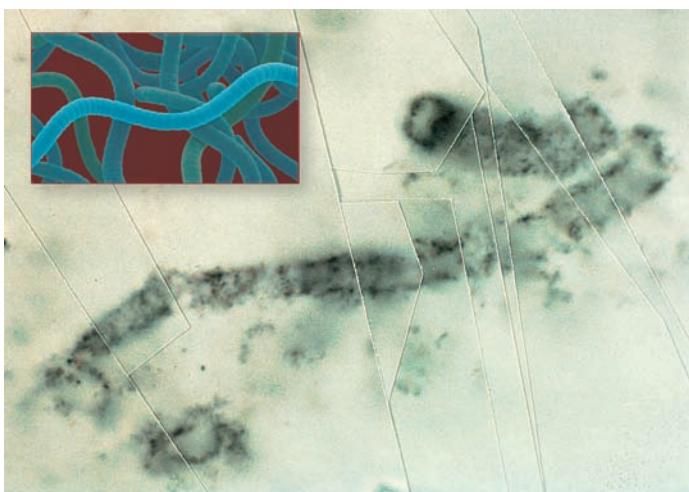
- Large molecules such as DNA or RNA could not pass through the bilayer to enter the protocells, but small molecules such as sugars and individual nucleotides could.
- Nucleic acids inside the protocells could replicate using the nucleotides from outside. When the investigators placed a short nucleic acid strand capable of self-replication inside protocells and added nucleotides to the watery environment outside, the nucleotides crossed the barrier, entered the protocells, and became incorporated into new polynucleotide

chains. This may have been the first step toward cell reproduction, and it took place without protein catalysis.

Were these protocells truly cells, and was the lipid bilayer produced in these experiments a true cell membrane? Certainly not. The protocells could not fully reproduce, nor could they carry out all the metabolic reactions that take place in modern cells. The simple lipid bilayer had few of the sophisticated functions



**4.13 Protocells** (A) In a series of experiments in the Szostak lab, researchers mixed fatty acid molecules in water. The molecules formed bilayers that have some of the properties of a cell membrane. The bilayers and the water “trapped” inside them are essential to form a protocell. (B) A model of the protocell. Nutrients and nucleotides (blue and white particles) pass through the “membrane” and enter the protocell, where they copy an already present DNA template. The new copies of DNA remain in the protocell.



**4.14 The Earliest Cells?** This fossil from Western Australia is 3.5 billion years old. Its form is similar to that of modern filamentous cyanobacteria (inset).

of modern cell membranes. Nevertheless, the protocell may be a reasonable facsimile of a cell as it evolved billions of years ago:

- It can act as a system of interacting parts
- It is capable of organization and self-catalysis
- It includes an interior that is distinct from the exterior environment.

These are all fundamental characteristics of living cells.

### Some ancient cells left a fossil imprint

In the 1990s, scientists made an extremely rare find: a formation of ancient rocks in Australia that had remained relatively unchanged since they first formed 3.5 billion years ago. In one of these rock samples, geologist J. William Schopf of the University of California, Los Angeles, saw chains and clumps of what looked tantalizingly like contemporary cyanobacteria, or “blue-green” bacteria (**Figure 4.14**). Cyanobacteria are believed to

have been among the first organisms, because they can perform photosynthesis, converting CO<sub>2</sub> from the atmosphere and water into carbohydrates. Schopf needed to prove that the chains were once alive, not just the results of simple chemical reactions. He and his colleagues looked for chemical evidence of photosynthesis in the rock samples.

The use of carbon dioxide in photosynthesis is a hallmark of life and leaves a unique chemical signature—a specific ratio of isotopes of carbon (<sup>13</sup>C:<sup>12</sup>C) in the resulting carbohydrates. Schopf showed that the Australian material had this isotope signature. Furthermore, microscopic examination of the chains revealed *internal* substructures that are characteristic of living systems and were not likely to be the result of simple chemical reactions. Schopf’s evidence suggests that the Australian sample is indeed the remains of a truly ancient living organism.

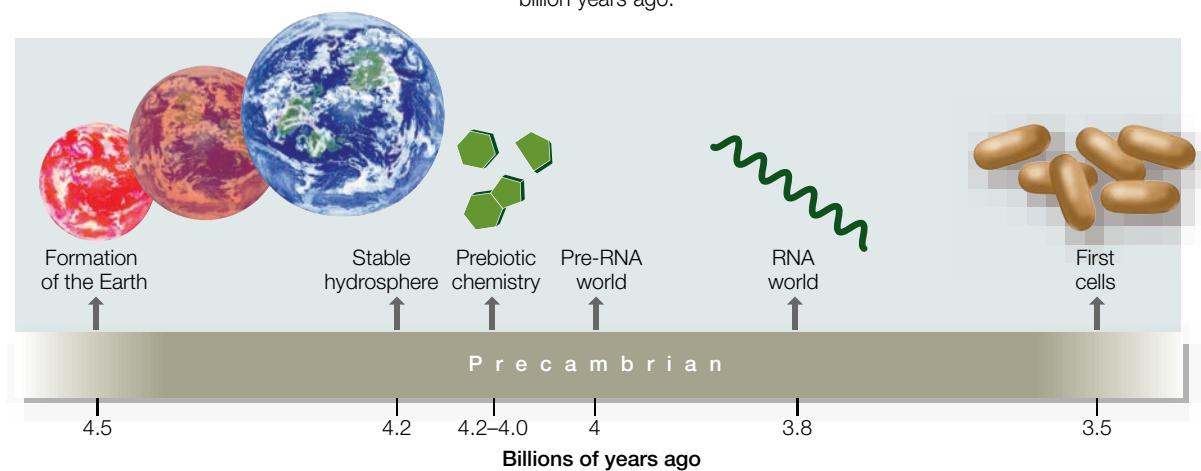
Taking geological, chemical, and biological evidence into account, it is plausible that it took about 500 million to a billion years from the formation of the Earth until the appearance of the first cells (**Figure 4.15**). Life has been cellular ever since. In the next chapter, we begin our study of cell structure and function.

## 4.4 RECAP

The chemical reactions that preceded living organisms probably occurred in specialized compartments, such as water droplets on the surfaces of minerals. Life as we know it did not begin until the emergence of cells. Protocells made in the laboratory have some of the properties of modern cells. Cell-like structures fossilized in ancient rocks date the first cells to about 3.5 billion years ago.

- Explain the importance of the cell membrane to the evolution of living organisms. **See p. 72**
- What is the evidence that ancient rocks contain the fossils of cells? **See p. 73**

**4.15 The Origin of Life** This highly simplified timeline gives a sense of the major events that culminated in the origin of life more than 3.5 billion years ago.



## CHAPTER SUMMARY

### 4.1 What Are the Chemical Structures and Functions of Nucleic Acids?

- The unique function of the nucleic acids—DNA and RNA—is information storage. They form the hereditary material that passes genetic information from one generation to the next.
- Nucleic acids are polymers of nucleotides. A **nucleotide** consists of a phosphate group, a pentose sugar (**ribose** in RNA and **deoxyribose** in DNA), and a nitrogen-containing **base**. **Review Figure 4.1**
- In DNA, the nucleotide bases are **adenine**, **guanine**, **cytosine**, and **thymine**. **Uracil** replaces thymine in RNA. The nucleotides are joined by **phosphodiester linkages** between the sugar of one and the phosphate of the next, forming a nucleic acid polymer. **WEB ACTIVITY 4.1**
- DNA is a **double helix** with two separate strands in which there is **complementary base pairing** based on hydrogen bonds between adenine and thymine (A-T) and between guanine and cytosine (G-C). The two strands of the DNA double helix run in opposite directions. RNA consists of one chain of nucleotides. Hydrogen bonding can occur within the single strand of RNA, forming double-stranded regions and giving the molecule a three-dimensional surface shape. **Review Figures 4.2 and 4.3; WEB ACTIVITY 4.2**
- The information content of DNA and RNA resides in their **base sequences**.
- DNA is expressed as RNA in **transcription**. RNA can then specify the amino acid sequence of a protein in **translation**. **Review Figures 4.5 and 4.6**

### 4.2 How and Where did the Small Molecules of Life Originate?

- Historically, many cultures believed that life originates repeatedly by **spontaneous generation**. This was disproven experimentally. **Review Figure 4.7; ANIMATED TUTORIAL 4.1**
- Life probably originated from chemical reactions. A prerequisite for life is the presence of water.

- The presence of chemical traces of life on meteorites that have landed on Earth suggests that life might have originated extraterrestrially.
- Chemical experiments modeling the prebiotic conditions on Earth have shown that the small molecules that characterize life could have been formed from atmospheric chemicals. **Review Figure 4.9; ANIMATED TUTORIAL 4.2**

### 4.3 How Did the Large Molecules of Life Originate?

- Polymerization of small molecules to polymers could occur in small compartments such as droplets or on surfaces. Both of these conditions concentrate molecules such that reactions are favored.
- The “metabolism first” theory of polymerization proposes that chemical reactions involving small molecules evolved first, and some of them formed polymers that acted as genetic information and catalysts.
- The “replicator first” theory proposes that RNA formed early, and acted as both genetic material and catalyst. Then reactions involving small molecules could occur. **Review Figure 4.10**
- In contemporary organisms, RNA can act as both an information molecule and as a catalyst. This favors the replicator first model. The **RNA world** may have been an important step on the way to life. **Review Figure 4.11**

### 4.4 How Did Cells Originate?

- A key to the emergence of living cells was the prebiotic chemical generation of compartments enclosed by **membranes**. Such enclosed compartments permitted the generation and maintenance of internal chemical conditions that were different from those in the exterior environment.
- In the laboratory, fatty acids and related lipids assemble into **protocells** that have some of the characteristics of cells. **Review Figure 4.13**
- Ancient rocks (3.5 billion years old) have been found with imprints that are probably fossils of early cells.

## SELF-QUIZ

- A nucleotide in DNA is made up of
  - four bases.
  - a base plus a ribose sugar.
  - a base plus a deoxyribose sugar plus phosphate.
  - a sugar plus a phosphate.
  - a sugar and a base.
- Nucleotides in RNA are connected to one another in the polynucleotide chain by
  - covalent bonds between bases.
  - covalent bonds between sugars.
  - covalent bonds between sugar and phosphate.
  - hydrogen bonds between purines.
  - hydrogen bonds between any bases.
- Which is a difference between DNA and RNA?
  - DNA is single-stranded and RNA is double-stranded.
  - DNA is only informational and RNA is only catalytic.
  - DNA contains deoxyribose and RNA contains ribose.
  - DNA is transcribed and RNA is replicated.
  - DNA contains uracil (U) and RNA contains thymine (T).
- The nucleotide sequence of DNA
  - is the same in all organisms of a species.
  - contains only information for translation.
  - evolved before RNA.
  - contains the four bases, A, T, G, and C.
  - is produced by prebiotic chemistry experiments.
- Spontaneous generation of life from nonliving materials
  - can occur in dark places.
  - has not been a belief of humans.
  - has never occurred.
  - requires only nucleotides and fatty acids.
  - was disproven for microorganisms by Pasteur’s experiment.
- The components in the atmosphere for the Miller–Urey experiment on prebiotic synthesis did not include
  - $H_2$ .
  - $H_2O$ .
  - $O_2$ .
  - $NH_3$ .
  - $CH_4$ .

7. All of the major building blocks of macromolecules were made in Miller–Urey prebiotic synthesis experiments *except*
  - a. amino acids.
  - b. hexose sugars.
  - c. bases for nucleotides.
  - d. fatty acids.
  - e. ribose.
8. The “RNA world” hypothesis proposes that
  - a. RNA formed from DNA.
  - b. RNA was both a catalyst and genetic material.
  - c. RNA was a catalyst only.
  - d. RNA formed after proteins.
  - e. DNA formed after RNA was broken down.
9. Ribozymes are
  - a. enzymes that are made up of ribose sugar.
  - b. ancient catalysts that no longer exist.
  - c. RNA catalysts.
  - d. present in bacterial cells only.
  - e. less active than protein enzymes.
10. Findings in ancient rocks indicate cells first appeared
  - a. about 4.5 billion years ago.
  - b. about 3.5 billion years ago.
  - c. about 2 billion years ago.
  - d. before rocks were formed.
  - e. before water arrived on Earth.

## FOR DISCUSSION

1. Are the statements “all life comes from pre-existing life” and “life on Earth could have arisen from prebiotic molecules” truly paradoxical? What conditions existing on Earth today might preclude the origin of life from such molecules?
2. Why might RNA have preceded proteins in the evolution of biological macromolecules?
3. Do you consider the two alternative theories presented in this chapter as possible explanations of the origin of life on Earth (that life came from outside of Earth, or that life arose on Earth through chemical evolution) to be equally plausible? Which do you favor, and why?
4. Why was the evolution of a self-contained cell essential for life as we know it?

## ADDITIONAL INVESTIGATION

1. The interpretation of Pasteur’s experiment (see Figure 4.7) depended on the inactivation of microorganisms by heat. We now know of microorganisms that can survive extremely high temperatures (see Chapter 26). Does this change the interpretation of Pasteur’s experiment? What experiments would you do to inactivate such microbes?
2. The Miller–Urey experiment (see Figure 4.9) showed that it was possible for amino acids to be formed from gases that were hypothesized to have been in Earth’s early atmosphere. These amino acids were dissolved in water. Knowing what you do about the polymerization of amino acids into proteins (see Figure 3.6), how would you set up experiments to show that proteins can form under the conditions of early Earth? What properties would you expect of those proteins?

## WORKING WITH DATA (GO TO [yourBioPortal.com](http://yourBioPortal.com))

### Synthesis of Prebiotic Molecules in an Experimental Atmosphere

In this hands-on exercise, you will examine the original research paper of Miller and Urey to see the experimental approach they used to show that amino acids could be made in a simulation of Earth’s early atmosphere (Figure 4.9). You will also analyze more recent data using the same apparatus.

### Disproving the Spontaneous Generation of Life

In this hands-on exercise, you will examine data from an experiment similar to Pasteur’s famous experiments (Figure 4.7). By calculating growth rates in the different flasks, you will be able to see how Pasteur came to the conclusion he did.

# Cells: The Working Units of Life

## How to mend a broken heart

It is a day in the not-too-distant future. Decades of eating fatty foods, combined with an inherited tendency to deposit cholesterol in his arteries, have finally caught up with 70-year-old Don. A blood clot has closed off blood flow to part of his heart, leading to a heart attack and severe damage to that vital organ.

If this had happened today, Don would have been faced with a long period of rehabilitation, taking medications to manage his weakened heart. Instead, his physicians take a pinch of skin tissue from his arm and bring it to a laboratory. After certain DNA sequences are added, Don's skin cells no longer look and act like skin cells: They are undifferentiated (unspecialized) and reproduce continuously in the laboratory dish. These cells are also multipotent stem

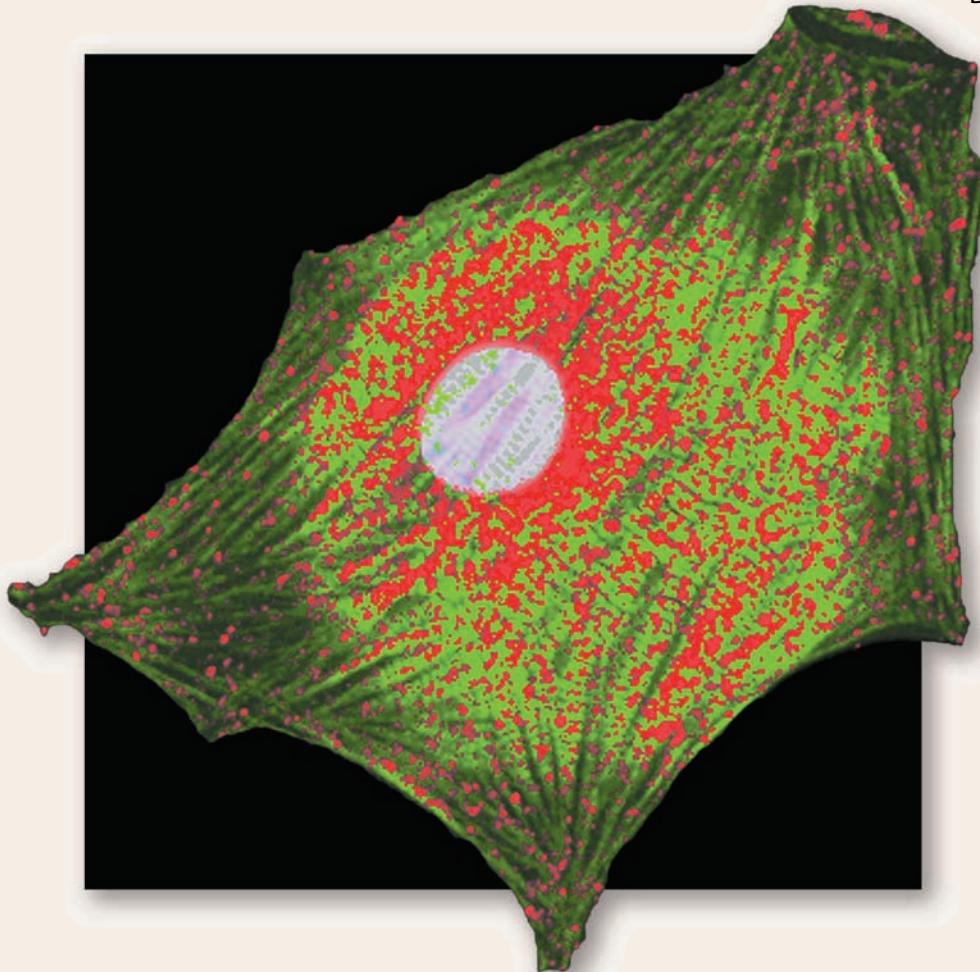
cells, able to differentiate into almost any type of cell in the body if given the right environment. When they are injected directly into Don's heart, his stem cells soon become heart muscle cells, repairing the damage caused by the heart attack. Don leaves the hospital with full cardiac function and recommendations for a healthy diet.

You are probably familiar with another type of multipotent cell, the fertilized human egg. This single cell ultimately produces the tens of trillions of cells that make up the human body. The fertilized egg is programmed to generate an entire organism—not just the heart and skin, but blood, nerves, liver, brain, and even bones—and for this reason is called totipotent (“toti” means all; “multi” means most). In contrast, the stem cells derived from

Don's skin need specific external signals to differentiate into other kinds of cells, and could not develop into an entire person.

The potential uses of stem cells in medicine have generated a lot of excitement in recent years. Such widely read periodicals as *Time* have hailed advances in stem cell research as “breakthroughs of the year.” Patients with the neurological disorder Parkinson’s disease dream of the day when their skin cells can be turned into brain cells to fix their damaged nervous systems. People with diabetes hope for stem cells to repair their pancreases. The list is long.

Behind all of this hope and the research it inspires is a cornerstone of biological science: the cell theory. As you saw in the last



**A New Heart Cell** This cardiac stem cell is developing into a fully differentiated heart cell. The hope is to be able to coax stem cells to follow this path or to produce other cell types to repair damaged tissues.



**Open Heart Surgery** Stem cell therapies may provide alternative approaches to treating heart disease in the future.

chapter, a key event in the emergence of life was the enclosure of biochemical reactions inside a cell, thus concentrating them and separating them from the external environment. These are the first two tenets of the cell theory, that the cell is the unit of life and that the activities of life either happen inside cells or are caused by them. Don's stem cells contain not just the activities of a living entity, but also the potential to change those activities in new directions. The third tenet of the cell theory—equally important—is that the cell is the unit of reproduction: all cells come from pre-existing cells. Stem cell therapy does not create new cells out of thin air; it coaxes existing ones to differentiate and reproduce along the desired path.

**IN THIS CHAPTER** we examine the structure and some of the functions of cells. We will begin with a fuller explanation of cell theory. Then, we will examine the relatively simple cells of prokaryotes. This is followed by a tour of the more complex eukaryotic cell and its various internal compartments, each of which performs specific functions. Finally, we discuss ideas on how complex cells evolved.

## CHAPTER OUTLINE

- 5.1 What Features Make Cells the Fundamental Units of Life?
- 5.2 What Features Characterize Prokaryotic Cells?
- 5.3 What Features Characterize Eukaryotic Cells?
- 5.4 What Are the Roles of Extracellular Structures?
- 5.5 How Did Eukaryotic Cells Originate?

### 5.1 What Features Make Cells the Fundamental Units of Life?

In Chapter 1 we introduced some of the characteristics of life: chemical complexity, growth and reproduction, the ability to refashion substances from the environment, and the ability to determine what substances can move into and out of the organism. These characteristics are all demonstrated by cells. Just as atoms are the building blocks of chemistry, cells are the building blocks of life.

The **cell theory** is described in Section 1.1 as the first unifying principle of biology. There are three critical components of the cell theory:

- Cells are the fundamental units of life.
- All living organisms are composed of cells.
- All cells come from preexisting cells.

Cells contain water and the other small and large molecules, which we examined in Chapters 2–4. Each cell contains at least 10,000 different types of molecules, most of them present in many copies. Cells use these molecules to transform matter and energy, to respond to their environments, and to reproduce themselves.

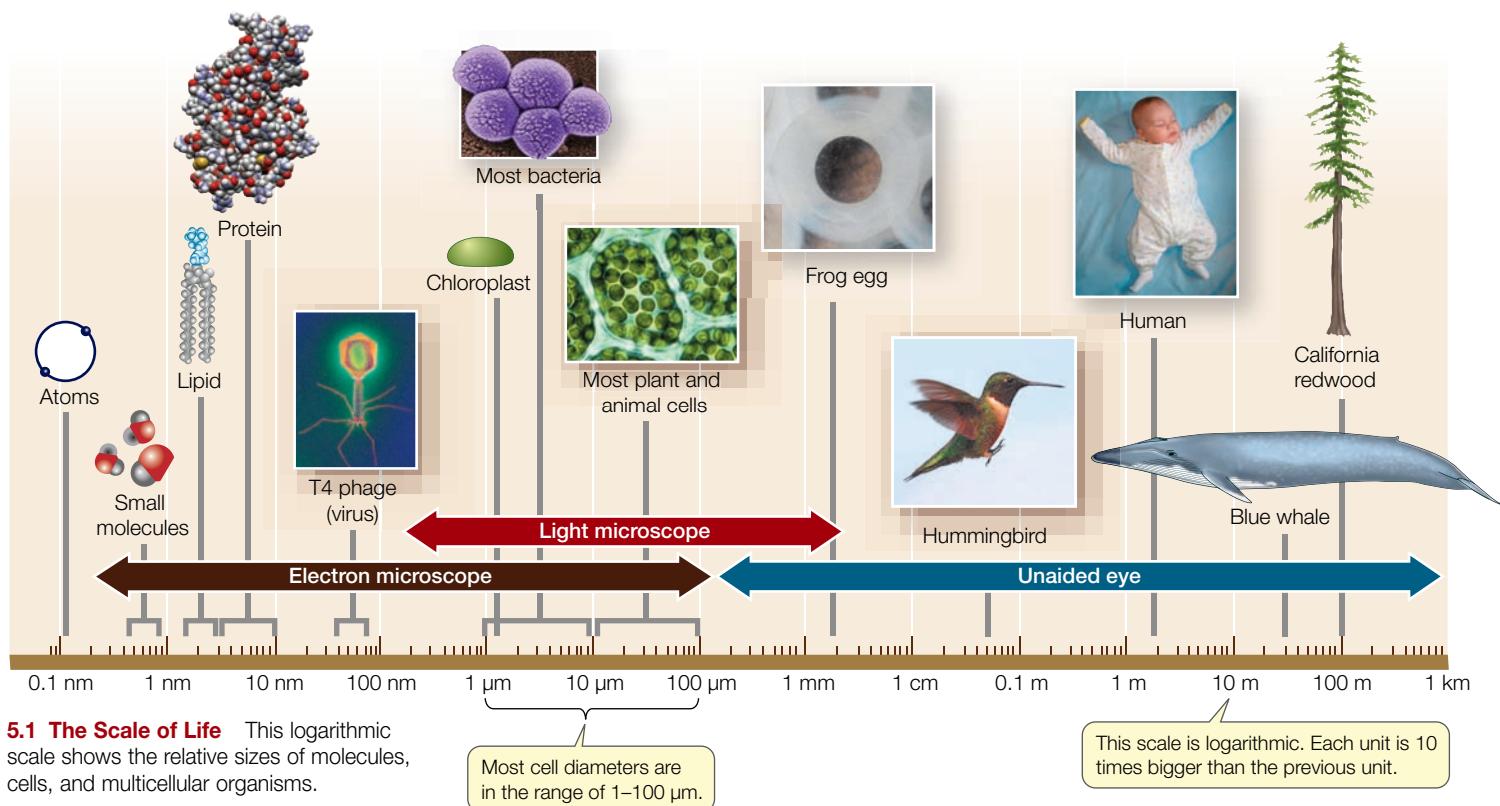
The cell theory has three important implications:

- Studying cell biology is in some sense the same as studying life. The principles that underlie the functions of the single cell of a bacterium are similar to those governing the approximately 60 trillion cells of your body.
- Life is continuous. All those cells in your body came from a single cell, a fertilized egg. That egg came from the fusion of two cells, a sperm and an egg, from your parents. The cells of your parents' bodies were all derived from their parents, and so on back through generations and evolution to the first living cell.
- The origin of life on Earth was marked by the origin of the first cells (see Chapter 4).

Even the largest creatures on Earth are composed of cells, but the cells themselves are usually too small for the naked eye to see. Why are cells so small?

#### Cell size is limited by the surface area-to-volume ratio

Most cells are tiny. In 1665, the early microscopist Robert Hooke estimated that in one square inch of cork, which he examined under his magnifying lens, there were 1,259,712,000 cells! The volumes of cells range from 1 to 1,000 cubic micrometers ( $\mu\text{m}^3$ ). There are some exceptions: the eggs of birds are single cells that



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are, relatively speaking, enormous, and individual cells of several types of algae and bacteria are large enough to be viewed with the unaided eye (**Figure 5.1**). And although neurons (nerve cells) have volumes that are within the “usual” range, they often have fine projections that may extend for meters, carrying signals from one part of a large animal to another. So there is enormous diversity among cells in their dimensions and volumes, but cells are usually very small.

Small cell size is a practical necessity arising from the change in the **surface area-to-volume ratio** of any object as it increases in size. As an object increases in volume, its surface area also increases, but not at the same rate (**Figure 5.2**). This phenomenon has great biological significance for two reasons:

- The volume of a cell determines the amount of chemical activity it carries out per unit of time.
- The surface area of a cell determines the amount of substances that can enter it from the outside environment, and the amount of waste products that can exit to the environment.

**5.2 Why Cells Are Small** Whether it is cuboid (A) or spheroid (B), as an object grows larger its volume increases more rapidly than its surface area. Cells must maintain a large surface area-to-volume ratio in order to function. This fact explains why large organisms must be composed of many small cells rather than a few huge ones.

(A) Cubes

Smaller surface area compared to volume.		
Larger surface area compared to volume.		
1-mm cube	2-mm cube	4-mm cube
Surface area $6 \text{ sides} \times 1^2 = 6 \text{ mm}^2$	Surface area $6 \text{ sides} \times 2^2 = 24 \text{ mm}^2$	Surface area $6 \text{ sides} \times 4^2 = 96 \text{ mm}^2$
Volume $1^3 = 1 \text{ mm}^3$	Volume $2^3 = 8 \text{ mm}^3$	Volume $4^3 = 64 \text{ mm}^3$
Surface area-to-volume ratio 6:1	Surface area-to-volume ratio 3:1	Surface area-to-volume ratio 1.5:1

(B) Spheres

Diameter 1 $\mu\text{m}$	Diameter 2 $\mu\text{m}$	Diameter 3 $\mu\text{m}$
Surface area $4\pi r^2$ $3.14 \mu\text{m}^2$	Surface area $4\pi r^2$ $12.56 \mu\text{m}^2$	Surface area $4\pi r^2$ $28.26 \mu\text{m}^2$
Volume $\frac{4}{3}\pi r^3$ $0.52 \mu\text{m}^3$	Volume $\frac{4}{3}\pi r^3$ $4.19 \mu\text{m}^3$	Volume $\frac{4}{3}\pi r^3$ $14.18 \mu\text{m}^3$
Surface area-to-volume ratio 6:1	Surface area-to-volume ratio 3:1	Surface area-to-volume ratio 2:1

As a living cell grows larger, its chemical activity, and thus its need for resources and its rate of waste production, increases faster than its surface area. (The surface area increases in proportion to the square of the radius, while the volume increases much more—in proportion to the cube of the radius.) In addition, substances must move from one site to another within the cell; the smaller the cell, the more easily this is accomplished. This explains why large organisms must consist of many small cells: cells must be small in volume in order to maintain a large enough surface area-to-volume ratio and an ideal internal volume. The large surface area represented by the many small cells of a multicellular organism enables it to carry out the many different functions required for survival.

### Microscopes reveal the features of cells

Microscopes do two different things to allow cells and details within them to be seen by the human eye. First, they increase the apparent size of the object: this is called *magnification*. But just increasing the magnification does not necessarily mean that the object will be seen clearly. In addition to being larger, a magnified object must be sharp, or clear. This is a property called *resolution*. Formally defined, resolution is the minimum distance two objects can be apart and still be seen as two objects. Resolution for the human eye is about 0.2 mm (200  $\mu\text{m}$ ). Most cells are much smaller than 200  $\mu\text{m}$ , and thus are invisible to the human eye. Microscopes magnify and increase resolution so that cells and their internal structures can be seen clearly (**Figure 5.3**).

There are two basic types of microscopes—*light microscopes* and *electron microscopes*—that use different forms of radiation (see Figure 5.3). While the resolution is better in electron microscopy, we should emphasize that because cells are prepared in a vacuum, only dead, dehydrated cells are visualized. Therefore, the preparation of cells for electron microscopy may alter them, and this must be taken into consideration when interpreting the images produced. On the other hand, light microscopes can be used to visualize living cells (for example, by phase-contrast microscopy; see Figure 5.3).

Before we delve into the details of cell structure, it is useful to consider the many uses of microscopy. An entire branch of medicine, *pathology*, makes use of many different methods of microscopy to aid in the analysis of cells and the diagnosis of diseases. For instance, a surgeon might remove from a body some tissue suspected of being cancerous. The pathologist might:

- examine the tissue quickly by phase-contrast microscopy or interference-contrast microscopy to determine the size, shape, and spread of the cells
- stain the tissue with a general dye and examine it by bright-field microscopy to bring out features such as the shape of the nucleus, or cell division characteristics
- stain the tissue with a fluorescent dye and examine it by fluorescence microscopy or confocal microscopy for the presence of specific proteins that are diagnostic of a particular cancer
- examine the tissue under the electron microscope to observe its most minute internal structures, such as the shapes

of the mitochondria and the chromatin. (These structures are described in Section 5.3.)

### The plasma membrane forms the outer surface of every cell

While the structural diversity of cells can often be observed using light microscopy, the **plasma membrane** is best observed with an electron microscope. This very thin structure forms the outer surface of every cell, and it has more or less the same thickness and molecular structure in all cells. Biochemical methods have shown that membranes have great functional diversity. These methods have revealed that the thin, almost invisible plasma membrane is actively involved in many cellular functions—it is not a static structure. The plasma membrane separates the interior of the cell from its outside environment, creating a segregated (but not isolated) compartment. The presence of this outer limiting membrane is a feature of all cells. What is the composition and molecular architecture of this amazing structure?

The plasma membrane is composed of a *phospholipid bilayer* (or simply *lipid bilayer*), with the hydrophilic “heads” of the lipids facing the cell’s aqueous interior on one side of the membrane and the extracellular environment on the other (see Figure 3.20). Proteins and other molecules are embedded in the lipids. The membrane is not a rigid, static structure. Rather, it is an oily fluid, in which the proteins and lipids are in constant motion. This allows the membrane to move and change the shape of the cell. A detailed description of the structure and functions of the plasma membrane is given in Chapter 6. Here is a brief summary:

- The plasma membrane acts as a *selectively permeable barrier*, preventing some substances from crossing it while permitting other substances to enter and leave the cell. For example, macromolecules such as DNA and proteins cannot normally cross the plasma membrane, but some smaller molecules such as oxygen can. In addition to size, other factors such as polarity determine a molecule’s ability to cross the plasma membrane: because the membrane is composed mostly of hydrophobic fatty acids, nonpolar molecules cross it more easily than polar or charged molecules.
- The plasma membrane allows the cell to maintain a more or less *constant internal environment*. A self-maintaining, constant internal environment (known as *homeostasis*) is a key characteristic of life that will be discussed in detail in Chapter 40. One way that the membrane does this is by actively regulating the transport of substances across it. This dynamic process is distinct from the more passive process of diffusion, which is dependent on the size of a molecule.
- As the cell’s boundary with the outside environment, the plasma membrane is important in *communicating* with adjacent cells and receiving signals from the environment. We will describe this function in Chapter 7.
- The plasma membrane often has proteins protruding from it that are responsible for *binding* and *adhering* to adjacent

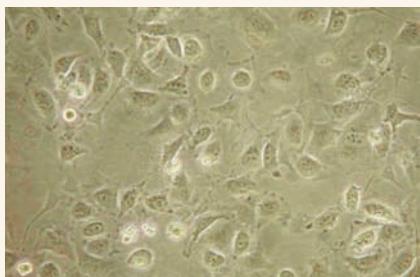
## TOOLS FOR INVESTIGATING LIFE

### 5.3 Looking at Cells

The six images on this page show some techniques used in light microscopy. The three images on the following page were created using electron microscopes. All of these images are of a particular type of cultured cell known as HeLa cells. Note that the images in most cases are flat, two-dimensional views. As you look at images of cells, keep in mind that they are three-dimensional structures.



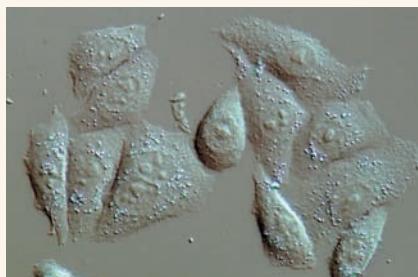
In a **light microscope**, glass lenses and visible light are used to form an image. The resolution is about  $0.2 \mu\text{m}$ , which is 1,000 times greater than that of the human eye. Light microscopy allows visualization of cell sizes and shapes and some internal cell structures. Internal structures are hard to see under visible light, so cells are often chemically treated and stained with various dyes to make certain structures stand out by increasing contrast.

140  $\mu\text{m}$ 

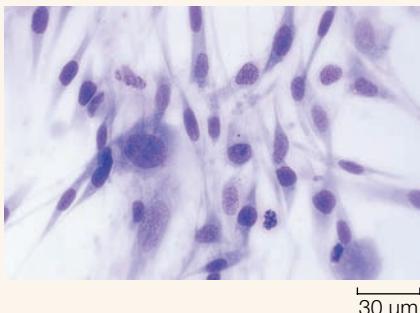
In **bright-field microscopy**, light passes directly through these human cells. Unless natural pigments are present, there is little contrast and details are not distinguished.

30  $\mu\text{m}$ 

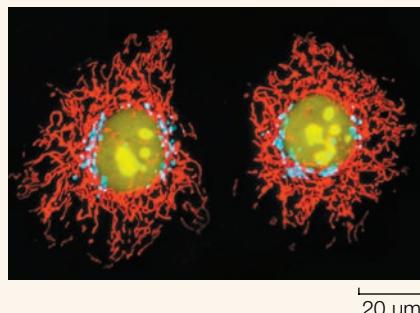
In **phase-contrast microscopy**, contrast in the image is increased by emphasizing differences in refractive index (the capacity to bend light), thereby enhancing light and dark regions in the cell.

30  $\mu\text{m}$ 

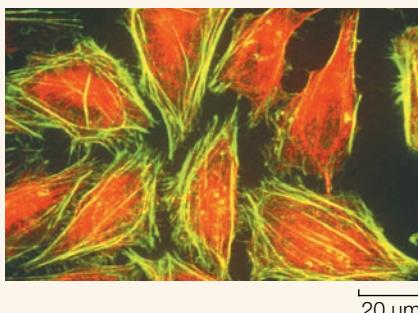
**Differential interference-contrast microscopy** uses two beams of polarized light. The combined images look as if the cell is casting a shadow on one side.

30  $\mu\text{m}$ 

In **stained bright-field microscopy**, a stain enhances contrast and reveals details not otherwise visible. Stains differ greatly in their chemistry and their capacity to bind to cell materials, so many choices are available.

20  $\mu\text{m}$ 

In **fluorescence microscopy**, a natural substance in the cell or a fluorescent dye that binds to a specific cell material is stimulated by a beam of light, and the longer-wavelength fluorescent light is observed coming directly from the dye.

20  $\mu\text{m}$ 

**Confocal microscopy** uses fluorescent materials but adds a system of focusing both the stimulating and emitted light so that a single plane through the cell is seen. The result is a sharper two-dimensional image than with standard fluorescence microscopy.

cells. Thus the plasma membrane plays an important structural role and contributes to cell shape.

### All cells are classified as either prokaryotic or eukaryotic

As we learned in Section 1.2, biologists classify all living things into three domains: Archaea, Bacteria, and Eukarya. The organ-

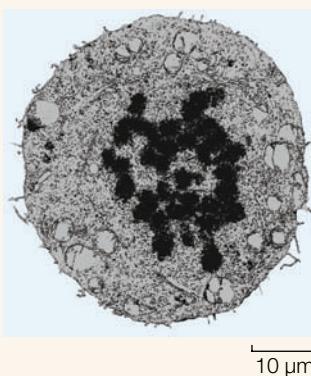
isms in Archaea and Bacteria are collectively called **prokaryotes** because they have in common a prokaryotic cell organization. A prokaryotic cell does not typically have membrane-enclosed internal compartments; in particular, it does not have a nucleus. The first cells were probably similar in organization to those of modern prokaryotes.

## TOOLS FOR INVESTIGATING LIFE

### 5.3 Looking at Cells (continued)

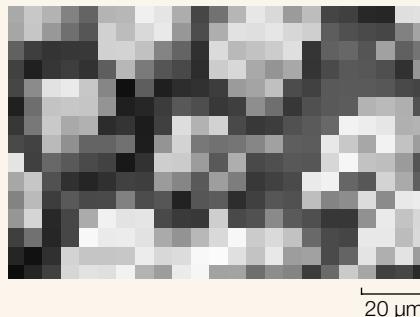


In an *electron microscope*, electromagnets are used to focus an electron beam, much as a light microscope uses glass lenses to focus a beam of light. Since we cannot see electrons, the electron microscope directs them through a vacuum at a fluorescent screen or photographic film to create a visible image. The resolution of electron microscopes is about 2 nm, which is about 100,000 times greater than that of the human eye. This resolution permits the details of many subcellular structures to be distinguished.



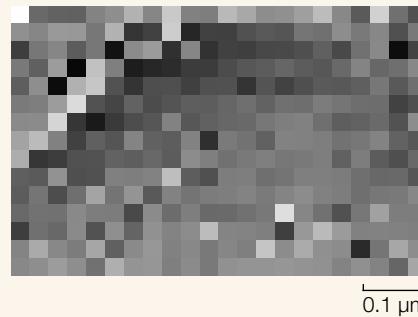
10 µm

In **transmission electron microscopy (TEM)**, a beam of electrons is focused on the object by magnets. Objects appear darker if they absorb the electrons. If the electrons pass through they are detected on a fluorescent screen.



20 µm

**Scanning electron microscopy (SEM)** directs electrons to the surface of the sample, where they cause other electrons to be emitted. These electrons are viewed on a screen. The three-dimensional surface of the object can be visualized.



0.1 µm

In **freeze-fracture microscopy**, cells are frozen and then a knife is used to crack them open. The crack often passes through the interior of plasma and internal membranes. The “bumps” that appear are usually large proteins or aggregates embedded in the interior of the membrane.

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Eukaryotic cell organization, on the other hand, is found in members of the domain Eukarya (**eukaryotes**), which includes the protists, plants, fungi, and animals. As we will discuss later in this chapter, eukaryotic cells probably evolved from prokaryotes. In contrast to the prokaryotes, the genetic material (DNA) of eukaryotic cells is contained in a special membrane-enclosed compartment called the **nucleus**. Eukaryotic cells also contain other membrane-enclosed compartments in which specific chemical reactions occur. For example, some of the key reactions that generate usable chemical energy for cells take place in mitochondria. The internal membranes that enclose these compartments have the same basic composition, structure and properties as the plasma membrane. The efficiency afforded by these compartments has led to the impressive functions that can occur in eukaryotic cells, and their specialization into tissues as diverse as the parts of a flower, muscles, and nerves.

### 5.1 RECAP

The cell theory is a unifying principle of biology. Surface area-to-volume ratios limit the sizes of cells. Both prokaryotic and eukaryotic cells are enclosed within a plasma membrane, but prokaryotic cells lack the membrane-enclosed internal compartments found in eukaryotes.

- How does cell biology embody all the principles of life? **See p. 77**
- Why are cells small? **See pp. 77–79 and Figure 5.2**
- Explain the importance of the plasma membrane to cells. **See pp. 79–80**

As we mentioned in this section, there are two structural themes in cell architecture: prokaryotic and eukaryotic. We now turn to the organization of prokaryotic cells.

## 5.2 What Features Characterize Prokaryotic Cells?

Prokaryotes can derive energy from more diverse sources than any other living organisms. They can tolerate environmental extremes—such as very hot springs with temperatures up to 100°C (*Thermus aquaticus*) or very salty water (*Halobacterium*)—that would kill other organisms. As we examine prokaryotic cells in this section, bear in mind that there are vast numbers of prokaryotic species, and that the Bacteria and Archaea are distinguished in numerous ways. These differences, and the vast diversity of organisms in these two domains, will be the subject of Chapter 26.

The volume of a prokaryotic cell is generally about one fiftieth of the volume of a eukaryotic cell. Prokaryotic cells range from about 1 to 10 µm in length or diameter. Each individual prokaryote is a single cell, but many types of prokaryotes are usually seen in chains or small clusters, and some occur in large clusters containing hundreds of cells. In this section we will first consider the features shared by cells in the domains Bacteria and Archaea. Then we will examine structural features that are found in some, but not all, prokaryotes.

### Prokaryotic cells share certain features

All prokaryotic cells have the same basic structure (Figure 5.4):

- The plasma membrane encloses the cell, regulating the traffic of materials into and out of the cell, and separating its interior from the external environment.

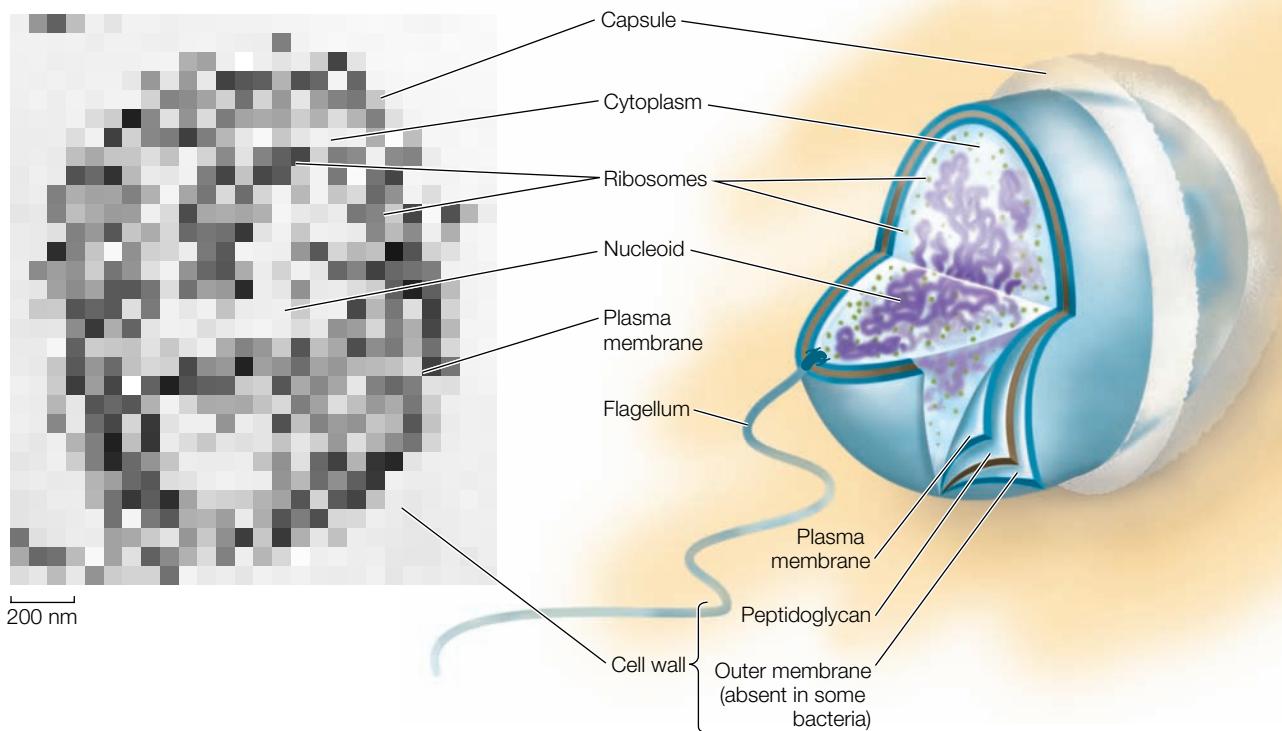
- The **nucleoid** is a region in the cell where the DNA is located. As we described in Section 4.1, DNA is the hereditary material that controls cell growth, maintenance, and reproduction.

The rest of the material enclosed in the plasma membrane is called the **cytoplasm**. The cytoplasm has two components: the cytosol and insoluble suspended particles, including ribosomes:

- The **cytosol** consists mostly of water that contains dissolved ions, small molecules, and soluble macromolecules such as proteins.
- **Ribosomes** are complexes of RNA and proteins that are about 25 nm in diameter. They can only be visualized with the electron microscope. They are the sites of protein synthesis, where information coded for in nucleic acids directs the sequential linking of amino acids to form proteins.

The cytoplasm is not a static region. Rather, the substances in this environment are in constant motion. For example, a typical protein moves around the entire cell within a minute, and it collides with many other molecules along the way.

Although they are structurally less complex than eukaryotic cells, prokaryotic cells are functionally complex, carrying out thousands of biochemical reactions. Based on our current knowledge about the origins of the first cells (see Section 4.4), some prokaryotic cell lineages must stretch back in time for more than 3 billion years. Thus, prokaryotes are very successful organisms from an evolutionary perspective.



**5.4 A Prokaryotic Cell** The bacterium *Pseudomonas aeruginosa* illustrates the typical structures shared by all prokaryotic cells. This bacterium also has a protective outer membrane that not all prokaryotes have. The flagellum and capsule are also structures found in some, but not all, prokaryotic cells.

### Specialized features are found in some prokaryotes

As they evolved, some prokaryotes developed specialized structures that gave a selective advantage to those that had them: cells with these structures were better able to survive and reproduce in particular environments than cells lacking them. These structures include a protective cell wall, an internal membrane for compartmentalization of some chemical reactions, flagella for cell movement through the watery environment, and a rudimentary internal skeleton.

**CELL WALLS** Most prokaryotes have a cell wall located outside the plasma membrane. The rigidity of the cell wall supports the cell and determines its shape. The cell walls of most bacteria, but not archaea, contain peptidoglycan, a polymer of amino sugars that are cross-linked by covalent bonds to peptides, to form a single giant molecule around the entire cell. In some bacteria, another layer, the outer membrane (a polysaccharide-rich phospholipid membrane), encloses the peptidoglycan layer (see Figure 5.4). Unlike the plasma membrane, this outer membrane is not a major barrier to the movement of molecules across it.

Enclosing the cell wall in some bacteria is a slimy layer composed mostly of polysaccharides, and referred to as a capsule. In some cases these capsules protect the bacteria from attack by white blood cells in the animals they infect. Capsules also help to keep the cells from drying out, and sometimes they help bacteria attach to other cells. Many prokaryotes produce no capsule, and those that do have capsules can survive even if they lose them, so the capsule is not essential to prokaryotic life.

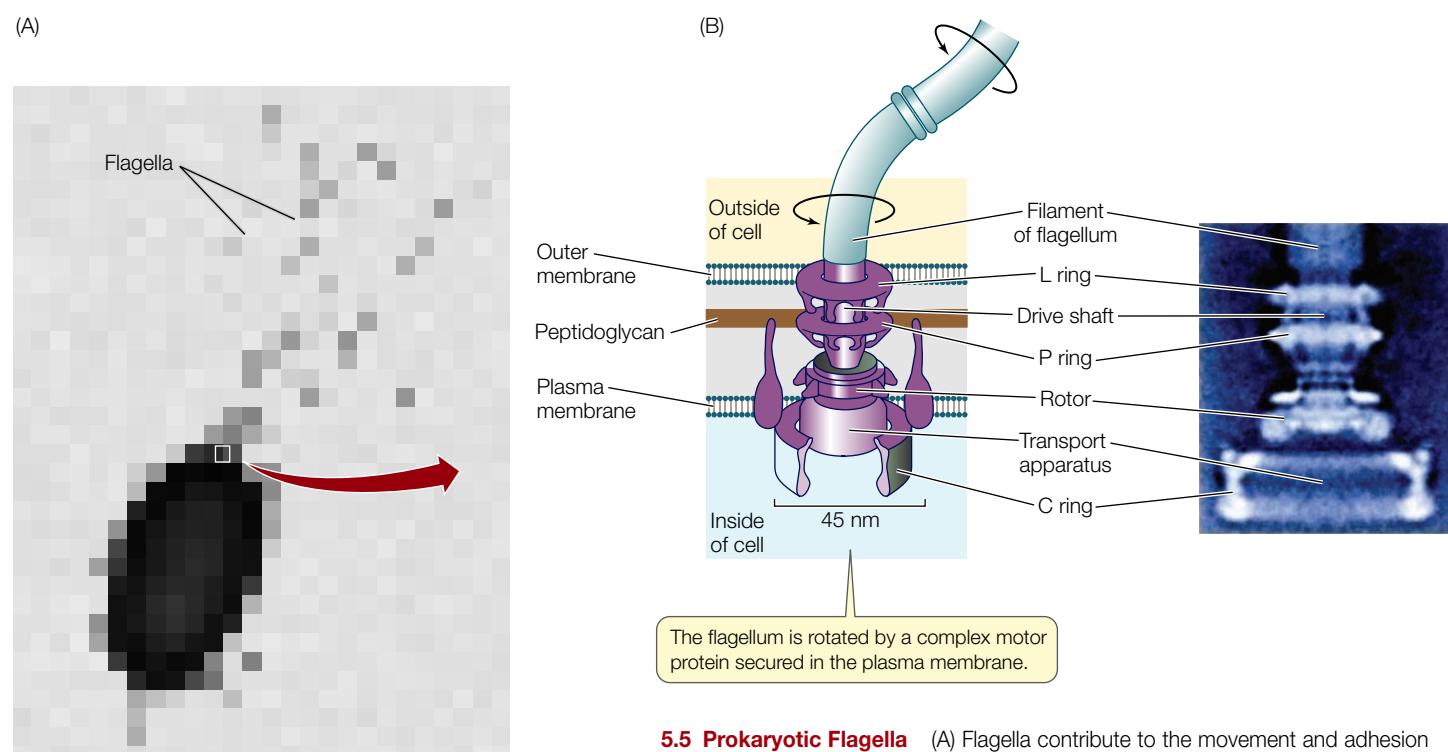
As you will see later in this chapter, eukaryotic plant cells also have a cell wall, but it differs in composition and structure from the cell walls of prokaryotes.

**INTERNAL MEMBRANES** Some groups of bacteria—including the cyanobacteria—carry out photosynthesis: they use energy from the sun to convert carbon dioxide and water into carbohydrates. These bacteria have an internal membrane system that contains molecules needed for photosynthesis. The development of photosynthesis, which requires membranes, was an important event in the early evolution of life on Earth. Other prokaryotes have internal membrane folds that are attached to the plasma membrane. These folds may function in cell division or in various energy-releasing reactions.

**FLAGELLA AND PILI** Some prokaryotes swim by using appendages called **flagella**, which sometimes look like tiny corkscrews (Figure 5.5A). In bacteria a single flagellum is made of a protein called flagellin. A complex motor protein spins the flagellum on its axis like a propeller, driving the cell along. The motor protein is anchored to the plasma membrane and, in some bacteria, to the outer membrane of the cell wall (Figure 5.5B).

We know that the flagella cause the motion of cells because if they are removed, the cells do not move.

**Pili** are structures made of protein that project from the surfaces of some types of bacterial cells. These hairlike structures are shorter than flagella, and are used for adherence. The sex-pili help bacteria join to one another to exchange genetic material. The *fimbriae* are similar to pili but shorter, and help cells to adhere to surfaces such as animal cells, for food and protection.



**5.5 Prokaryotic Flagella** (A) Flagella contribute to the movement and adhesion of prokaryotic cells. (B) Complex protein ring structures anchored in the plasma membrane form a motor unit that rotates the flagellum and propels the cell.

**CYTOSKELETON** Some prokaryotes, especially rod-shaped bacteria, have a helical network of filamentous structures that extend down the length of the cell just inside the plasma membrane. The proteins that make up this structure are similar in amino acid sequence to actin in eukaryotic cells. Since actin is part of the cytoskeleton in eukaryotes (see Section 5.3), it has been suggested that the helical filaments in prokaryotes play a role in maintaining the rod-like cell shape.

## 5.2 RECAP

**Prokaryotic organisms can live on diverse energy sources and in extreme environments. Unlike eukaryotic cells, prokaryotic cells do not have extensive internal compartments.**

- What structures are present in all prokaryotic cells? **See p. 82 and Figure 5.4**
- Describe the structure and function of a specialized prokaryotic cell feature, such as the cell wall, capsule, flagellum, or pilus. **See pp. 83–84 and Figure 5.5**

As we mentioned earlier, the prokaryotic cell is one of two types of cell structure recognized in cell biology. The other is the eukaryotic cell. Eukaryotic cells, and multicellular eukaryotic organisms, are more structurally and functionally complex than prokaryotic cells.

## 5.3 What Features Characterize Eukaryotic Cells?

Eukaryotic cells generally have dimensions up to 10 times greater than those of prokaryotes; for example, the spherical yeast cell has a diameter of about 8  $\mu\text{m}$ , in contrast to a typical bacterium with a diameter of 1  $\mu\text{m}$ . Like prokaryotic cells, eukaryotic cells have a plasma membrane, cytoplasm, and ribosomes. But as you learned earlier in this chapter, eukaryotic cells also have compartments within the cytoplasm whose interiors are separated from the cytosol by membranes.

### Compartmentalization is the key to eukaryotic cell function

The membranous compartments of eukaryotic cells are called **organelles**. Each type of organelle has a specific role in its particular cell. Some of the organelles have been characterized as factories that make specific products. Others are like power plants that take in energy in one form and convert it into a more useful form. These functional roles are defined by the chemical reactions each organelle can carry out:

- The *nucleus* contains most of the cell's genetic material (DNA). The replication of the genetic material and the first steps in expressing genetic information take place in the nucleus.
- The *mitochondrion* is a power plant and industrial park, where energy stored in the bonds of carbohydrates and

fatty acids is converted into a form that is more useful to the cell (ATP; see Section 9.1).

- The *endoplasmic reticulum* and *Golgi apparatus* are compartments in which some proteins synthesized by the ribosomes are packaged and sent to appropriate locations in the cell.
- *Lysosomes* and *vacuoles* are cellular digestive systems in which large molecules are hydrolyzed into usable monomers.
- *Chloroplasts* (found in only some cells) perform photosynthesis.

The membrane surrounding each organelle has two essential roles. First, it keeps the organelle's molecules away from other molecules in the cell, to prevent inappropriate reactions. Second, it acts as a traffic regulator, letting important raw materials into the organelle and releasing its products to the cytoplasm. In some organelles, the membrane also has proteins that have functional roles in chemical reactions that occur at the organelle surface.

There are a number of other structures in eukaryotic cells that have specialized functions, but are not generally called organelles because they lack membranes:

- Ribosomes, where protein synthesis takes place
- The cytoskeleton, composed of several types of protein-based filaments, which has both structural and functional roles
- The extracellular matrix, which also has structural and functional roles

The evolution of compartments was an important development that enabled eukaryotic cells to specialize, forming the organs and tissues of complex multicellular organisms.

### Organelles can be studied by microscopy or isolated for chemical analysis

Cell organelles and structures were first detected by light and then by electron microscopy. The functions of the organelles could sometimes be inferred by observations and experiments, leading, for example, to the hypothesis (later confirmed) that the nucleus contained the genetic material. Later, the use of stains targeted to specific macromolecules allowed cell biologists to determine the chemical compositions of organelles (see Figure 5.17, which shows a single cell stained for three different proteins).

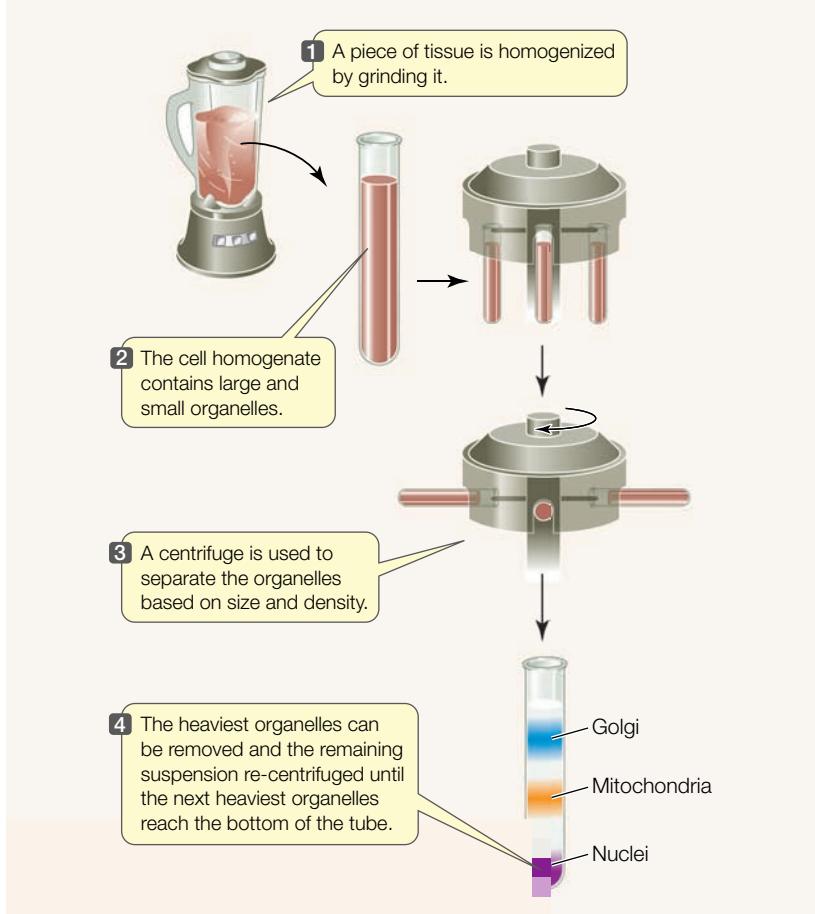
Another way to analyze cells is to take them apart in a process called cell fractionation. This process permits cell organelles and other cytoplasmic structures to be separated from each other and examined using chemical methods. Cell fractionation begins with the destruction of the plasma membrane, which allows the cytoplasmic components to flow out into a test tube. The various organelles can then be separated from one another on the basis of size or density (**Figure 5.6**). Biochemical analyses can then be done on the isolated organelles.

Microscopy and cell fractionation have complemented each other, giving us a more complete picture of the composition and function of each organelle and structure.

## TOOLS FOR INVESTIGATING LIFE

### 5.6 Cell Fractionation

Organelles can be separated from one another after cells are broken open and their contents suspended in an aqueous medium. The medium is placed in a tube and spun in a centrifuge, which rotates about an axis at high speed. Centrifugal forces cause particles to sediment at the bottom of the tube where they may be collected for biochemical study. Heavier particles sediment at lower speeds than do lighter particles. By adjusting the speed of centrifugation, cellular organelles and even large particles like ribosomes can be separated and partially purified.



Microscopy of plant and animal cells has revealed that many of the organelles are similar in appearance in each cell type (**Figure 5.7**). By comparing the illustrations in Figure 5.7 and Figure 5.4 you can see some of the prominent differences between eukaryotic cells and prokaryotic cells.

### Ribosomes are factories for protein synthesis

The ribosomes of prokaryotes and eukaryotes are similar in that both types consist of two different-sized subunits. Eukaryotic ribosomes are somewhat larger than those of prokaryotes, but the structure of prokaryotic ribosomes is better understood. Chemically, ribosomes consist of a special type of RNA called ribosomal RNA (rRNA). Ribosomes also contain more than 50

different protein molecules, which are noncovalently bound to the rRNA.

In prokaryotic cells, ribosomes float freely in the cytoplasm. In eukaryotic cells they are found in two places: in the cytoplasm, where they may be free or attached to the surface of the endoplasmic reticulum (a membrane-bound organelle, see below), and inside mitochondria and chloroplasts. In each of these locations, the ribosomes are molecular factories where proteins are synthesized with their amino acid sequences specified by nucleic acids. Although they seem small in comparison to the cells that contain them, by molecular standards ribosomes are huge complexes (about 25 nm in diameter), made up of several dozen different molecules.

### The nucleus contains most of the genetic information

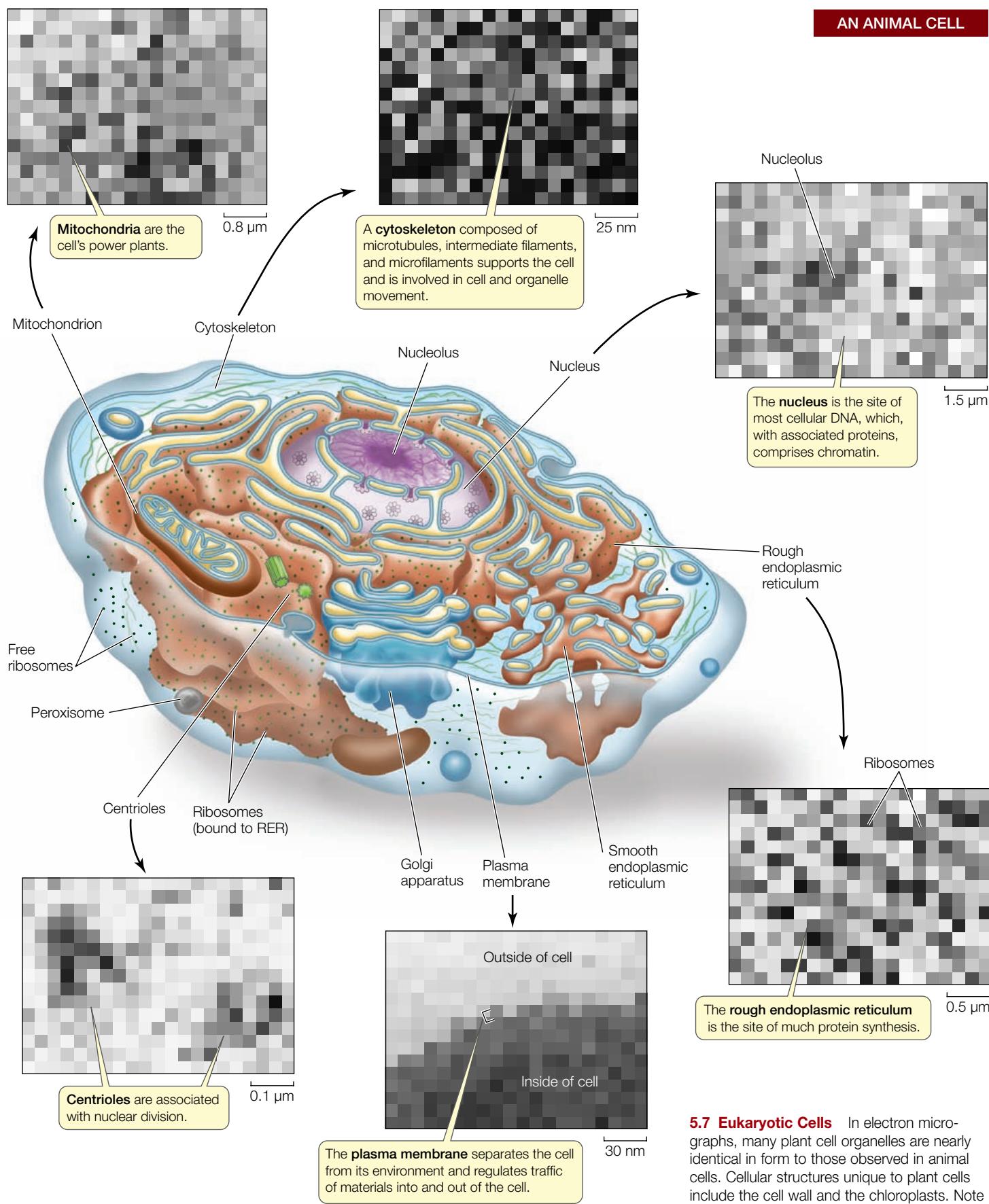
Organisms depend on accurate information—internal signals, environmental cues, and stored instructions—in order to respond appropriately to changing conditions, to maintain a constant internal environment, and to reproduce. In the cell, hereditary information is stored in the sequence of nucleotides in DNA molecules. Most of the DNA in eukaryotic cells resides in the nucleus (see Figure 5.7). Information encoded in the DNA is *translated* into proteins at the ribosomes. This process is described in detail in Chapter 14.

Most cells have a single nucleus, which is usually the largest organelle (**Figure 5.8**). The nucleus of a typical animal cell is approximately 5  $\mu\text{m}$  in diameter—substantially larger than most prokaryotic cells. The nucleus has several functions in the cell:

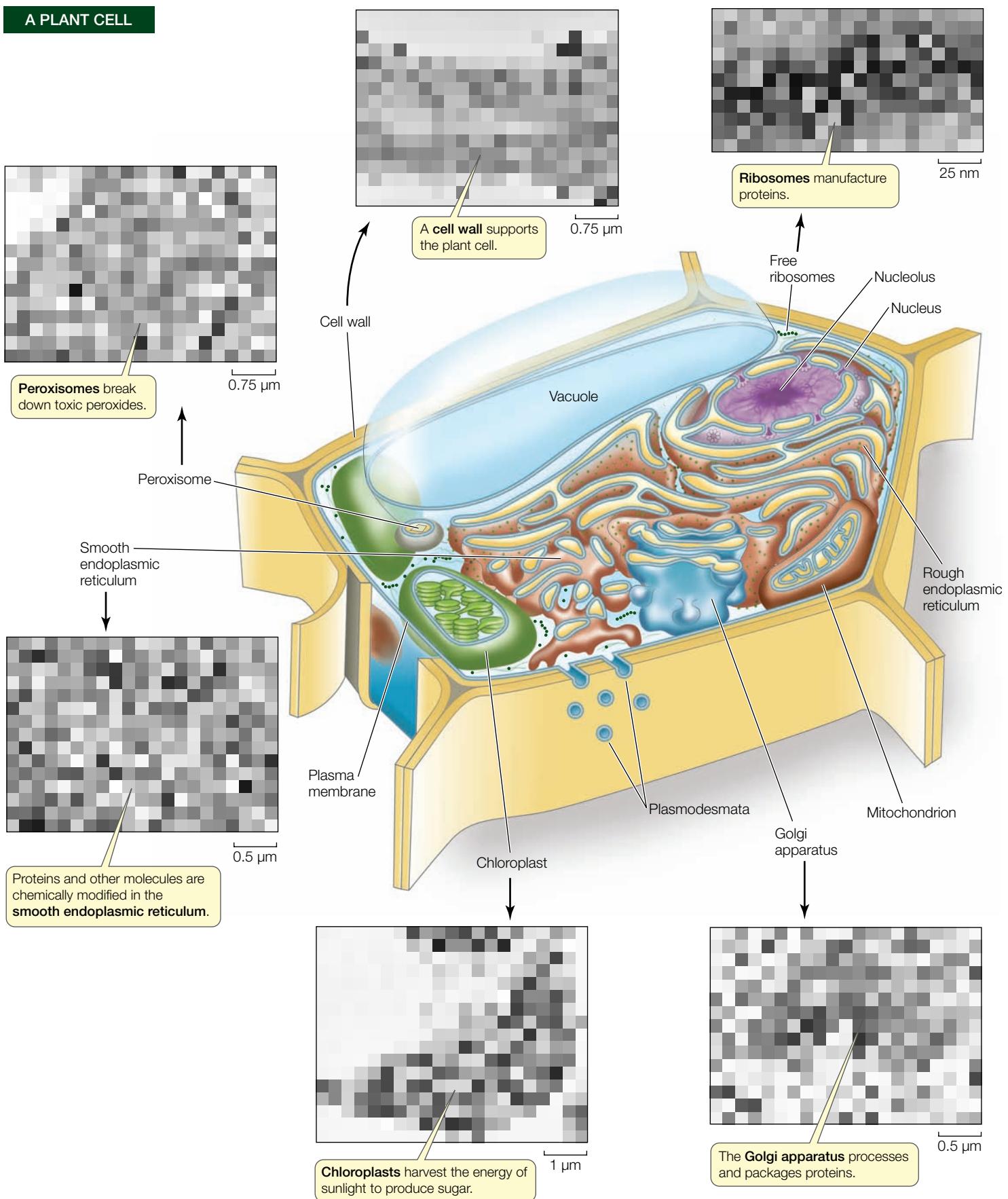
- It is the location of the DNA and the site of DNA replication.
- It is the site where gene transcription is turned on or off.
- A region within the nucleus, the **nucleolus**, is where ribosomes begin to be assembled from RNA and proteins.

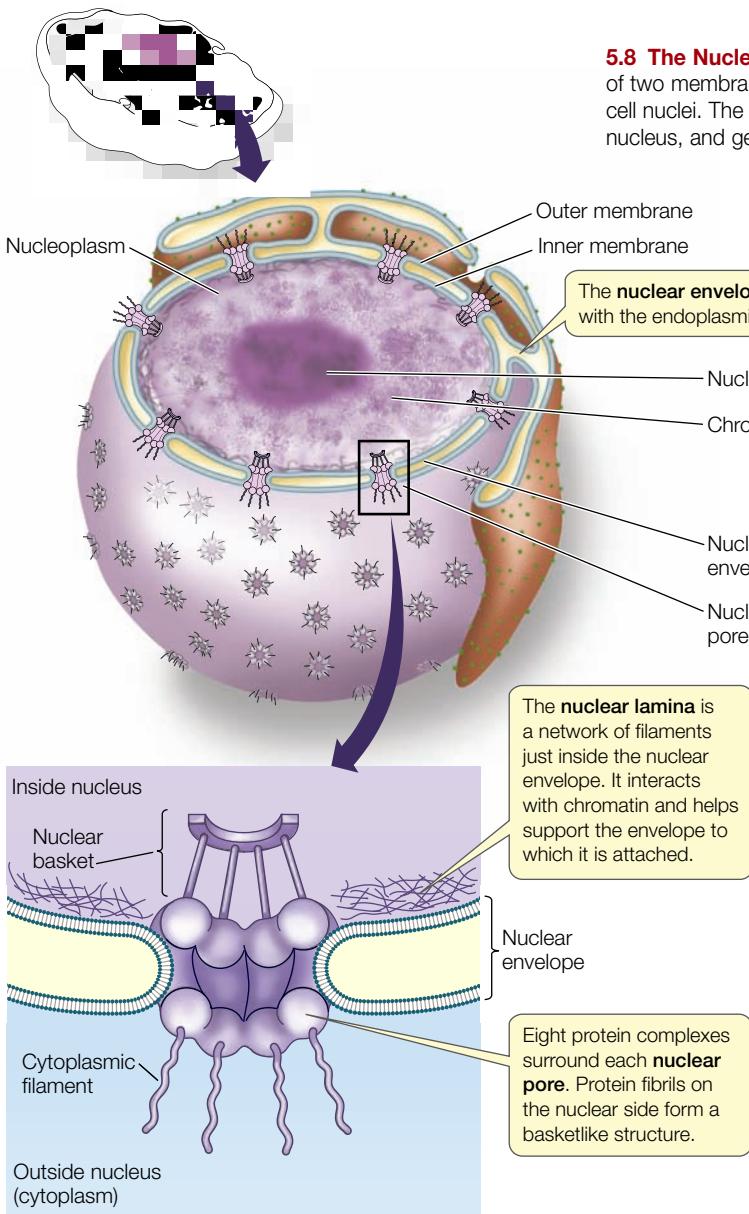
The nucleus is surrounded by two membranes, which together form the *nuclear envelope* (see Figure 5.8). This structure separates the genetic material from the cytoplasm. Functionally, it separates DNA transcription (which occurs in the nucleus) from translation (in the cytoplasm) (see Figure 4.5). The two membranes of the nuclear envelope are perforated by thousands of nuclear pores, each measuring approximately 9 nm in diameter, which connect the interior of the nucleus with the cytoplasm (see Figure 5.8). The pores regulate the traffic between these two cellular compartments by allowing some molecules to enter the nucleus and blocking others. This allows the nucleus to regulate the information-processing functions.

At the nuclear pore, small substances, including ions and other molecules with molecular weights of less than 10,000 dal-

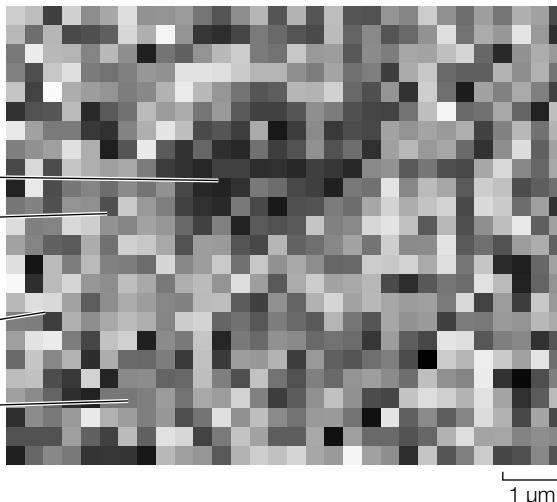


**5.7 Eukaryotic Cells** In electron micrographs, many plant cell organelles are nearly identical in form to those observed in animal cells. Cellular structures unique to plant cells include the cell wall and the chloroplasts. Note that the images are two-dimensional “slices,” while cells are three-dimensional structures.





**5.8 The Nucleus Is Enclosed by a Double Membrane** The nuclear envelope (made up of two membranes), nucleolus, nuclear lamina, and nuclear pores are common features of all cell nuclei. The pores are the gateways through which proteins from the cytoplasm enter the nucleus, and genetic material (mRNA) exits the nucleus into the cytoplasm.



The NLS binds to a receptor protein at the pore, and the signaled protein slides through the pore and across the nuclear envelope.

Inside the nucleus, DNA is combined with proteins to form a fibrous complex called *chromatin*. Chromatin occurs in the form of exceedingly long, thin threads called *chromosomes*. Different eukaryotic organisms have different numbers of chromosomes (ranging from two in one kind of Australian ant to hundreds in some plants). Prior to cell division, the chromatin becomes tightly compacted and condensed so that the individual chromosomes are visible under a light microscope. This occurs to facilitate distribution of the DNA during cell division. (Figure 5.9). Surrounding the chromatin are water and dissolved substances collectively referred to as the *nucleoplasm*. Within the nucleoplasm, a network of structural proteins called the *nuclear matrix* helps organize the chromatin.

At the interior periphery of the nucleus, the chromatin is attached to a protein meshwork, called the *nuclear lamina*, which is formed by the polymerization of proteins called lamins into long thin structures called intermediate filaments. The nuclear lamina maintains the shape of the nucleus by its attachment to both the chromatin and the nuclear envelope. There is some evidence that the nuclear lamina may be involved with human aging. As people age, the nuclear lamina begins to disintegrate and in the process the structural integrity of the nucleus declines. In people with the rare disease called progeria, this decline begins very early in life and their aging is accelerated.

During most of a cell's life cycle, the nuclear envelope is a stable structure. When the cell reproduces, however, the nuclear envelope breaks down into small, membrane-bound droplets, called *vesicles*, containing pore complexes. The envelope reforms after the replicated DNA has been distributed to the daughter cells (see Section 11.3).

At certain sites, the outer membrane of the nuclear envelope folds outward into the cytoplasm and is continuous with the

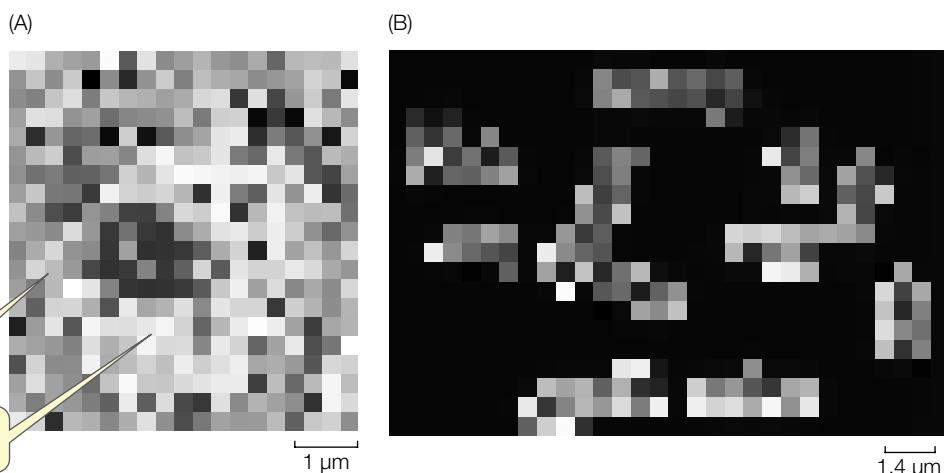
tons, freely diffuse through the pore. Larger molecules, such as many proteins that are made in the cytoplasm and imported into the nucleus, cannot get through without a certain short sequence of amino acids that is part of the protein. We know that this sequence is the *nuclear localization signal* (NLS) from several lines of evidence (see also Figure 14.20):

- The NLS occurs in most proteins targeted to the nucleus, but not in proteins that remain in the cytoplasm.
- If the NLS is removed from a protein, the protein stays in the cytoplasm.
- If the NLS is added to a protein that normally stays in the cytoplasm, that protein moves into the nucleus.
- Some viruses have an NLS that allows them to enter the nucleus; viruses without the signal sequence do not enter the nucleus as virus particles.

### 5.9 Chromatin and Chromosomes

(A) When a cell is not dividing, the nuclear DNA is aggregated with proteins to form chromatin, which is dispersed throughout the nucleus. This two-dimensional image was made using a transmission electron microscope. (B) The chromosomes in dividing cells become highly condensed. This three-dimensional image of isolated metaphase chromosomes was produced by a scanning electron microscope.

Dense chromatin (dark) near the nuclear envelope is attached to the nuclear lamina.  
Diffuse chromatin (light) is in the nucleoplasm.



membrane of another organelle, the endoplasmic reticulum, which we will discuss next.

### The endomembrane system is a group of interrelated organelles

Much of the volume of some eukaryotic cells is taken up by an extensive **endomembrane system**. This is an interconnected system of membrane-enclosed compartments that are sometimes flattened into sheets and sometimes have other characteristic shapes (see Figure 5.7). The endomembrane system includes the plasma membrane, nuclear envelope, endoplasmic reticulum, Golgi apparatus, and lysosomes, which are derived from the Golgi. Tiny, membrane-surrounded droplets called vesicles shuttle substances between the various components of the endomembrane system (Figure 5.10). In drawings and electron microscope pictures this system appears static, fixed in space and time. But these depictions are just snapshots; in the living cell, membranes and the materials they contain are in constant motion. Membrane components have been observed to shift from one organelle to another within the endomembrane system. Thus, all these membranes must be functionally related.

**ENDOPLASMIC RETICULUM** Electron micrographs of eukaryotic cells reveal networks of interconnected membranes branching throughout the cytoplasm, forming tubes and flattened sacs. These membranes are collectively called the **endoplasmic reticulum**, or **ER**. The interior compartment of the ER, referred to as the lumen, is separate and distinct from the surrounding cytoplasm (see Figure 5.10). The ER can enclose up to 10 percent of the interior volume of the cell, and its foldings result in a surface area many times greater than that of the plasma membrane. There are two types of endoplasmic reticulum, the so-called rough and smooth.

**Rough endoplasmic reticulum (RER)** is called “rough” because of the many ribosomes attached to the outer surface of the membrane, giving it a “rough” appearance in electron microscopy (see Figure 5.7). The attached ribosomes are actively involved in protein synthesis, but that is not the entire story:

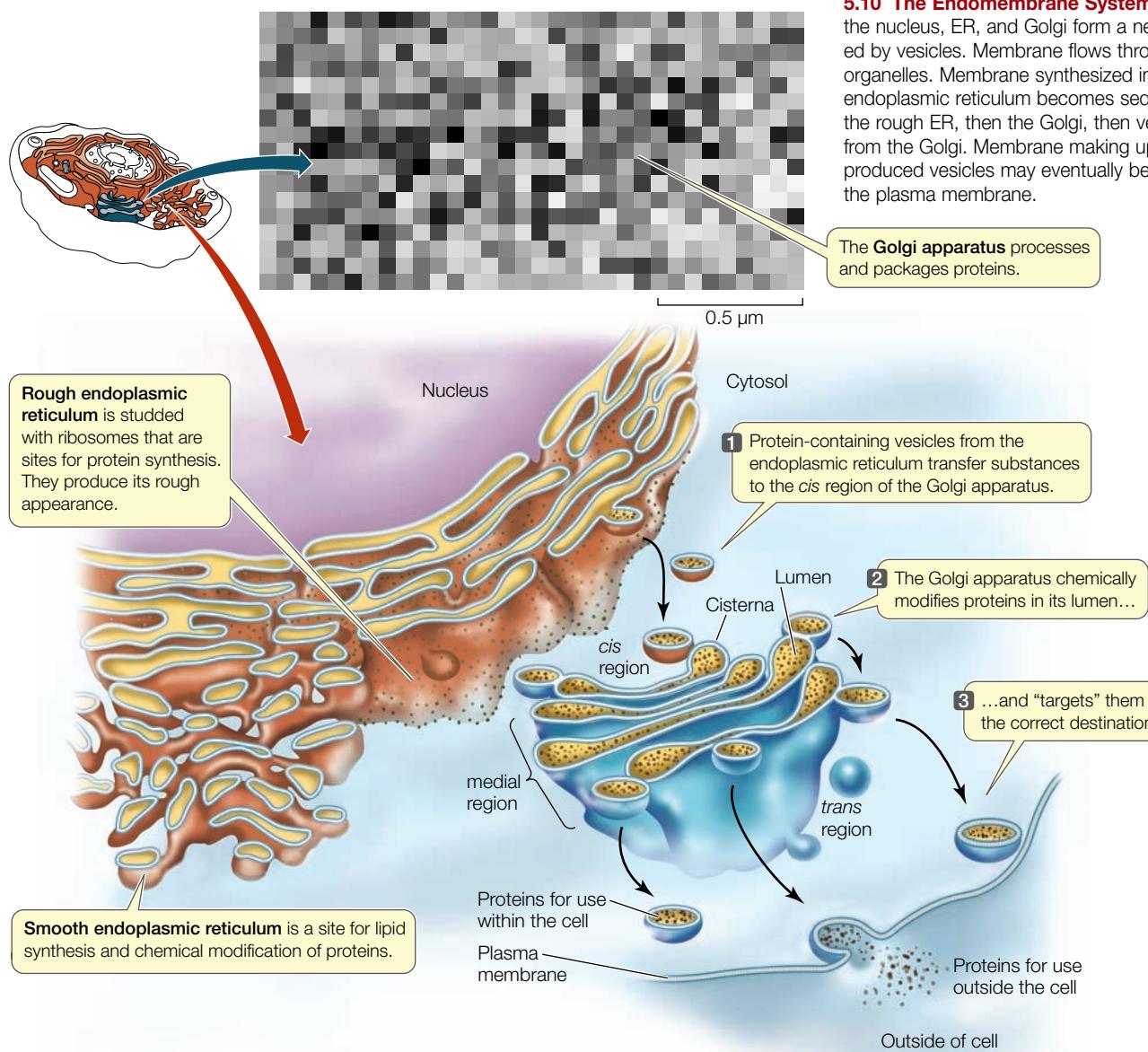
- The RER receives into its lumen certain newly synthesized proteins, segregating them away from the cytoplasm. The RER also participates in transporting these proteins to other locations in the cell.
- While inside the RER, proteins can be chemically modified to alter their functions and to chemically ‘tag’ them for delivery to specific cellular destinations.
- Proteins are shipped to cellular destinations enclosed within vesicles that pinch off from the ER.
- Most membrane-bound proteins are made in the RER.

A protein enters the lumen of the RER through a pore as it is synthesized. As with a protein passing through a nuclear pore, this is accomplished via a sequence of amino acids on the protein, which acts as a RER localization signal (see Section 14.6). Once in the lumen of the RER, proteins undergo several changes, including the formation of disulfide bridges and folding into their tertiary structures (see Figure 3.7).

Some proteins are covalently linked to carbohydrate groups in the RER, thus becoming glycoproteins. In the case of proteins directed to the lysosomes, the carbohydrate groups are part of an “addressing” system that ensures that the right proteins are directed to those organelles. This addressing system is very important because the enzymes within the lysosomes are some of the most destructive the cell makes. Were they not properly addressed and contained, they could destroy the cell.

The **smooth endoplasmic reticulum (SER)** lacks ribosomes and is more tubular (and less like flattened sacs) than the RER, but it shows continuity with portions of the RER (see Figure 5.10). Within the lumen of the SER, some proteins that have been synthesized on the RER are chemically modified. In addition, the SER has three other important roles:

- It is responsible for the chemical modification of small molecules taken in by the cell, including drugs and pesticides. These modifications make the targeted molecules more polar, so they are more water-soluble and more easily removed.
- It is the site for glycogen degradation in animal cells. We discuss this important process in Chapter 9.
- It is the site for the synthesis of lipids and steroids.



Cells that synthesize a lot of protein for export are usually packed with RER. Examples include glandular cells that secrete digestive enzymes and white blood cells that secrete antibodies. In contrast, cells that carry out less protein synthesis (such as storage cells) contain less RER. Liver cells, which modify molecules (including toxins) that enter the body from the digestive system, have abundant SER.

**GOLGI APPARATUS** The **Golgi apparatus** (or Golgi complex), more often referred to merely as the Golgi, is another part of the diverse, dynamic, and extensive endomembrane system (see Figure 5.10). The exact appearance of the Golgi apparatus (named for its discoverer, Camillo Golgi) varies from species to species, but it almost always consists of two components: flattened membranous sacs called *cisternae* (singular *cisterna*) that are piled up like saucers, and small membrane-enclosed vesicles. The entire apparatus is about 1 μm long.

**5.10 The Endomembrane System** Membranes of the nucleus, ER, and Golgi form a network, connected by vesicles. Membrane flows through these organelles. Membrane synthesized in the smooth endoplasmic reticulum becomes sequentially part of the rough ER, then the Golgi, then vesicles formed from the Golgi. Membrane making up the Golgi-produced vesicles may eventually become part of the plasma membrane.

The **Golgi apparatus** processes and packages proteins.

1 Protein-containing vesicles from the endoplasmic reticulum transfer substances to the *cis* region of the Golgi apparatus.

2 The Golgi apparatus chemically modifies proteins in its lumen...

...and “targets” them to the correct destinations.

Outside of cell

The Golgi has several roles:

- When protein-containing vesicles from the RER fuse with the Golgi membranes, the Golgi receives the proteins and may further modify them.
- It concentrates, packages, and sorts proteins before they are sent to their cellular or extracellular destinations.
- It adds some carbohydrates to proteins and modifies others that were attached to proteins in the ER.
- It is where some polysaccharides for the plant cell wall are synthesized.

While there is a characteristic form for all Golgi, there are also variations in its size and appearance in different cell types. In the cells of plants, protists, fungi, and many invertebrate animals, the stacks of cisternae are individual units scattered throughout the cytoplasm. In vertebrate cells, a few such stacks usually form a single, larger, more complex Golgi apparatus.

The cisternae of the Golgi apparatus appear to have three functionally distinct regions: the *cis* region lies nearest to the nucleus or a patch of RER, the *trans* region lies closest to the plasma membrane, and the *medial* region lies in between (see Figure 5.10). (The terms *cis*, *trans*, and *medial* derive from Latin words meaning, respectively, “on the same side,” “on the opposite side,” and “in the middle.”) These three parts of the Golgi apparatus contain different enzymes and perform different functions.

The Golgi apparatus receives proteins from the ER, packages them, and sends them on their way. Since there is often no direct membrane continuity between the ER and Golgi apparatus, how does a protein get from one organelle to the other? The protein could simply leave the ER, travel across the cytoplasm, and enter the Golgi apparatus. But that would expose the protein to interactions with other molecules in the cytoplasm. On the other hand, segregation from the cytoplasm could be maintained if a piece of the ER could “bud off,” forming a membranous vesicle that contains the protein—and that is exactly what happens.

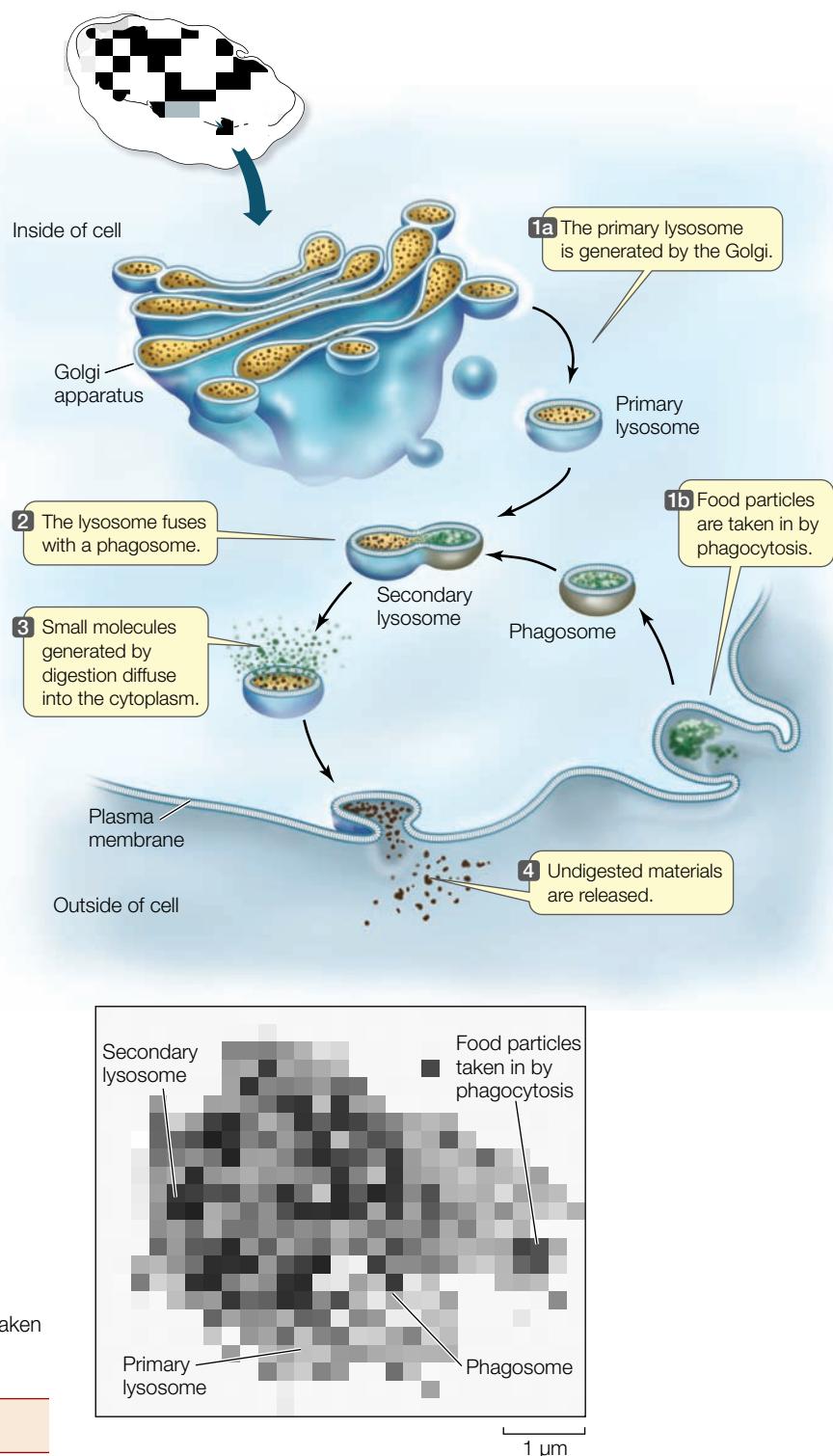
Proteins make the passage from the ER to the Golgi apparatus safely enclosed in vesicles. Once it arrives, a vesicle fuses with the *cis* membrane of the Golgi apparatus, releasing its cargo into the lumen of the Golgi cisterna. Other vesicles may move between the cisternae, transporting proteins, and it appears that some proteins move from one cisterna to the next through tiny channels. Vesicles budding off from the *trans* region carry their contents away from the Golgi apparatus. These vesicles go to the plasma membrane, or to another organelle in the endomembrane system called the lysosome.

**LYSOSOMES** The **primary lysosomes** originate from the Golgi apparatus. They contain digestive enzymes, and they are the sites where macromolecules—proteins, polysaccharides, nucleic acids, and lipids—are hydrolyzed into their monomers (see Figure 3.4). Lysosomes are about 1  $\mu\text{m}$  in diameter; they are surrounded by a single membrane and have a featureless interior (Figure 5.11). There may be dozens of lysosomes in a cell, depending on its needs.

Lysosomes are sites for the breakdown of food, other cells, or foreign objects that are taken up by the cell. These materials get into the cell by a process called *phagocytosis* (*phago*, “eat”; *cytosis*, “cellular”). In this process, a pocket forms in the plasma membrane and then deepens and encloses material from outside

the cell. The pocket becomes a small vesicle called a phagosome, containing food or other material, which breaks free of the plasma membrane to move into the cytoplasm. The phagosome fuses with a primary lysosome to form a **secondary lysosome**, in which digestion occurs.

The effect of this fusion is rather like releasing hungry foxes into a chicken coop: the enzymes in the secondary lysosome quickly hydrolyze the food particles. These reactions are en-



### 5.11 Lysosomes Isolate Digestive Enzymes from the Cytoplasm

Lysosomes are sites for the hydrolysis of material taken into the cell by phagocytosis.

hanced by the mild acidity of the lysosome's interior, where the pH is lower than in the surrounding cytoplasm. The products of digestion pass through the membrane of the lysosome, providing energy and raw materials for other cellular processes. The "used" secondary lysosome, now containing undigested particles, then moves to the plasma membrane, fuses with it, and releases the undigested contents to the environment.

Phagocytes are specialized cells that have an essential role in taking up and breaking down materials; they are found in nearly all animals and many protists. You will encounter them and their activities again at many places in this book, but at this point one example suffices: in the human liver and spleen, phagocytes digest approximately 10 billion aged or damaged blood cells each day! The digestion products are then used to make new cells to replace those that are digested.

Lysosomes are active even in cells that do not perform phagocytosis. Because cells are such dynamic systems, some cell components are frequently destroyed and replaced by new ones. The programmed destruction of cell components is called *autophagy*, and lysosomes are where the cell breaks down its own materials. With the proper signal, lysosomes can engulf entire organelles, hydrolyzing their constituents.

How important is autophagy? An entire class of human diseases called lysosomal storage diseases occur when lysosomes fail to digest internal components; these diseases are invariably very harmful or fatal. An example is Tay-Sachs disease, in which a particular lipid called a ganglioside is not broken down in lysosomes and instead accumulates in brain cells. In the most common form of this disease, a baby starts exhibiting neurological symptoms and becomes blind, deaf, and unable to swallow after six months of age. Death occurs before age 4.

Plant cells do not appear to contain lysosomes, but the central vacuole of a plant cell (which we will describe below) may function in an equivalent capacity because it, like lysosomes, contains many digestive enzymes.

### Some organelles transform energy

All living things require external sources of energy. The energy from such sources must be transformed so that it can be used by cells. A cell requires energy to make the molecules it needs for activities such as growth, reproduction, responsiveness, and movement. Energy is transformed from one form to another in mitochondria (found in all eukaryotic cells) and in chloroplasts (found in eukaryotic cells that harvest energy from sunlight). In contrast, energy transformations in prokaryotic cells are associated with enzymes attached to the inner surface of the plasma membrane or to extensions of the plasma membrane that protrude into the cytoplasm.

**MITOCHONDRIA** In eukaryotic cells, the breakdown of fuel molecules such as glucose begins in the cytosol. The molecules that result from this partial degradation enter the **mitochondria** (singular *mitochondrion*), whose primary function is to convert the chemical energy of those fuel molecules into a form that the cell can use, namely the energy-rich molecule ATP (adenosine triphosphate) (see Section 8.2). The production of ATP in the mi-

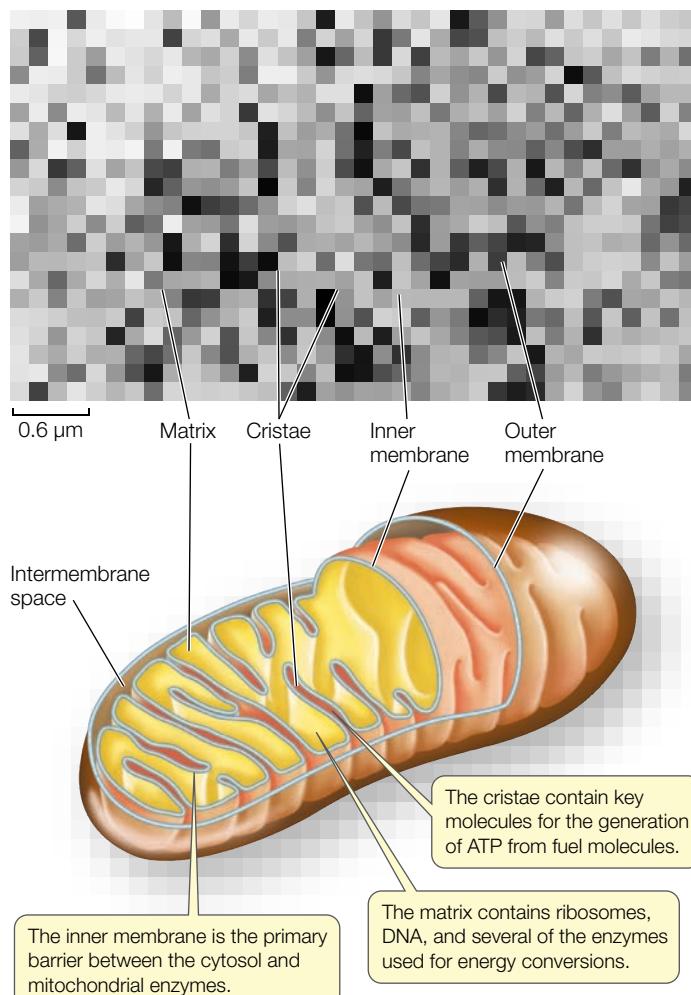
tochondria, using fuel molecules and molecular oxygen ( $O_2$ ), is called *cellular respiration*.

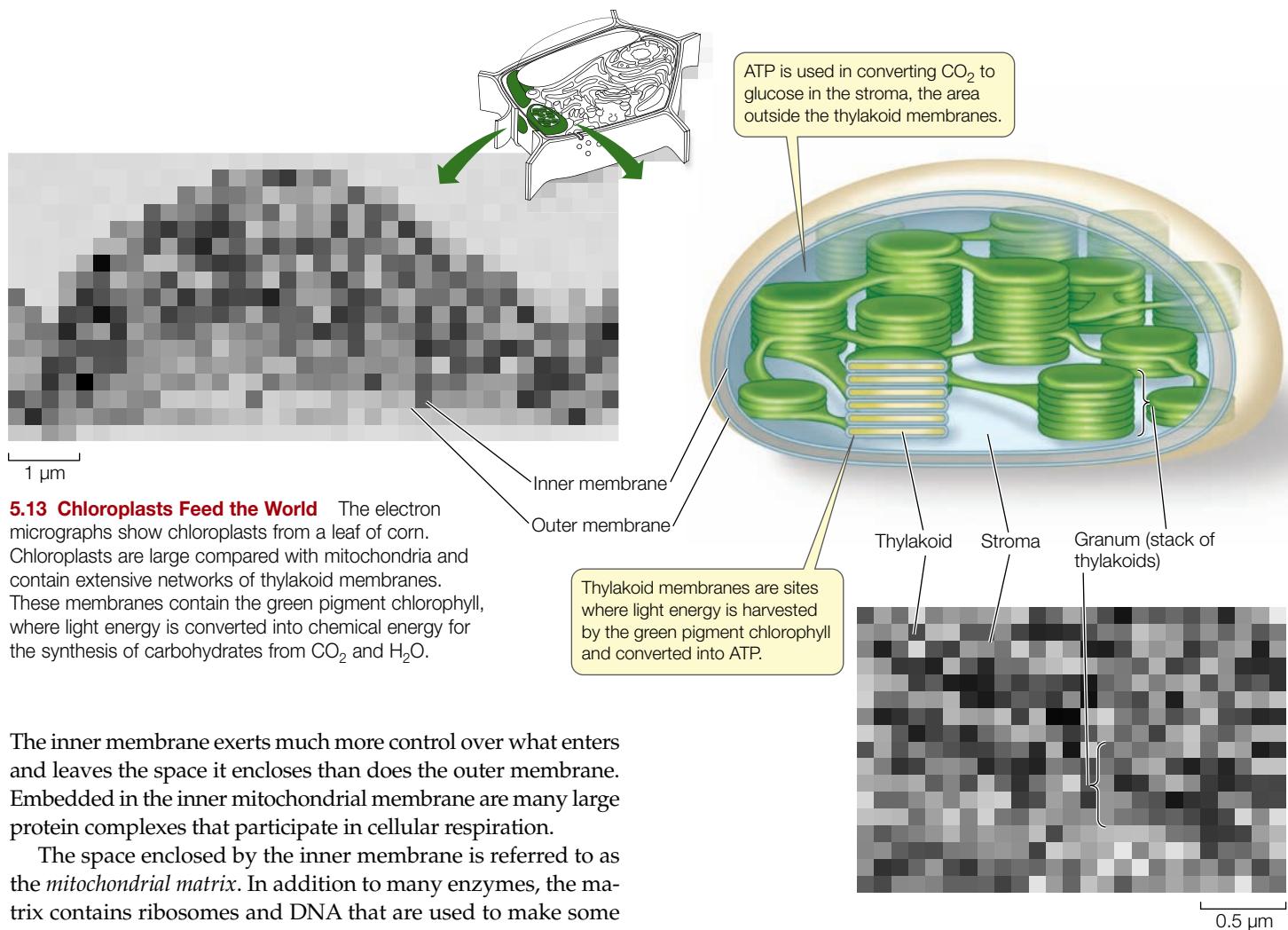
Typical mitochondria are somewhat less than 1.5  $\mu m$  in diameter and 2–8  $\mu m$  in length—about the size of many bacteria. They can divide independently of the central nucleus. The number of mitochondria per cell ranges from one gigantic organelle in some unicellular protists to a few hundred thousand in large egg cells. An average human liver cell contains more than a thousand mitochondria. Cells that are active in movement and growth require the most chemical energy, and these tend to have the most mitochondria per unit of volume.

Mitochondria have two membranes. The outer membrane is smooth and protective, and it offers little resistance to the movement of substances into and out of the organelle. Immediately inside the outer membrane is an inner membrane, which folds inward in many places, and thus has a surface area much greater than that of the outer membrane (Figure 5.12). The folds tend to be quite regular, giving rise to shelf-like structures called *cristae*.

### 5.12 A Mitochondrion Converts Energy from Fuel Molecules into ATP

The electron micrograph is a two-dimensional slice through a three-dimensional organelle. As the drawing emphasizes, the cristae are extensions of the inner mitochondrial membrane.



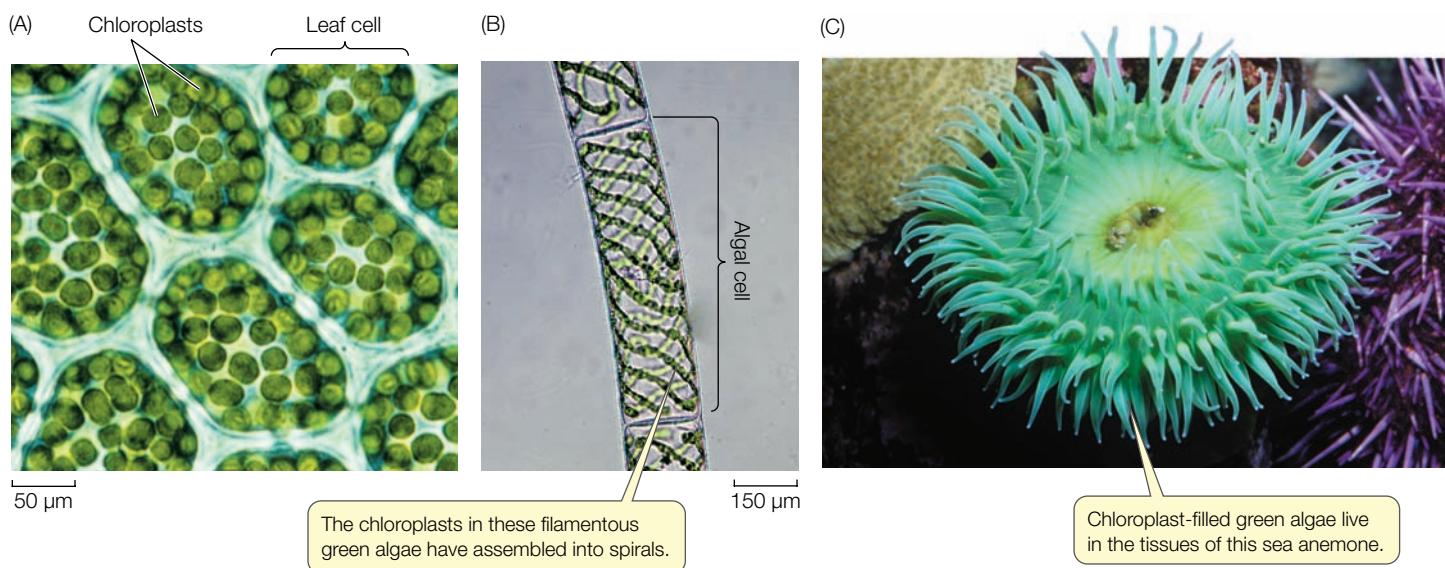


*grana*), consists of a series of flat, closely packed, circular compartments called **thylakoids** (see Figure 5.13). Thylakoid lipids are distinctive: only 10 percent are phospholipids, while the rest are galactose-substituted diglycerides and sulfolipids. Because of the abundance of chloroplasts, these are the most abundant lipids in the biosphere.

In addition to lipids and proteins, the membranes of the thylakoids contain chlorophyll and other pigments that harvest light energy for photosynthesis (we see how they do this in Section 10.2). The thylakoids of one grana may be connected to those of other grana, making the interior of the chloroplast a highly developed network of membranes, much like the ER.

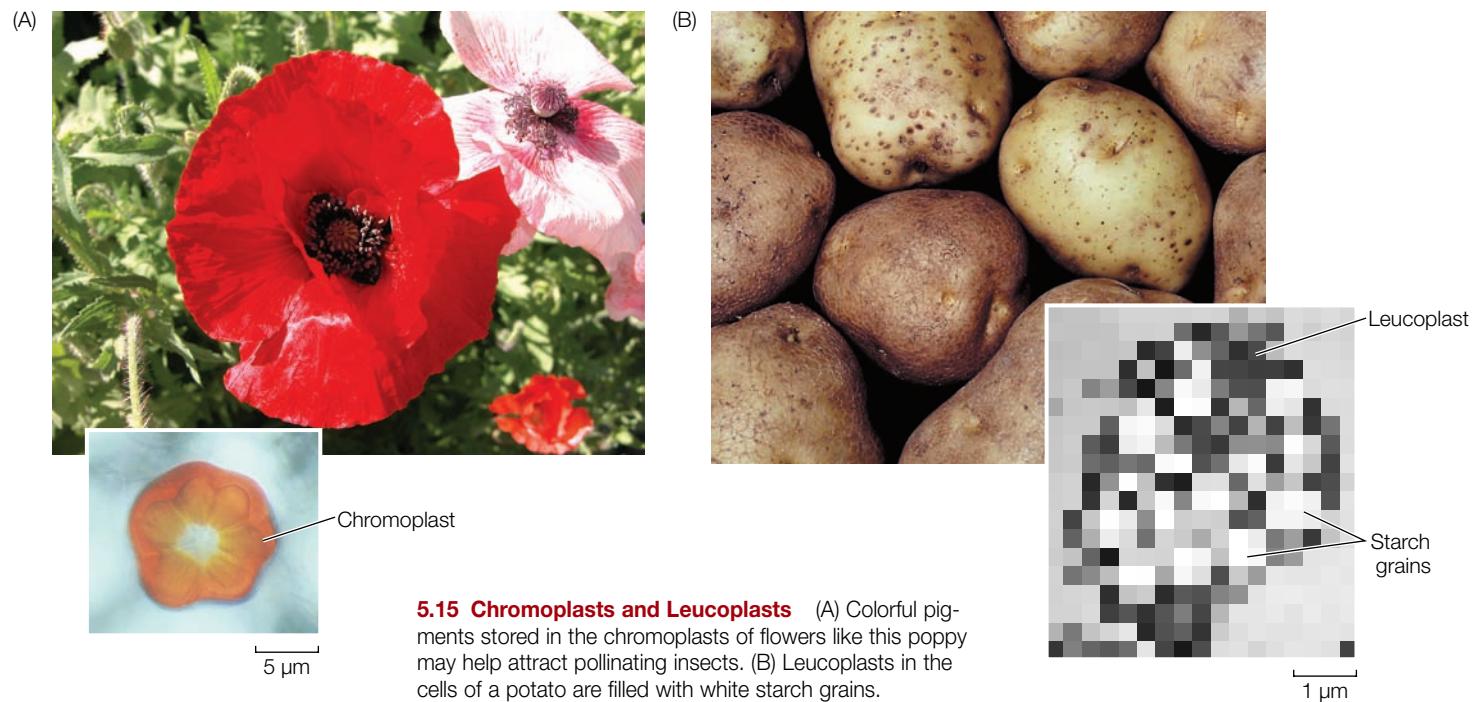
The fluid in which the grana are suspended is called the *stroma*. Like the mitochondrial matrix, the chloroplast stroma contains ribosomes and DNA, which are used to synthesize some, but not all, of the proteins that make up the chloroplast.

Animal cells typically do not contain chloroplasts, but some do contain functional photosynthetic organisms. The green color of some corals and sea anemones comes from chloroplasts in algae that live within those animals (see Figure 5.14C). The animals derive some of their nutrition from the photosynthesis that their chloroplast-containing “guests” carry out. Such an intimate relationship between two different organisms is called **symbiosis**.

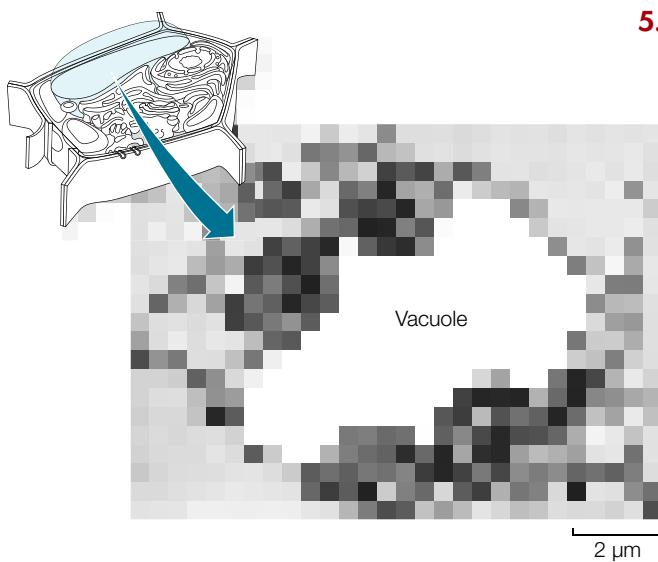


**5.14 Chloroplasts Are Everywhere** (A) In green plants, chloroplasts are concentrated in the leaf cells. (B) Green algae are photosynthetic and filled with chloroplasts. (C) No animal species produces its own chloroplasts, but this sea anemone (an animal) is nourished by the chloroplasts of unicellular green algae living within its tissues, in what is termed a symbiotic relationship.

Other types of plastids such as *chromoplasts* and *leucoplasts* have functions different from those of chloroplasts (Figure 5.15). Chromoplasts make and store red, yellow, and orange pigments, especially in flowers and fruits. Leucoplasts are storage organelles that do not contain pigments. An amyloplast is a leucoplast that stores starch.



**5.15 Chromoplasts and Leucoplasts** (A) Colorful pigments stored in the chromoplasts of flowers like this poppy may help attract pollinating insects. (B) Leucoplasts in the cells of a potato are filled with white starch grains.



**5.16 Vacuoles in Plant Cells Are Usually Large** The large central vacuole in this cell is typical of mature plant cells. Smaller vacuoles are visible toward each end of the cell.

**Glyoxysomes** are similar to peroxisomes and are found only in plants. They are most abundant in young plants, and are the locations where stored lipids are converted into carbohydrates for transport to growing cells.

**Vacuoles** occur in many eukaryotic cells, but particularly those of plants and protists. Plant vacuoles (Figure 5.16) have several functions:

- **Storage:** Plant cells produce a number of toxic by-products and waste products, many of which are simply stored within vacuoles. Because they are poisonous or distasteful, these stored materials deter some animals from eating the plants, and may thus contribute to plant defenses and survival.
- **Structure:** In many plant cells, enormous vacuoles take up more than 90 percent of the cell volume and grow as the cell grows. The presence of dissolved substances in the vacuole causes water to enter it from the cytoplasm, making the vacuole swell like a balloon. The plant cell does not swell when the vacuole fills with water, since it has a rigid cell wall. Instead, it stiffens from the increase in water pressure (called turgor), which supports the plant (see Figure 6.10).
- **Reproduction:** Some pigments (especially blue and pink ones) in the petals and fruits of flowering plants are contained in vacuoles. These pigments—the anthocyanins—are visual cues that help attract the animals that assist in pollination or seed dispersal.
- **Digestion:** In some plants, vacuoles in seeds contain enzymes that hydrolyze stored seed proteins into monomers that the developing plant embryo can use as food.

*Contractile vacuoles* are found in many freshwater protists. Their function is to get rid of the excess water that rushes into the cell because of the imbalance in solute concentration between the interior of the cell and its freshwater environment. The contractile vacuole enlarges as water enters, then abruptly contracts, forcing the water out of the cell through a special pore structure.

So far, we have discussed numerous membrane-enclosed organelles. Now we turn to a group of cytoplasmic structures without membranes.

### The cytoskeleton is important in cell structure and movement

From the earliest observations, light microscopy revealed distinctive shapes of cells that would sometimes change, and within cells rapid movements were observed. With the advent of electron microscopy, a new world of cellular substructure was revealed, including a meshwork of filaments inside cells. Experimentation showed that this **cytoskeleton** fills several important roles:

- It supports the cell and maintains its shape.
- It holds cell organelles in position within the cell.
- It moves organelles within the cell.
- It is involved with movements of the cytoplasm, called cytoplasmic streaming.
- It interacts with extracellular structures, helping to anchor the cell in place.

There are three components of the cytoskeleton: microfilaments (smallest diameter), intermediate filaments, and microtubules (largest diameter). These filaments have very different functions.

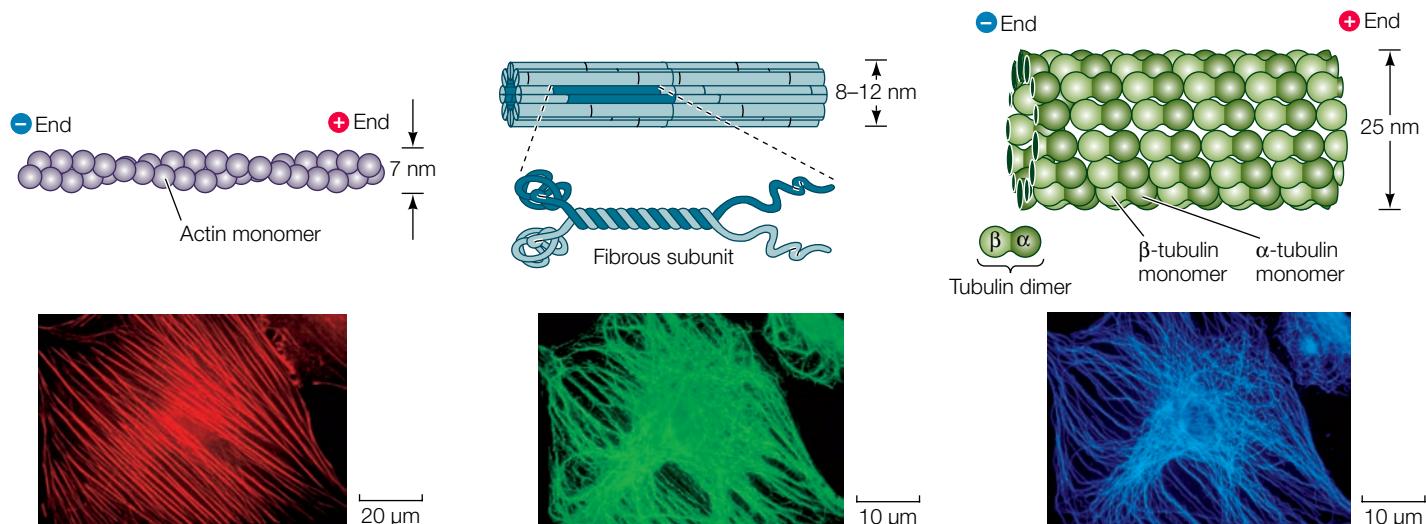
**MICROFILAMENTS** **Microfilaments** can exist as single filaments, in bundles, or in networks. They are about 7 nm in diameter and up to several micrometers long. Microfilaments have two major roles:

- They help the entire cell or parts of the cell to move.
- They determine and stabilize cell shape.

Microfilaments are assembled from *actin* monomers, a protein that exists in several forms and has many functions, especially in animals. The actin found in microfilaments (which are also known as actin filaments) has distinct ends designated “plus” and “minus.” These ends permit actin monomers to interact with one another to form long, double helical chains (Figure 5.17A). Within cells, the polymerization of actin into microfilaments is reversible, and the microfilaments can disappear from cells by breaking down into monomers of free actin. Special actin-binding proteins mediate these events.

In the muscle cells of animals, actin filaments are associated with another protein, the “motor protein” *myosin*, and the interactions of these two proteins account for the contraction of muscles (described in Section 48.1). In non-muscle cells, actin filaments are associated with localized changes in cell shape. For example, microfilaments are involved in the flowing movement of the cytoplasm called cytoplasmic streaming, in amoeboid movement, and in the “pinching” contractions that divide an animal cell into two daughter cells. Microfilaments are also involved in the formation of cellular extensions called pseudopodia (*pseudo*, “false”; *podia*, “feet”) that enable some cells to move (Figure 5.18). As you will see in Chapter 42, cells of the immune system must move toward other cells during the immune response.

In some cell types, microfilaments form a meshwork just inside the plasma membrane. Actin-binding proteins then cross-link the microfilaments to form a rigid net-like structure that supports the cell. For example, microfilaments support the tiny

**(A) Microfilaments**

Made up of strands of the protein actin; often interact with strands of other proteins.

**(B) Intermediate filaments**

Made up of fibrous proteins organized into tough, ropelike assemblages that stabilize a cell's structure and help maintain its shape.

**(C) Microtubules**

Long, hollow cylinders made up of many molecules of the protein tubulin. Tubulin consists of two subunits,  $\alpha$ -tubulin and  $\beta$ -tubulin.

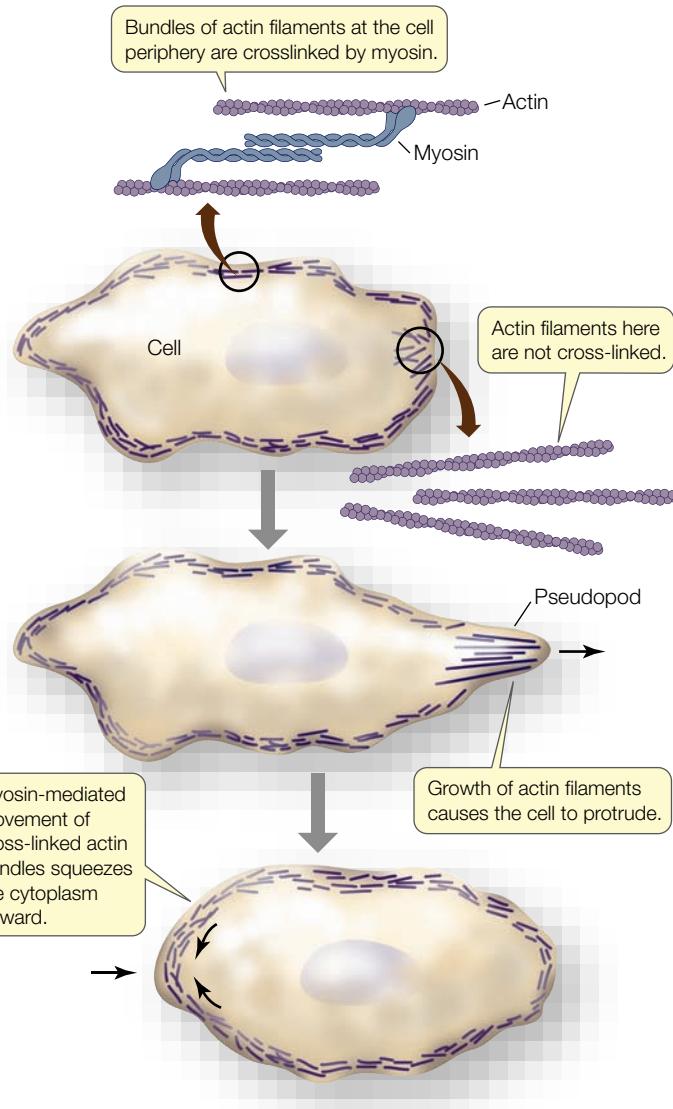
**5.17 The Cytoskeleton** Three highly visible and important structural components of the cytoskeleton are shown here in detail. These structures maintain and reinforce cell shape and contribute to cell movement.

microvilli that line the human intestine, giving it a larger surface area through which to absorb nutrients (**Figure 5.19**).

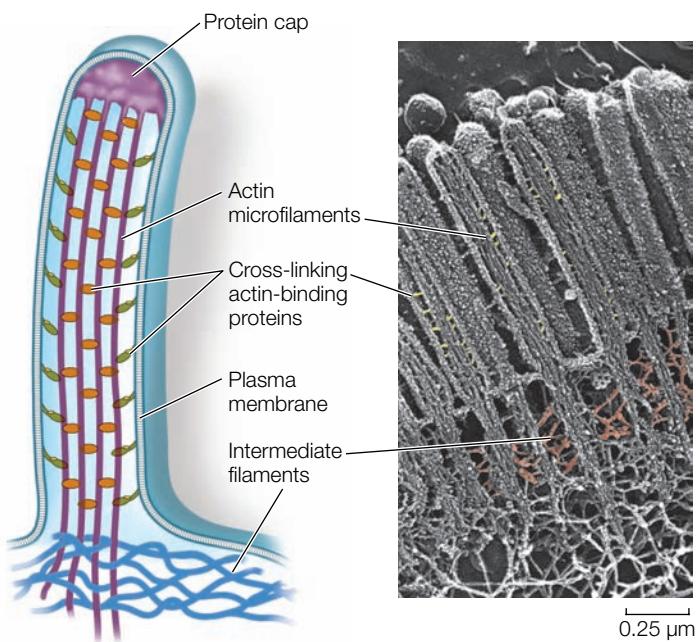
**INTERMEDIATE FILAMENTS** There are at least 50 different kinds of **intermediate filaments**, many of them specific to a few cell types. They generally fall into six molecular classes (based on amino acid sequence) that share the same general structure. One of these classes consists of fibrous proteins of the keratin family, which also includes the proteins that make up hair and fingernails. The intermediate filaments are tough, ropelike protein assemblages 8 to 12 nm in diameter (**Figure 5.17B**). Intermediate filaments are more permanent than the other two types; in cells they do not form and re-form, as the microtubules and microfilaments do.

Intermediate filaments have two major structural functions:

- They anchor cell structures in place. In some cells, intermediate filaments radiate from the nuclear envelope and help maintain the positions of the nucleus and other organelles in the cell. The lamins of the nuclear lamina are intermediate filaments (see Figure 5.8). Other kinds of intermediate filaments help hold in place the complex apparatus of microfilaments in the microvilli of intestinal cells (see Figure 5.19).
- They resist tension. For example, they maintain rigidity in body surface tissues by stretching through the cytoplasm and connecting specialized membrane structures called desmosomes (see Figure 6.7).



**5.18 Microfilaments and Cell Movements** Microfilaments mediate the movement of whole cells (as illustrated here for amoebic movement), as well as the movement of cytoplasm within a cell.



**5.19 Microfilaments for Support** Cells that line the intestine are folded into tiny projections called microvilli, which are supported by microfilaments. The microfilaments interact with intermediate filaments at the base of each microvillus. The microvilli increase the surface area of the cells, facilitating their absorption of small molecules.

**MICROTUBULES** The largest diameter components of the cytoskeletal system, **microtubules**, are long, hollow, unbranched cylinders about 25 nm in diameter and up to several micrometers long. Microtubules have two roles in the cell:

- They form a rigid internal skeleton for some cells.
- They act as a framework along which motor proteins can move structures within the cell.

Microtubules are assembled from dimers of the protein *tubulin*. A dimer is a molecule made up of two monomers. The polypeptide monomers that make up a tubulin dimer are known as  $\alpha$ -tubulin and  $\beta$ -tubulin. Thirteen chains of tubulin dimers surround the central cavity of the microtubule (Figure 5.17C; see also Figure 5.20). The two ends of a microtubule are different: one is designated the plus (+) end, and the other the minus (-) end. Tubulin dimers can be rapidly added or subtracted, mainly at the plus end, lengthening or shortening the microtubule. This capacity to change length rapidly makes microtubules dynamic structures, permitting some animal cells to rapidly change shape.

Many microtubules radiate from a region of the cell called the microtubule organizing center. Tubulin polymerization results in a rigid structure, and tubulin depolymerization leads to its collapse.

In plants, microtubules help control the arrangement of the cellulose fibers of the cell wall. Electron micrographs of plants frequently show microtubules lying just inside the plasma membranes of cells that are forming or extending their cell walls. Experimental alteration of the orientation of these microtubules leads to a similar change in the cell wall and a new shape for the cell.

Microtubules serve as tracks for **motor proteins**, specialized molecules that use cellular energy to change their shape and move. Motor proteins bond to and move along the microtubules, carrying materials from one part of the cell to another. Microtubules are also essential in distributing chromosomes to daughter cells during cell division. Because of this, drugs such as vincristine and taxol that disrupt microtubule dynamics also disrupt cell division. These drugs are useful for treating cancer, where cell division is excessive.

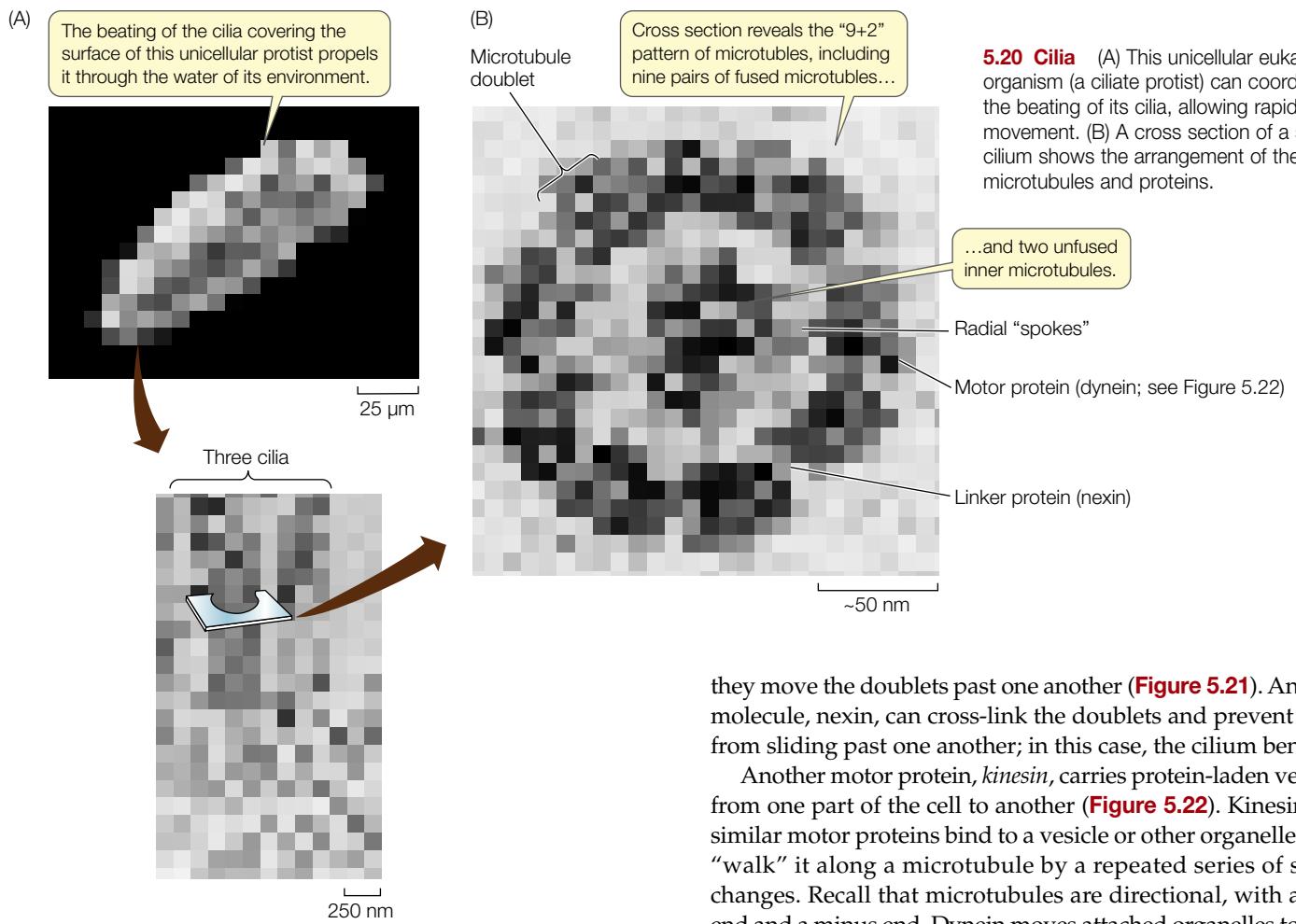
**CILIA AND FLAGELLA** Microtubules are also intimately associated with movable cell appendages: the **cilia** and **flagella**. Many eukaryotic cells have one or both of these appendages. Cilia are smaller than flagella—only 0.25  $\mu\text{m}$  in length. They may move surrounding fluid over the surface of the cell (for example, protists or cells lining tubes through which eggs move, the oviducts). Eukaryotic flagella are 0.25  $\mu\text{m}$  in diameter and 100–200  $\mu\text{m}$  in length. (The structure and operation of eukaryotic flagella are very different from those of prokaryotic flagella; see Figure 5.5.) They may push or pull the cell through its aqueous environment (for example, protists or sperm). Cilia and eukaryotic flagella are both assembled from specialized microtubules and have identical internal structures, but differ in their length and pattern of beating:

- Cilia (singular *cilium*) are usually present in great numbers (Figure 5.20A). They beat stiffly in one direction and recover flexibly in the other direction (like a swimmer’s arm), so that the recovery stroke does not undo the work of the power stroke.
- Eukaryotic flagella are usually found singly or in pairs. Waves of bending propagate from one end of a flagellum to the other in a snakelike undulation. Forces exerted by these waves on the surrounding fluid medium move the cell.

In cross section, a typical *cilium* or eukaryotic flagellum is surrounded by the plasma membrane and contains a “9 + 2” array of microtubules. As Figure 5.20B shows, nine fused pairs of microtubules—called doublets—form an outer cylinder, and one pair of unfused microtubules runs up the center. A spoke radiates from one microtubule of each doublet and connects the doublet to the center of the structure. These structures are essential to the bending motions of both cilia and flagella.

In the cytoplasm at the base of every eukaryotic flagellum and cilium is an organelle called a **basal body**. The nine microtubule doublets extend into the basal body. In the basal body, each doublet is accompanied by another microtubule, making nine sets of three microtubules. The central, unfused microtubules in the cilium do not extend into the basal body.

**Centrioles** are almost identical to the basal bodies of cilia and flagella. Centrioles are found in the microtubule organizing centers (sites of tubulin storage where microtubules polymerize) of all eukaryotes except the seed plants and some protists. Under the light microscope, a centriole looks like a small, featureless particle, but the electron microscope reveals that it contains a precise bundle of microtubules arranged in nine sets of three. Centrioles are involved in the formation of the mitotic spindle, to which the chromosomes attach during cell division (see Figure 11.10).

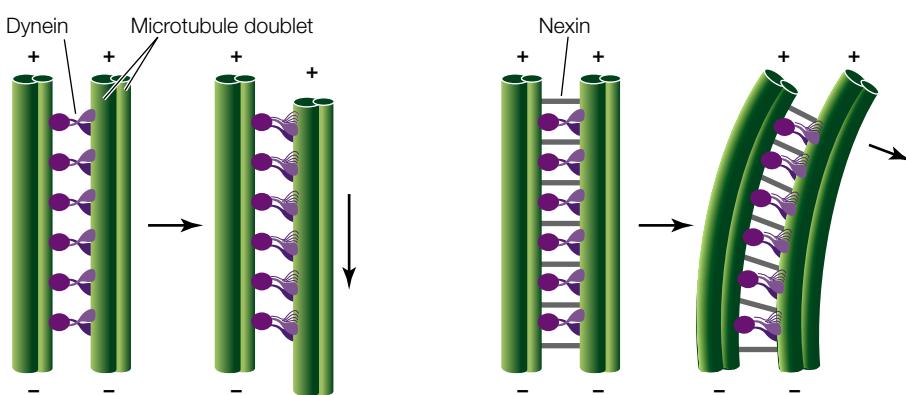


**MOTOR PROTEINS AND MOVEMENT** The nine microtubule doublets of cilia and flagella are linked by proteins. The motion of cilia and flagella results from the sliding of the microtubule doublets past each other. This sliding is driven by a motor protein called *dynein*, which can change its three-dimensional shape. All motor proteins work by undergoing reversible shape changes powered by energy from ATP hydrolysis. Dynein molecules that are attached to one microtubule doublet bind to a neighboring doublet. As the dynein molecules change shape, they move the doublets past one another (Figure 5.21). Another molecule, *nexin*, can cross-link the doublets and prevent them from sliding past one another; in this case, the cilium bends.

they move the doublets past one another (Figure 5.21). Another molecule, *nexin*, can cross-link the doublets and prevent them from sliding past one another; in this case, the cilium bends.

Another motor protein, *kinesin*, carries protein-laden vesicles from one part of the cell to another (Figure 5.22). Kinesin and similar motor proteins bind to a vesicle or other organelle, then “walk” it along a microtubule by a repeated series of shape changes. Recall that microtubules are directional, with a plus end and a minus end. Dynein moves attached organelles toward the minus end, while kinesin moves them toward the plus end (see Figure 5.17).

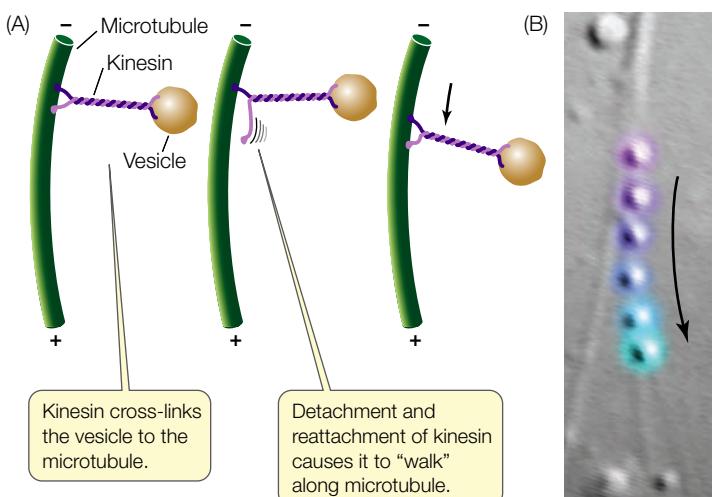
**DEMONSTRATING CYTOSKELETON FUNCTIONS** How do we know that the structural fibers of the cytoskeleton can achieve all these dynamic functions? We can observe an individual structure under the microscope and a function in a living cell that contains that structure. These observations may suggest that the structure carries out that function, but in science mere correlation does not show cause and effect. For example, light microscopy of living cells reveals that the cytoplasm is actively streaming around the cell, and that cytoplasm flows into an extended portion of an amoeboid cell during movement. The observed presence of cytoskeletal components suggests, but does not prove, their role in this process. Science seeks to show the specific links that relate one process, “A,” to a function, “B.” In cell biology, there are two ways to show that a structure or process “A” causes function “B”:



In isolated cilia without nexin cross-links, movement of dynein motor proteins causes microtubule doublets to slide past one another.

When nexin is present to cross-link the doublets, they cannot slide and the force generated by dynein movement causes the cilium to bend.

**5.21 A Motor Protein Moves Microtubules in Cilia and Flagella** A motor protein, dynein, causes microtubule doublets to slide past one another. In a flagellum or cilium, anchorage of the microtubule doublets to one another results in bending.



### 5.22 A Motor Protein Drives Vesicles along Microtubules

(A) Kinesin delivers vesicles or organelles to various parts of the cell by moving along microtubule "railroad tracks." Kinesin moves things from the minus toward the plus end of a microtubule; dynein works similarly, but moves from the plus toward the minus end. (B) Powered by kinesin, a vesicle moves along a microtubule track in the protist *Dictyostelium*. The time sequence (time-lapse micrography at half-second intervals) is shown by the color gradient of purple to blue.

- **Inhibition:** use a drug that inhibits A and see if B still occurs. If it does not, then A is probably a causative factor for B. **Figure 5.23** shows an experiment with such a drug (an inhibitor) that demonstrates cause and effect in the case of the cytoskeleton and cell movement.
- **Mutation:** examine a cell that lacks the gene (or genes) for A and see if B still occurs. If it does not, then A is probably a causative factor for B. Part Four of this book describes many experiments using this genetic approach.

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GO TO Animated Tutorial 5.2 • Eukaryotic Cell Tour

### 5.3 RECAP

The hallmark of eukaryotic cells is compartmentalization. Membrane-enclosed organelles process information, transform energy, form internal compartments for transporting proteins, and carry out intracellular digestion. An internal cytoskeleton plays several structural roles.

- What are some advantages of organelle compartmentalization? **See p. 84**
- Describe the structural and functional differences between rough and smooth endoplasmic reticulum. **See pp. 89–90 and Figure 5.10**
- Explain how motor proteins and microtubules move materials within the cell. **See pp. 95–98 and Figures 5.21 and 5.22**

## INVESTIGATING LIFE

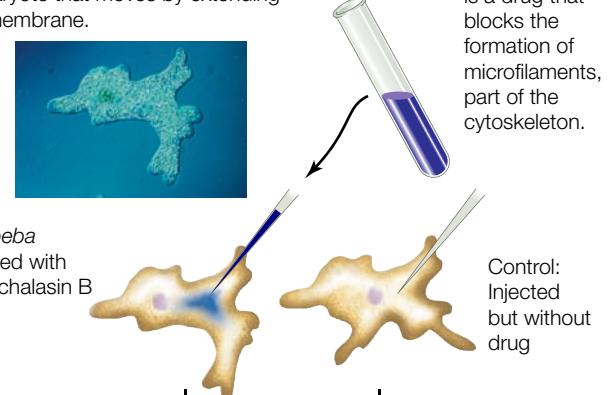
### 5.23 The Role of Microfilaments in Cell Movement—Showing Cause and Effect in Biology

After a test tube demonstration that the drug cytochalasin B prevented microfilament formation from monomeric precursors, the question was asked: Will the drug work like this in living cells and inhibit cell movement in *Amoeba*? Complementary experiments showed that the drug did not poison other cellular processes.

**HYPOTHESIS** Amoeboid cell movements are caused by the cytoskeleton.

#### METHOD

*Amoeba proteus* is a single-celled eukaryote that moves by extending its membrane.

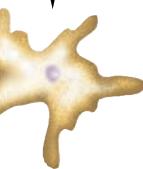


#### RESULTS

Treated Amoeba rounds up and does not move



Control Amoeba continues to move



**CONCLUSION** Microfilaments of the cytoskeleton are essential for amoeboid cell movement.

**FURTHER INVESTIGATION:** The drug colchicine breaks apart microtubules. How would you show that these components of the cytoskeleton are not involved in cell movement in *Amoeba*?

Go to [yourBioPortal.com](http://yourBioPortal.com) for original citations, discussions, and relevant links for all INVESTIGATING LIFE figures.

All cells interact with their environments, and many eukaryotic cells are parts of multicellular organisms and must interact, and closely coordinate activities, with other cells. The plasma membrane plays a crucial role in these interactions, but other structures outside that membrane are involved as well.

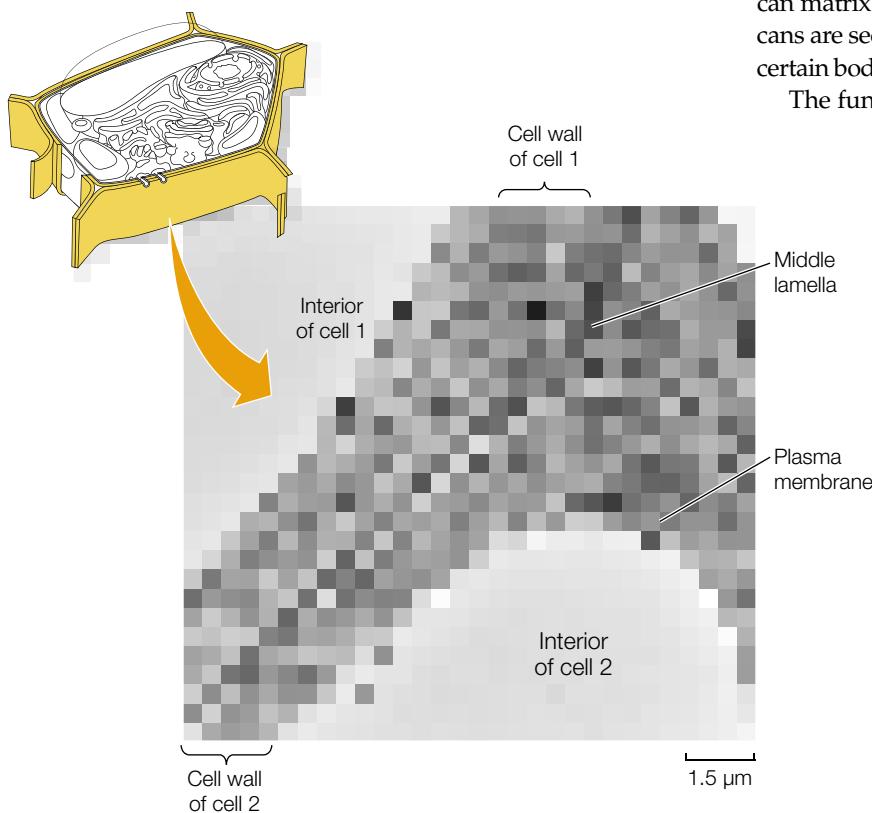
## 5.4 What Are the Roles of Extracellular Structures?

Although the plasma membrane is the functional barrier between the inside and the outside of a cell, many structures are produced by cells and secreted to the outside of the plasma membrane, where they play essential roles in protecting, supporting, or attaching cells to each other. Because they are outside the plasma membrane, these structures are said to be *extracellular*. The peptidoglycan cell wall of bacteria is an example of an extracellular structure (see Figure 5.4). In eukaryotes, other extracellular structures—the cell walls of plants and the extracellular matrices found between the cells of animals—play similar roles. Both of these structures are made up of two components:

- a prominent fibrous macromolecule
- a gel-like medium in which the fibers are embedded

### The plant cell wall is an extracellular structure

The plant **cell wall** is a semirigid structure outside the plasma membrane (Figure 5.24). We consider the structure and role of the cell wall in more detail in Chapter 34. For now, we note that it is typical of a two-component extracellular matrix, with cellulose fibers (see Figure 3.16) embedded in other complex polysaccharides and proteins. The plant cell wall has three major roles:



**5.24 The Plant Cell Wall** The semirigid cell wall provides support for plant cells. It is composed of cellulose fibrils embedded in a matrix of polysaccharides and proteins.

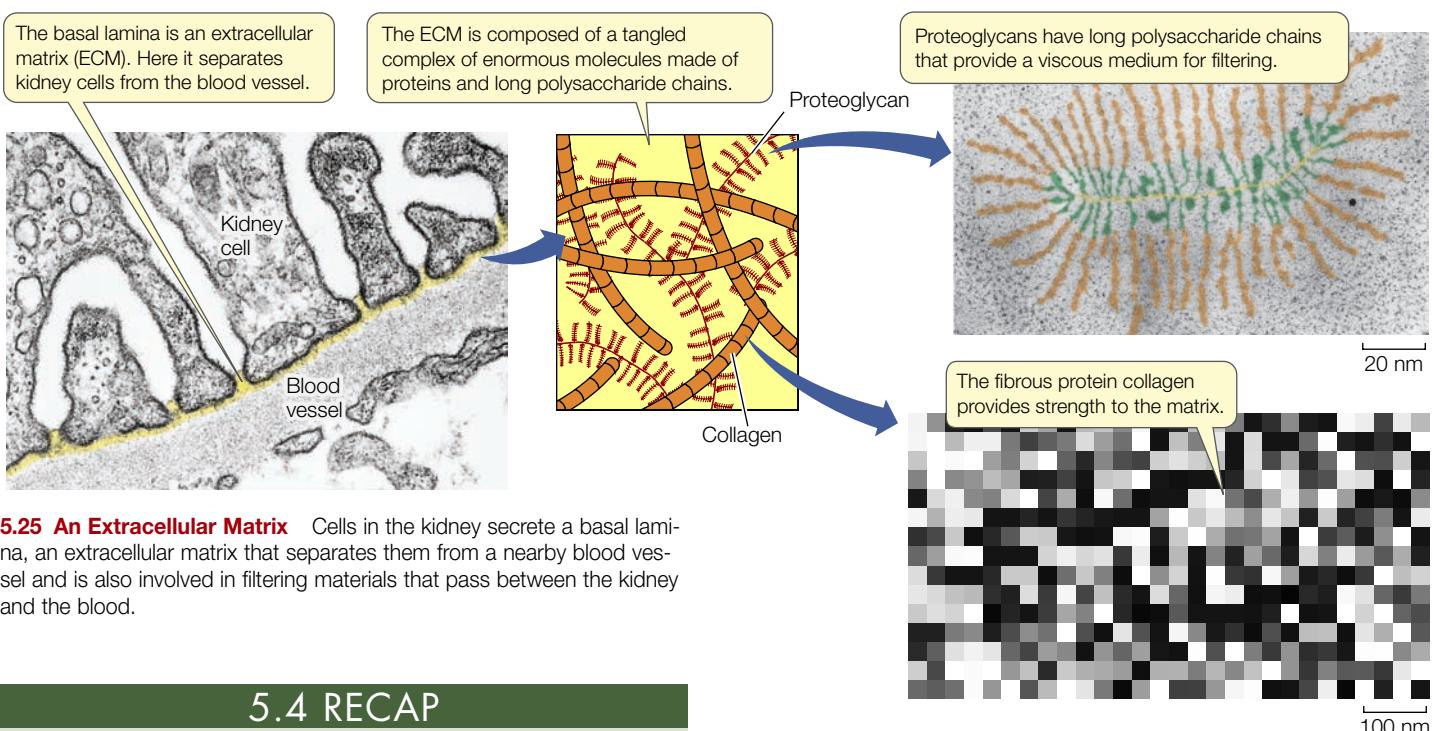
- It provides support for the cell and limits its volume by remaining rigid.
- It acts as a barrier to infection by fungi and other organisms that can cause plant diseases.
- It contributes to plant form by growing as plant cells expand. Because of their thick cell walls, plant cells viewed under a light microscope appear to be entirely isolated from one another. But electron microscopy reveals that this is not the case. The cytoplasms of adjacent plant cells are connected by numerous plasma membrane-lined channels, called **plasmodesmata**, that are about 20–40 nm in diameter and extend through the cell walls (see Figures 5.7 and 6.7). Plasmodesmata permit the diffusion of water, ions, small molecules, RNA, and proteins between connected cells, allowing for utilization of these substances far from their site of synthesis.

### The extracellular matrix supports tissue functions in animals

Animal cells lack the semirigid wall that is characteristic of plant cells, but many animal cells are surrounded by, or in contact with, an **extracellular matrix**. This matrix is composed of three types of molecules: fibrous proteins such as **collagen** (the most abundant protein in mammals, constituting over 25 percent of the protein in the human body); a matrix of glycoproteins termed **proteoglycans**, consisting primarily of sugars; and a third group of proteins that link the fibrous proteins and the gel-like proteoglycan matrix together (Figure 5.25). These proteins and proteoglycans are secreted, along with other substances that are specific to certain body tissues, by cells that are present in or near the matrix.

The functions of the extracellular matrix are many:

- It holds cells together in tissues. In Chapter 6 we see how there is an intercellular “glue” that is involved in both cell recognition and adhesion.
- It contributes to the physical properties of cartilage, skin, and other tissues. For example, the mineral component of bone is laid down on an organized extracellular matrix.
- It helps filter materials passing between different tissues. This is especially important in the kidney.
- It helps orient cell movements during embryonic development and during tissue repair.
- It plays a role in chemical signaling from one cell to another. Proteins connect the cell’s plasma membrane to the extracellular matrix. These proteins (for example, *integrin*) span the plasma membrane and are involved with transmitting signals to the interior of the cell. This allows communication between the extracellular matrix and the cytoplasm of the cell.



**5.25 An Extracellular Matrix** Cells in the kidney secrete a basal lamina, an extracellular matrix that separates them from a nearby blood vessel and is also involved in filtering materials that pass between the kidney and the blood.

## 5.4 RECAP

Extracellular structures are produced by cells and secreted outside the plasma membrane. Most consist of a fibrous component in a gel-like medium.

- What are the functions of the cell wall in plants and the extracellular matrix in animals? See p. 100

We have now discussed the structures and some functions of prokaryotic and eukaryotic cells. Both exemplify the cell theory, showing that cells are the basic units of life and of biological continuity. Much of the rest of this part of the book will deal with these two aspects of cells. There is abundant evidence that the simpler prokaryotic cells are more ancient than eukaryotic cells, and that the first cells were probably prokaryotic. We now turn to the next step in cellular evolution, the origin of eukaryotic cells.

## 5.5 How Did Eukaryotic Cells Originate?

For about 2 billion years, life on Earth was entirely prokaryotic—from the time when prokaryotic cells first appeared until about 1.5 billion years ago, when eukaryotic cells arrived on the scene. The advent of compartmentalization—the hallmark of eukaryotes—was a major event in the history of life, as it permitted many more biochemical functions to coexist in the same cell than had previously been possible. Compared to the typical eukaryote, a single prokaryotic cell is often biochemically specialized, limited in the resources it can use and the functions it can perform.

What is the origin of compartmentalization? We will describe the evolution of eukaryotic organelles in more detail in Section 27.1. Here, we outline two major themes in this process.

### Internal membranes and the nuclear envelope probably came from the plasma membrane

We noted earlier that some bacteria contain internal membranes. How could these arise? In electron micrographs, the internal

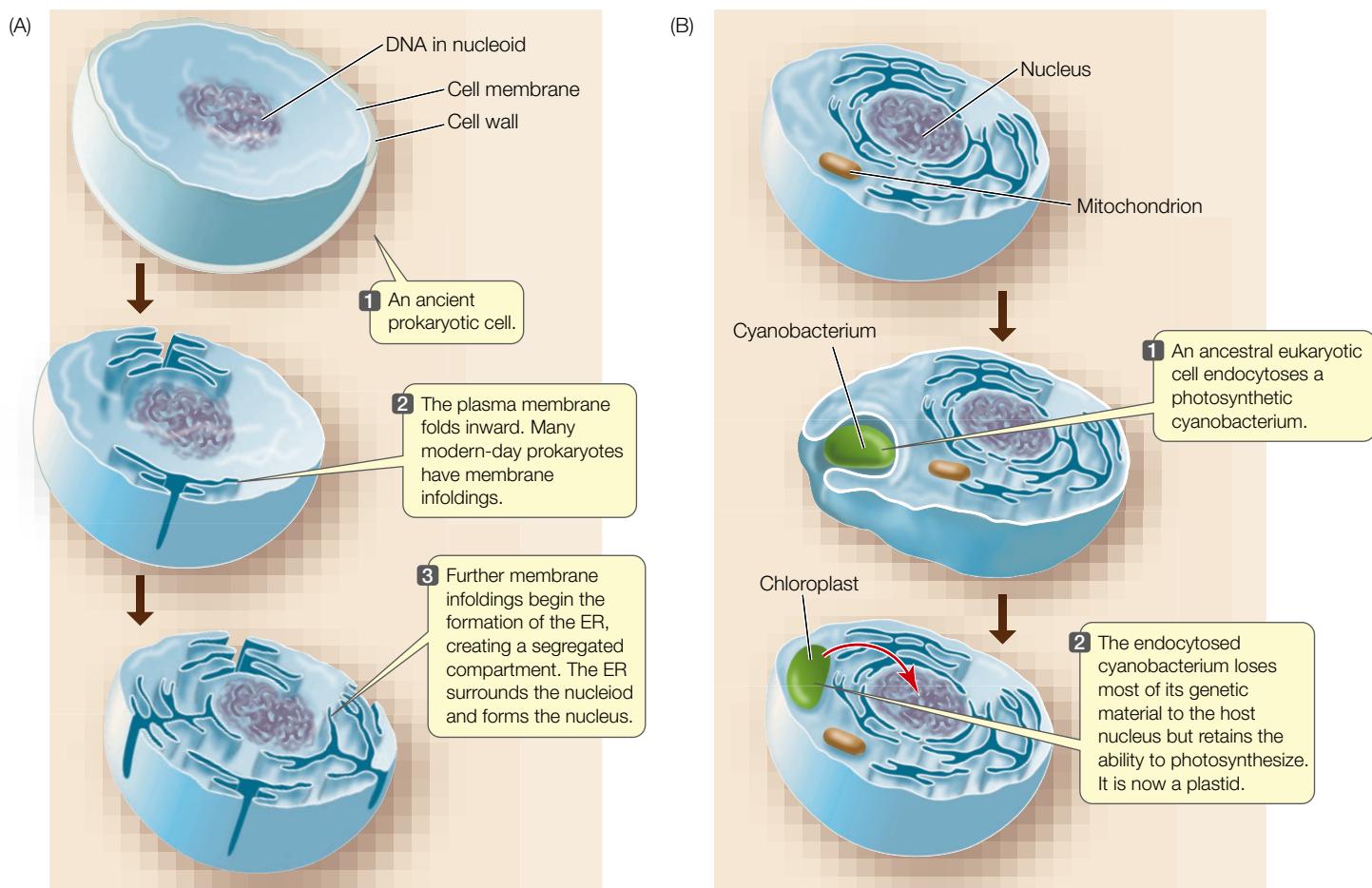
membranes of prokaryotes often appear to be inward folds of the plasma membrane. This has led to a theory that the endomembrane system and cell nucleus originated by a related process (**Figure 5.26A**). The close relationship between the ER and the nuclear envelope in today's eukaryotes is consistent with this theory.

A bacterium with enclosed compartments would have several evolutionary advantages. Chemicals could be concentrated within particular regions of the cell, allowing chemical reactions to proceed more efficiently. Biochemical activities could be segregated within organelles with, for example, a different pH from the rest of the cell, creating more favorable conditions for certain metabolic processes. Finally, gene transcription could be separated from translation, providing more opportunities for separate control of these steps in gene expression.

### Some organelles arose by endosymbiosis

**Symbiosis** means “living together,” and often refers to two organisms that coexist, each one supplying something that the other needs. Biologists have proposed that some organelles—the mitochondria and the plastids—arose not by an infolding of the plasma membrane but by one cell ingesting another cell, giving rise to a symbiotic relationship. Eventually, the ingested cell lost its autonomy and some of its functions. In addition, many of the ingested cell’s genes were transferred to the host’s DNA. Mitochondria and plastids in today’s eukaryotic cells are the remnants of these *symbionts*, retaining some specialized functions that benefit their host cells. This is the essence of the **endosymbiosis theory** for the origin of organelles.

Consider the case of the plastid. About 2.5 billion years ago some prokaryotes (the cyanobacteria) developed photosynthesis (see Figure 1.9). The emergence of these prokaryotes was a key event in the evolution of complex organisms, because they increased the O<sub>2</sub> concentration in Earth’s atmosphere (see Section 1.2).



**5.26 The Origin of Organelles** (A) The endomembrane system and cell nucleus may have been formed by infolding and then fusion of the plasma membrane. (B) The endosymbiosis theory proposes that some organelles may be descended from prokaryotes that were engulfed by other, larger cells.

According to endosymbiosis theory, photosynthetic prokaryotes also provided the precursor of the modern-day plastid. Cells without cell walls can engulf relatively large particles by phagocytosis (see Figure 5.11). In some cases, such as that of phagocytes in the human immune system, the engulfed particle can be an entire cell, such as a bacterium. Plastids may have arisen by a similar event involving an ancestral eukaryote and a cyanobacterium (**Figure 5.26B**).

Among the abundant evidence supporting the endosymbiotic origin of plastids (see Section 27.1), perhaps the most remarkable comes from a sandy beach in Japan. Noriko Okamoto and Isao Inouye recently discovered a single-celled eukaryote that contains a large “chloroplast,” and named it *Hatena* (**Figure 5.27**). It turns out that the “chloroplast” is the remains of a green alga, *Nephroselmis*, which lives among the *Hatena* cells. When living autonomously, this algal cell has flagella, a cytoskeleton, ER, Golgi, and mitochondria in addition to a plastid. Once ingested by *Hatena*, all of these structures, and presumably their associated functions, are lost. What remains is essentially a plastid.

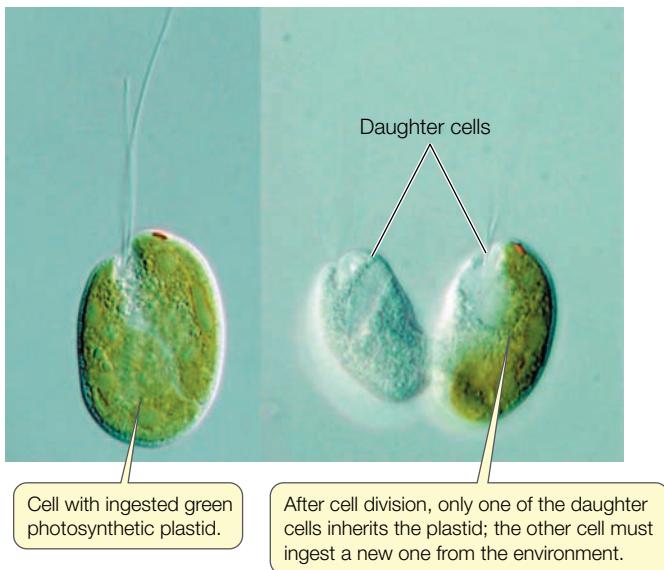
When *Hatena* divides, only one of the two daughter cells ends up with the “chloroplast.” The other cell finds and ingests its own *Nephroselmis* alga—almost like a “replay” of what may have occurred in the evolution of eukaryotic cells. No wonder the Japanese scientists call the host cell *Hatena*: in Japanese, it means “how odd”!

## 5.5 RECAP

Eukaryotic cells arose long after prokaryotic cells. Some organelles may have evolved by infolding of the plasma membrane, while others evolved by endosymbiosis.

- How could membrane infolding in a prokaryotic cell lead to the endomembrane system? **See p. 101 and Figure 5.26A**
- Explain the endosymbiosis theory for the origin of chloroplasts. **See Figure 5.26B**

In this chapter, we presented an overview of the structures of cells, with some ideas about their relationships and origins. As you now embark on the study of major cell functions, keep in



**5.27 Endosymbiosis in Action** A *Hatena* cell engulfs an algal cell, which then loses most of its cellular functions other than photosynthesis. This re-enacts a possible event in the origin of plastids in eukaryotic cells.

mind that the structures in a cell do not exist in isolation. They are part of a dynamic, interacting cellular system. In Chapter 6 we show that the plasma membrane is far from a passive barrier, but instead is a multi-functional system that connects the inside of the cell with its extracellular environment.

## CHAPTER SUMMARY

### 5.1 What Features Make Cells the Fundamental Units of Life?

#### SEE WEB ACTIVITIES 5.1 AND 5.2

- All cells come from preexisting cells.
- Cells are small because a cell's surface area must be large compared with its volume to accommodate exchanges with its environment. **Review Figure 5.2**
- All cells are enclosed by a selectively permeable **plasma membrane** that separates their contents from the external environment.
- While certain biochemical processes, molecules, and structures are shared by all kinds of cells, two categories of cells—**prokaryotes** and **eukaryotes**—are easily distinguished.

### 5.2 What Features Characterize Prokaryotic Cells?

- Prokaryotic cells have no internal compartments, but have a **nucleoid** region containing DNA, and a **cytoplasm** containing **cytosol**, **ribosomes**, proteins, and small molecules. Some prokaryotes have additional protective structures, including a **cell wall**, an **outer membrane**, and a **capsule**. **Review Figure 5.4**
- Some prokaryotes have folded membranes that may be photosynthetic membranes, and some have **flagella** or **pili** for motility or attachment. **Review Figure 5.5**

### 5.3 What Features Characterize Eukaryotic Cells?

- Eukaryotic cells are larger than prokaryotic cells and contain many membrane-enclosed **organelles**. The membranes that envelop organelles ensure compartmentalization of their functions. **Review Figure 5.7**
- **Ribosomes** are sites of protein synthesis.
- The **nucleus** contains most of the cell's DNA and participates in the control of protein synthesis. **Review Figure 5.8**
- The **endomembrane system**—consisting of the **endoplasmic reticulum** and **Golgi apparatus**—is a series of interrelated compartments enclosed by membranes. It segregates proteins and

modifies them. **Lysosomes** contain many digestive enzymes. **Review Figures 5.10 and 5.11**, **WEB ACTIVITY 5.3**, **ANIMATED TUTORIAL 5.1**

- **Mitochondria** and **chloroplasts** are semi-autonomous organelles that process energy. Mitochondria are present in most eukaryotic organisms and contain the enzymes needed for cellular respiration. The cells of photosynthetic eukaryotes contain chloroplasts that harvest light energy for photosynthesis. **Review Figures 5.12 and 5.13**
- **Vacuoles** are prominent in many plant cells and consist of a membrane-enclosed compartment full of water and dissolved substances.
- The **microfilaments**, **intermediate filaments**, and **microtubules** of the **cytoskeleton** provide the cell with shape, strength, and movement. **Review Figure 5.18**

#### SEE ANIMATED TUTORIAL 5.2

### 5.4 What Are the Roles of Extracellular Structures?

- The plant **cell wall** consists principally of **cellulose**. Cell walls are pierced by **plasmodesmata** that join the cytoplasms of adjacent cells.
- In animals, the **extracellular matrix** consists of different kinds of proteins, including collagen and proteoglycans. **Review Figure 5.25**

### 5.5 How Did Eukaryotic Cells Originate?

- Infoldings of the plasma membrane could have led to the formation of some membrane-enclosed organelles, such as the endomembrane system and the nucleus. **Review Figure 5.26A**
- The **endosymbiosis theory** states that mitochondria and chloroplasts originated when larger prokaryotes engulfed, but did not digest, smaller prokaryotes. Mutual benefits permitted this symbiotic relationship to be maintained, allowing the smaller cells to evolve into the eukaryotic organelles observed today. **Review Figure 5.26B**

## SELF-QUIZ

1. Which structure is generally present in both prokaryotic cells and eukaryotic plant cells?
  - a. Chloroplasts
  - b. Cell wall
  - c. Nucleus
  - d. Mitochondria
  - e. Microtubules
2. The major factor limiting cell size is the
  - a. concentration of water in the cytoplasm.
  - b. need for energy.
  - c. presence of membrane-enclosed organelles.
  - d. ratio of surface area to volume.
  - e. composition of the plasma membrane.
3. Which statement about mitochondria is *not* true?
  - a. The inner mitochondrial membrane folds to form cristae.
  - b. The outer membrane is relatively permeable to macromolecules.
  - c. Mitochondria are green because they contain chlorophyll.
  - d. Fuel molecules from the cytosol are used for respiration in mitochondria.
  - e. ATP is synthesized in mitochondria.
4. Which statement about plastids is true?
  - a. They are found in prokaryotes.
  - b. They are surrounded by a single membrane.
  - c. They are the sites of cellular respiration.
  - d. They are found only in fungi.
  - e. They may contain several types of pigments or polysaccharides.
5. If all the lysosomes within a cell suddenly ruptured, what would be the most likely result?
  - a. The macromolecules in the cytosol would break down.
  - b. More proteins would be made.
  - c. The DNA within mitochondria would break down.
  - d. The mitochondria and chloroplasts would divide.
  - e. There would be no change in cell function.
6. The Golgi apparatus
  - a. is found only in animals.
  - b. is found in prokaryotes.
  - c. is the appendage that moves a cell around in its environment.
  - d. is a site of rapid ATP production.
  - e. modifies and packages proteins.
7. Which structure is *not* surrounded by one or more membranes?
  - a. Ribosome
  - b. Chloroplast
  - c. Mitochondrion
  - d. Peroxisome
  - e. Vacuole
8. The cytoskeleton consists of
  - a. cilia, flagella, and microfilaments.
  - b. cilia, microtubules, and microfilaments.
  - c. internal cell walls.
  - d. microtubules, intermediate filaments, and microfilaments.
  - e. calcified microtubules.
9. Microfilaments
  - a. are composed of polysaccharides.
  - b. are composed of actin.
  - c. allow cilia and flagella to move.
  - d. make up the spindle that aids the movement of chromosomes.
  - e. maintain the position of the chloroplast in the cell.
10. Which statement about the plant cell wall is *not* true?
  - a. Its principal chemical components are polysaccharides.
  - b. It lies outside the plasma membrane.
  - c. It provides support for the cell.
  - d. It completely isolates adjacent cells from one another.
  - e. It is semirigid.

## FOR DISCUSSION

1. The drug vincristine is used to treat many cancers. It apparently works by causing microtubules to depolymerize. Vincristine use has many side effects, including loss of dividing cells and nerve problems. Explain why this might be so.
2. Through how many membranes would a molecule have to pass in moving from the interior (stroma) of a chloroplast to the interior (matrix) of a mitochondrion? From the interior of a lysosome to the outside of a cell? From one ribosome to another?
3. How does the possession of double membranes by chloroplasts and mitochondria relate to the endosymbiosis theory of the origins of these organelles? What other evidence supports the theory?
4. Compare the extracellular matrix of the animal cell with the plant cell wall, with respect to composition of the fibrous and nonfibrous components, rigidity, and connectivity of cells.

## ADDITIONAL INVESTIGATION

The pathway of newly synthesized proteins can be followed through the cell using a “pulse-chase” experiment. During synthesis, proteins are tagged with a radioactive isotope (the “pulse”), and then the cell is allowed to process the proteins for varying periods of time. The locations of the radioactive pro-

teins are then determined by isolating cell organelles and quantifying their radioactivity. How would you use this method, and what results would you expect for (a) a lysosomal enzyme and (b) a protein that is released from the cell?

# 6

# Cell Membranes

## Membranes and memory

James noticed the changes in his grandfather when he was home from college for the winter holiday. He and grandpa John had always joked about grandpa John's missing keys and glasses; the old man, who had lived with James' family since his wife died, was forever searching for them. Now the memory lapses had become more pronounced. When James introduced his new girlfriend to the family, he was relieved (as was she) when she was welcomed with open arms. But an hour later, grandpa John just stared at her, unable to remember who she was. By the time James came home for the summer, his grandfather had become withdrawn; he could no longer talk about current events, and often he became confused and lashed out in anger.

James' grandfather had Alzheimer's disease. This condition is most common in (but not limited to) the elderly, and as more people today are living to advanced ages, more and more Alzheimer's cases are diagnosed. But the symptoms are not new to human experience or to medicine. The condition was first recognized as a disease in 1901. That year, the family of 51-year-old Frau Auguste D. brought her to Dr. Alois Alzheimer at the Frankfurt hospital in Germany. She had severe memory lapses, accused her husband of infidelity, and had difficulty communicating. These symptoms got worse before she died several years later. When Alzheimer autopsied her brain, he saw that the parts of the brain that are important in thought and speech were shrunken. Moreover, when he examined these areas

through the microscope he saw abnormal protein deposits in and around the brain cells.

In the century since Alzheimer's original case, cell biologists have investigated the nature of these abnormal deposits, now known as *plaques*. It turns out that the key events that produce plaques take place in the plasma membrane of nerve cells in the brain. Plaques are clumps of the protein amyloid beta, which at high levels is toxic to brain cells. Amyloid beta is a small piece of a larger amyloid precursor protein (APP), which is embedded in the nerve cell plasma membrane; APP is cut twice by two other membrane proteins,  $\beta$ -secretase and  $\gamma$ -secretase, to produce amyloid beta, which is released from the membrane to fall outside of the cell. All these proteins are present in a variety of animal cells and have multiple important



**Dr. Alzheimer's Patient** Frau Auguste D., who died in 1906, was the first patient described with progressive dementia by Dr. Alois Alzheimer.



**Plaques in the Brain** At autopsy, the brain of an Alzheimer's disease patient accumulates plaques (dark fibers in this micrograph) composed of protein fragments produced by an enzyme in the nerve cell membrane.

roles in the dynamic cell membrane; they may even be essential for normal nervous system development and function.

So what goes wrong in Alzheimer's disease? Cells in the diseased brain might be producing too much amyloid beta (e.g., because  $\gamma$ -secretase is too active) or producing it at the wrong time (e.g., in old age instead of infancy). One form of the disease is caused by a mutant form of  $\gamma$ -secretase, which has a tendency to cut APP in the "wrong" place, thereby producing a particularly toxic form of amyloid beta. Because of their role in producing plaques, APP and  $\gamma$ -secretase are potential targets for Alzheimer's disease therapies.

Learning how membranes are made and how they work has been a key to understanding, and perhaps treating, this increasingly prevalent disease.

**IN THIS CHAPTER** we focus on the structure and functions of biological membranes. First we describe the composition and structure of biological membranes. We go on to discuss their functions—how membranes are involved in intercellular interactions, and how membranes regulate which substances enter and leave the cell.

## CHAPTER OUTLINE

- 6.1** What Is the Structure of a Biological Membrane?
- 6.2** How Is the Plasma Membrane Involved in Cell Adhesion and Recognition?
- 6.3** What Are the Passive Processes of Membrane Transport?
- 6.4** What are the Active Processes of Membrane Transport?
- 6.5** How Do Large Molecules Enter and Leave a Cell?
- 6.6** What Are Some Other Functions of Membranes?

### 6.1 What Is the Structure of a Biological Membrane?

The physical organization and functioning of all biological membranes depend on their constituents: lipids, proteins, and carbohydrates. You are already familiar with these molecules from Chapter 3; it may be useful to review that chapter now. The lipids establish the physical integrity of the membrane and create an effective barrier to the rapid passage of hydrophilic materials such as water and ions. In addition, the phospholipid bilayer serves as a lipid "lake" in which a variety of proteins "float" (Figure 6.1). This general design is known as the **fluid mosaic model**.

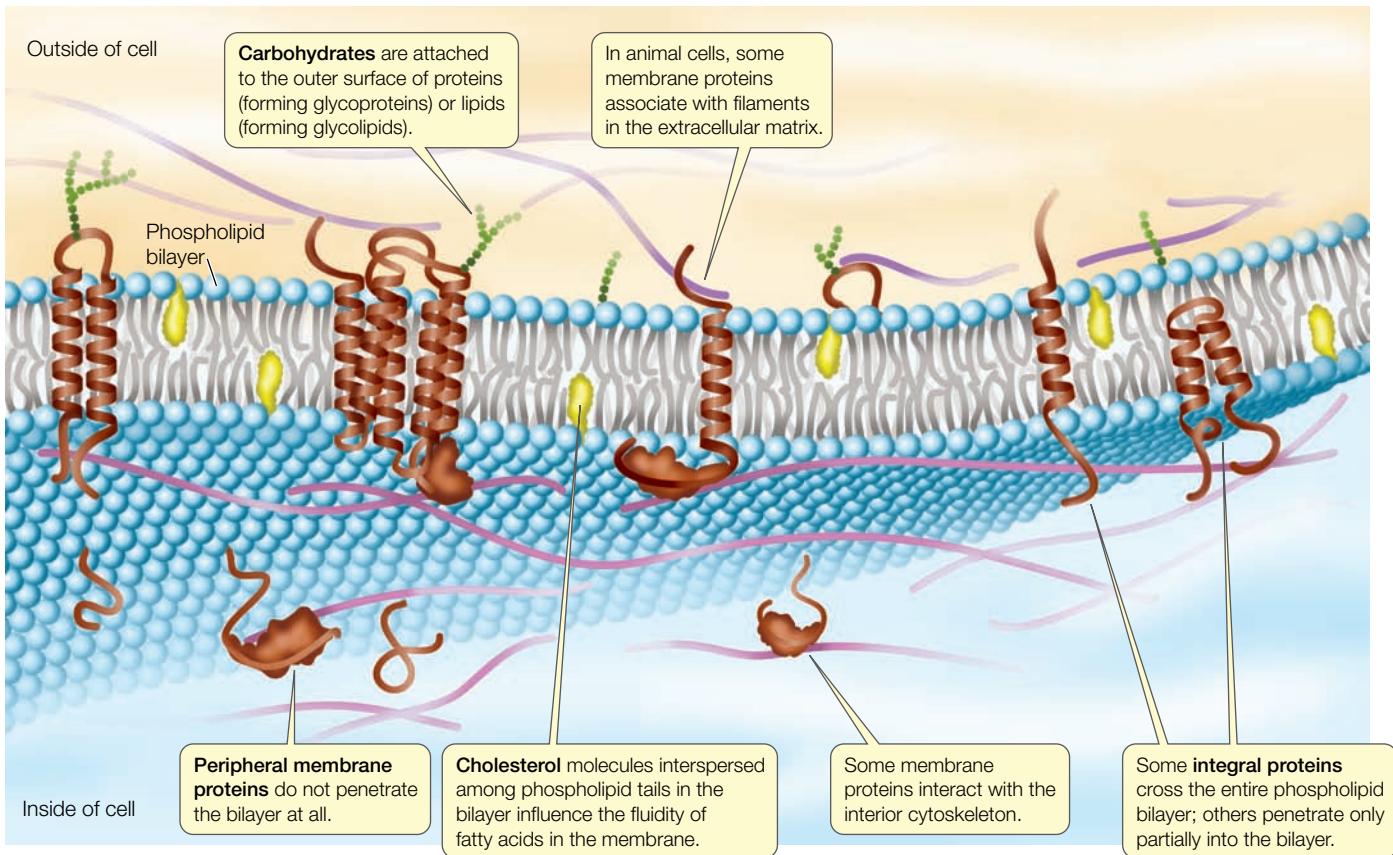
In the fluid mosaic model for biological membranes, the proteins are noncovalently embedded in the phospholipid bilayer by their hydrophobic regions (or *domains*), but their hydrophilic domains are exposed to the watery conditions on either side of the bilayer. These membrane proteins have a number of functions, including moving materials through the membrane and receiving chemical signals from the cell's external environment. Each membrane has a set of proteins suitable for the specialized functions of the cell or organelle it surrounds.

The carbohydrates associated with membranes are attached either to the lipids or to protein molecules. In plasma membranes, carbohydrates are located on the outside of the cell, where they may interact with substances in the external environment. Like some of the membrane proteins, carbohydrates are crucial in recognizing specific molecules, such as those on the surfaces of adjacent cells.

Although the fluid mosaic model is largely valid for membrane structure, it does not say much about membrane composition. As you read about the different molecules in membranes in the next sections, keep in mind that some membranes have more protein than lipids, others are lipid-rich, others have significant amounts of cholesterol or other sterols, and still others are rich in carbohydrates.

#### Lipids form the hydrophobic core of the membrane

The lipids in biological membranes are usually *phospholipids*. Recall from Section 2.2 that some compounds are hydrophilic ("water-loving") and others are hydrophobic ("water-hating"), and from Section 3.4 that a phospholipid molecule has regions of both kinds:



**6.1 The Fluid Mosaic Model** The general molecular structure of biological membranes is a continuous phospholipid bilayer which has proteins embedded in or associated with it.

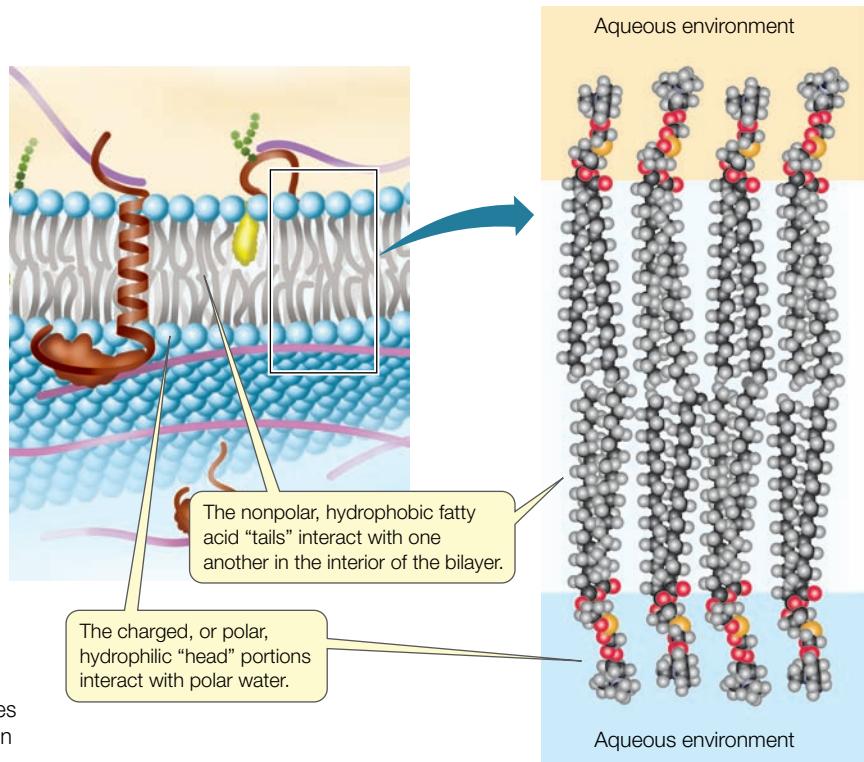
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**GO TO** Web Activity 6.1 • The Fluid-Mosaic Model

- **Hydrophilic regions:** The phosphorus-containing “head” of the phospholipid is electrically charged and therefore associates with polar water molecules.
- **Hydrophobic regions:** The long, nonpolar fatty acid “tails” of the phospholipid associate with other nonpolar materials, but they do not dissolve in water or associate with hydrophilic substances.

Because of these properties, one way in which phospholipids can coexist with water is to form a **bilayer**, with the fatty acid “tails” of the two layers interacting with each other and the polar “heads” facing the outside aqueous environment (**Figure 6.2**). The thickness of a biological membrane is about 8 nm (0.008  $\mu\text{m}$ ), which is twice the length of a typical phospholipid—another indication that the membrane consists of a lipid bilayer. This thickness is about 8,000 times thinner than a piece of paper.

**6.2 A Phospholipid Bilayer** The phospholipid bilayer separates two aqueous regions. The eight phospholipid molecules shown on the right represent a small cross section of a membrane bilayer.



In the laboratory, it is easy to make artificial bilayers with the same organization as natural membranes. Small holes in such bilayers seal themselves spontaneously. This capacity of lipids to associate with one another and maintain a bilayer organization helps biological membranes to fuse during vesicle formation, phagocytosis, and related processes.

All biological membranes have a similar structure, but differ in the kinds of proteins and lipids they contain. Membranes from different cells or organelles may differ greatly in their *lipid composition*. Not only are phospholipids highly variable, but a significant proportion of the lipid content in an animal cell membrane may be cholesterol.

Phospholipids can differ in terms of fatty acid chain length (number of carbon atoms), degree of unsaturation (double bonds) in the fatty acids, and the polar (phosphate-containing) groups present. The most common fatty acids with their chain length and degree of unsaturation are:

- Palmitic: C<sub>14</sub>, no double bonds, saturated
- Palmitoleic: C<sub>16</sub>, one double bond
- Stearic: C<sub>18</sub>, no double bonds, saturated
- Oleic: C<sub>18</sub>, one double bond
- Linoleic: C<sub>18</sub>, two double bonds
- Linolenic: C<sub>18</sub>, three double bonds

The saturated fatty acid chains allow close packing of fatty acids in the bilayer, while the “kinks” in unsaturated fatty acids (see Figure 3.19) make for a less dense, more fluid packing. These less-dense membranes in animal cells can accommodate cholesterol molecules.

Up to 25 percent of the lipid content of an animal cell plasma membrane may be cholesterol. When present, cholesterol is important for membrane integrity; the cholesterol in your membranes is not hazardous to your health. A molecule of cholesterol is usually situated next to an unsaturated fatty acid.

The phospholipid bilayer stabilizes the entire membrane structure, but leaves it flexible. The fatty acids of the phospholipids make the hydrophobic interior of the membrane somewhat fluid—about as fluid as lightweight machine oil. This fluidity permits some molecules to move laterally within the plane of the membrane. A given phospholipid molecule in the plasma membrane can travel from one end of the cell to the other in a little more than a second! On the other hand, seldom does a phospholipid molecule in one half of the bilayer spontaneously flip over to the other side. For that to happen, the polar part of the molecule would have to move through the hydrophobic interior of the membrane. Since spontaneous phospholipid flip-flops are rare, the inner and outer halves of the bilayer may be quite different in the kinds of phospholipids they contain.

The fluidity of a membrane is affected by its lipid composition and by its temperature. Long-chain, saturated fatty acids pack tightly beside one another, with little room for movement. Cholesterol interacts hydrophobically with the fatty acid chains. A membrane with these components is less fluid than one with shorter-chain fatty acids, unsaturated fatty acids, or less cholesterol. Adequate membrane fluidity is essential for many of the

functions we will describe in this chapter. Because molecules move more slowly and fluidity decreases at reduced temperatures, membrane functions may decline under cold conditions in organisms that cannot keep their bodies warm. To address this problem, some organisms simply change the lipid composition of their membranes when they get cold, replacing saturated with unsaturated fatty acids and using fatty acids with shorter tails. These changes play a role in the survival of plants, bacteria, and hibernating animals during the winter.

### Membrane proteins are asymmetrically distributed

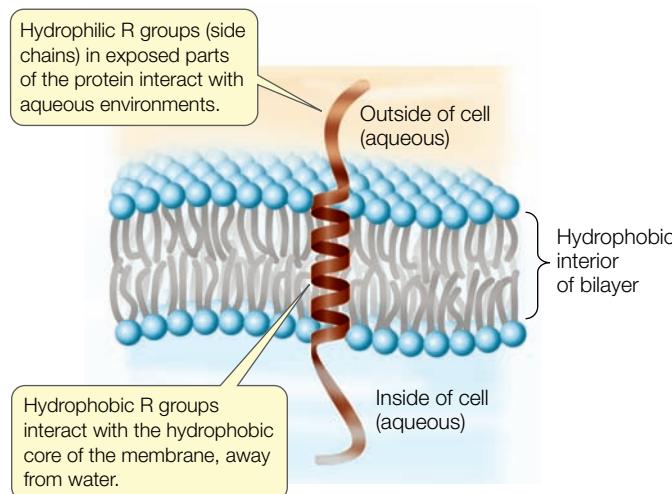
All biological membranes contain proteins. Typically, plasma membranes have one protein molecule for every 25 phospholipid molecules. This ratio varies depending on membrane function. In the inner membrane of the mitochondrion, which is specialized for energy processing, there is one protein for every 15 lipids. On the other hand, myelin—a membrane that encloses portions of some neurons (nerve cells) and acts as an electrical insulator—has only one protein for every 70 lipids.

There are two general types of membrane proteins: peripheral proteins and integral proteins.

**Peripheral membrane proteins** lack exposed hydrophobic groups and are not embedded in the bilayer. Instead, they have polar or charged regions that interact with exposed parts of integral membrane proteins, or with the polar heads of phospholipid molecules (see Figure 6.1).

**Integral membrane proteins** are at least partly embedded in the phospholipid bilayer (see Figure 6.1). Like phospholipids, these proteins have both hydrophilic and hydrophobic regions (Figure 6.3).

- *Hydrophilic domains*: Stretches of amino acids with hydrophilic side chains (see Table 3.1) give certain regions of the



**6.3 Interactions of Integral Membrane Proteins** An integral membrane protein is held in the membrane by the distribution of the hydrophilic and hydrophobic side chains on its amino acids. The hydrophilic parts of the protein extend into the aqueous cell exterior and the internal cytoplasm. The hydrophobic side chains interact with the hydrophobic lipid core of the membrane.

protein a polar character. These hydrophilic domains interact with water and stick out into the aqueous environment inside or outside the cell.

- **Hydrophobic domains:** Stretches of amino acids with hydrophobic side chains give other regions of the protein a nonpolar character. These domains interact with the fatty acids in the interior of the phospholipid bilayer, away from water.

A special preparation method for electron microscopy, called **freeze-fracturing**, reveals proteins that are embedded in the phospholipid bilayers of cellular membranes (**Figure 6.4**). When the two lipid *leaflets* (or layers) that make up the bilayer are separated, the proteins can be seen as bumps that protrude from the interior of each membrane. The bumps are not observed when artificial bilayers of pure lipid are freeze-fractured.

According to the fluid mosaic model, the proteins and lipids in a membrane are somewhat independent of each other and interact only noncovalently. The polar ends of proteins can interact with the polar ends of lipids, and the nonpolar regions of both molecules can interact hydrophobically.

However, some membrane proteins have fatty acids or other lipid groups covalently attached to them. Proteins in this subgroup of integral membrane proteins are referred to as *anchored membrane proteins*, because their hydrophobic lipid components allow them to insert themselves into the phospholipid bilayer.

Proteins are asymmetrically distributed on the inner and outer surfaces of membranes. An integral protein that extends all the way through the phospholipid bilayer and protrudes on both sides is known as a **transmembrane protein**. In addition to one or more *transmembrane domains* that extend through the bilayer, such a protein may have domains with other specific functions on the inner and outer sides of the membrane. Peripheral membrane proteins are localized on one side of the membrane or the other. This asymmetrical arrangement of membrane proteins gives the two surfaces of the membrane different properties. As we will soon see, these differences have great functional significance.

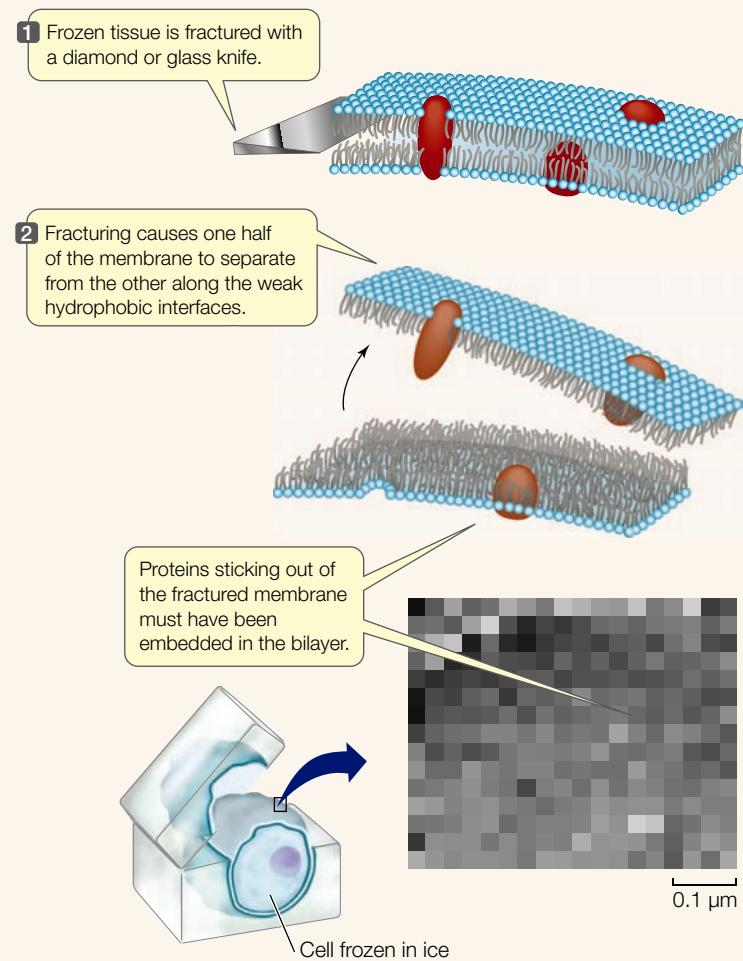
Like lipids, some membrane proteins move around relatively freely within the phospholipid bilayer. Experiments that involve the technique of cell fusion illustrate this migration dramatically. When two cells are fused, a single continuous membrane forms and surrounds both cells, and some proteins from each cell distribute themselves uniformly around this membrane (**Figure 6.5**).

Although some proteins are free to migrate in the membrane, others are not, but rather appear to be “anchored” to a specific region of the membrane. These membrane regions are like a corral of horses on a farm: the horses are free to move around within the fenced area, but not outside it. An example is the protein in the plasma membrane of a muscle cell that recognizes a chemical signal from a neuron. This protein is normally found only at the specific region where the neuron meets the muscle cell.

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### 6.4 Membrane Proteins Revealed by the Freeze-Fracture Technique

This HeLa cell (a human cell) membrane was first frozen to immobilize the lipids and proteins, and then fractured so that the bilayer was split open.



Proteins inside the cell can restrict the movement of proteins within a membrane. The cytoskeleton may have components just below the inner face of the membrane that are attached to membrane proteins protruding into the cytoplasm. The stability of the cytoskeletal components may thus restrict movement of attached membrane proteins.

### Membranes are constantly changing

Membranes in eukaryotic cells are constantly forming, transforming from one type to another, fusing with one another, and breaking down. As we discuss in Chapter 5, fragments of membrane move, in the form of vesicles, from the endoplasmic reticulum (ER) to the Golgi, and from the Golgi to the plasma membrane (see Figure 5.10). Secondary lysosomes form when primary lysosomes from the Golgi fuse with phagosomes from the plasma membrane (see Figure 5.11).

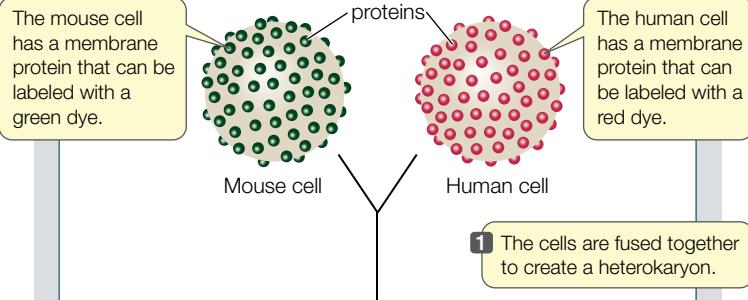
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## 6.5 Rapid Diffusion of Membrane Proteins

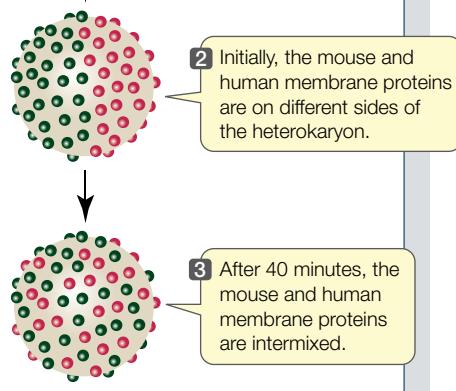
Two animal cells can be fused together in the laboratory, forming a single large cell (heterokaryon). This phenomenon was used to test whether membrane proteins can diffuse independently in the plane of the plasma membrane.

**HYPOTHESIS** Proteins embedded in a membrane can diffuse freely within the membrane.

### METHOD



### RESULTS



**CONCLUSION** Membrane proteins can diffuse rapidly in the plane of the membrane.

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Because all membranes appear similar under the electron microscope, and because they interconvert readily, we might expect all subcellular membranes to be chemically identical. However, that is not the case, for there are major chemical differences among the membranes of even a single cell. Membranes are changed chemically when they form parts of certain organelles. In the Golgi apparatus, for example, the membranes of the *cis* face closely resemble those of the endoplasmic reticulum in chemical composition, but those of the *trans* face are more similar to the plasma membrane.

### Plasma membrane carbohydrates are recognition sites

In addition to lipids and proteins, the plasma membrane contains carbohydrates. The carbohydrates are located on the outer

surface of the plasma membrane and serve as recognition sites for other cells and molecules, as you will see in Section 6.2.

Membrane-associated carbohydrates may be covalently bonded to lipids or to proteins:

- A **glycolipid** consists of a carbohydrate covalently bonded to a lipid. Extending outside the cell surface, the carbohydrate may serve as a recognition signal for interactions between cells. For example, the carbohydrates on some glycolipids change when cells become cancerous. This change may allow white blood cells to target cancer cells for destruction.
- A **glycoprotein** consists of a carbohydrate covalently bonded to a protein. The bound carbohydrate is an oligosaccharide, usually not exceeding 15 monosaccharide units in length (see Section 3.3). The oligosaccharides of glycoproteins often function as signaling sites, as do the carbohydrates attached to glycolipids.

The “alphabet” of monosaccharides on the outer surfaces of membranes can generate a large diversity of messages. Recall from Section 3.3 that sugar molecules consist of three to seven carbons that are attached at different sites to one another. They may form linear or branched oligosaccharides with many different three-dimensional shapes. An oligosaccharide of a specific shape on one cell can bind to a complementary shape on an adjacent cell. This binding is the basis of cell–cell adhesion.

## 6.1 RECAP

The fluid mosaic model applies to both the plasma membrane and the membranes of organelles. An integral membrane protein has both hydrophilic and hydrophobic domains, which affect its position and function in the membrane. Carbohydrates that attach to lipids and proteins on the outside of the membrane serve as recognition sites.

- What are some of the features of the fluid mosaic model of biological membranes?  
*See p. 106*
- Explain how the hydrophobic and hydrophilic regions of phospholipids cause a membrane bilayer to form. *See Figures 6.1 and 6.2*
- What differentiates an integral protein from a peripheral protein? *See p. 108 and Figure 6.1*
- What is the experimental evidence that membrane proteins can diffuse in the plane of the membrane?  
*See pp. 109–110 and Figure 6.5*

Now that you understand the structure of biological membranes, let’s see how their components function. In the next section we’ll focus on the membrane that surrounds individual cells: the plasma membrane. We’ll look at how the plasma membrane allows individual cells to be grouped together into multicellular systems of tissues.

## 6.2 How Is the Plasma Membrane Involved in Cell Adhesion and Recognition?

Some organisms, such as bacteria, are unicellular; that is, the entire organism is a single cell. Others, such as plants and animals, are multicellular—composed of many cells. Often these cells exist in specialized groups with similar functions, called tissues. Your body has about 60 trillion cells, arranged in different kinds of tissues (such as muscle, nerve, and epithelium).

Two processes allow cells to arrange themselves in groups:

- **Cell recognition**, in which one cell specifically binds to another cell of a certain type
- **Cell adhesion**, in which the connection between the two cells is strengthened

Both processes involve the plasma membrane. They are most easily studied if a tissue is separated into its individual cells, which are then allowed to adhere to one another again. Simple organisms provide a good model for studying processes that also occur in the complex tissues of larger species. Studies of sponges, for example, have revealed how cells associate with one another.

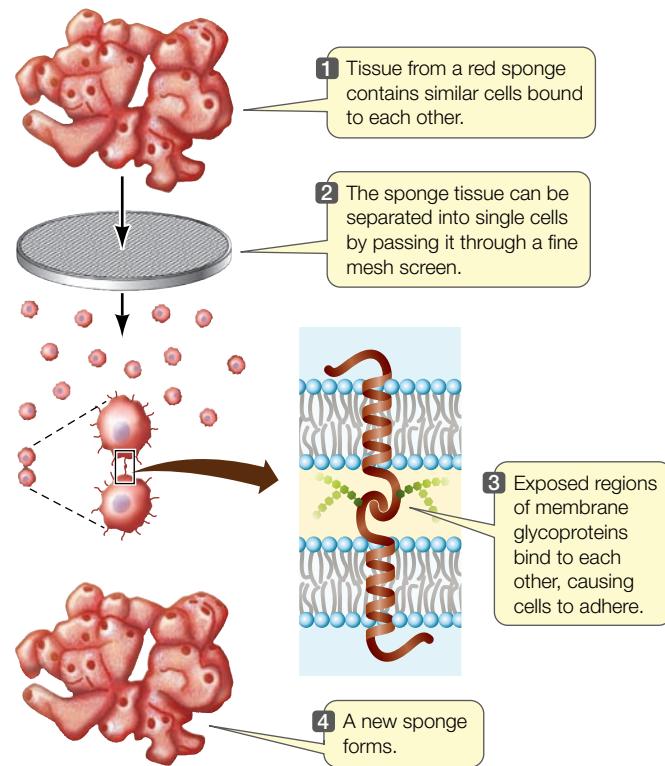
A sponge is a multicellular marine animal with a simple body plan that consists of only a few distinct tissues (see Section 31.5). The cells of a sponge adhere to one another, but can be separated mechanically by passing the animal several times through a fine wire screen (**Figure 6.6**). Through this process, what was a single animal becomes hundreds of individual cells suspended in seawater. Remarkably, if the cell suspension is shaken for a few hours, the cells bump into one another and stick together in the same shape and organization as the original sponge! The cells recognize and adhere to one another, and re-form the original tissues.

There are many different species of sponges. If disaggregated sponge cells from two different species are placed in the same container and shaken, individual cells will stick only to other cells of the same species. Two different sponges form, just like the ones at the start of the experiment. This demonstrates not just adhesion, but species-specific cell recognition.

Such tissue-specific and species-specific cell recognition and cell adhesion are essential to the formation and maintenance of tissues and multicellular organisms. Think of your own body. What keeps muscle cells bound to muscle cells and skin to skin? Specific cell adhesion is so obvious a characteristic of complex organisms that it is easy to overlook. You will see many examples of specific cell adhesion throughout this book; here, we describe its general principles. As you will see, cell recognition and cell adhesion depend on plasma membrane proteins.

### Cell recognition and cell adhesion involve proteins at the cell surface

The molecule responsible for cell recognition and adhesion in sponges is a huge integral membrane glycoprotein (which is 80 percent carbohydrate by molecular weight) that is partly embedded in the plasma membrane, with the carbohydrate part sticking out and exposed to the environment (and to other



**6.6 Cell Recognition and Adhesion** In most cases (including the aggregation of animal cells into tissues), protein binding is homotypic.

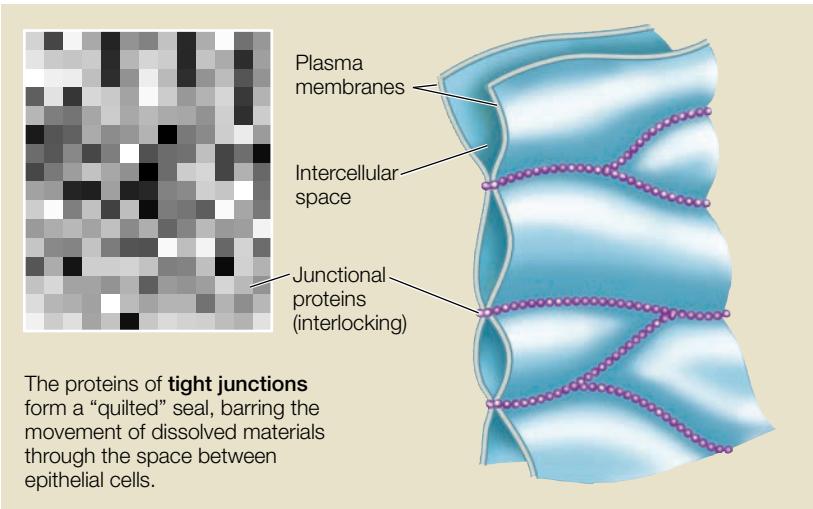
sponge cells). As we describe in Section 3.2, a protein not only has a specific shape, but also has specific chemical groups exposed on its surface where they can interact with other substances, including other proteins. Both of these features allow binding to other specific molecules. The cells of the disaggregated sponge in Figure 6.6 find one another again through the recognition of exposed chemical groups on their membrane glycoproteins. Adhesion proteins are not restricted to animal cells. In most plant cells, the plasma membrane is covered with a thick cell wall, but this structure also has adhesion proteins that allow cells to bind to one another.

In most cases, the binding of cells in a tissue is **homotypic**; that is, the same molecule sticks out of both cells, and the exposed surfaces bind to each other. But **heterotypic** binding (of cells with different proteins) can also occur. In this case, different chemical groups on different surface molecules have an affinity for one another. For example, when the mammalian sperm meets the egg, different proteins on the two types of cells have complementary binding surfaces. Similarly, some algae form male and female reproductive cells (analogous to sperm and eggs) that have flagella to propel them toward each other. Male and female cells can recognize each other by heterotypic proteins on their flagella.

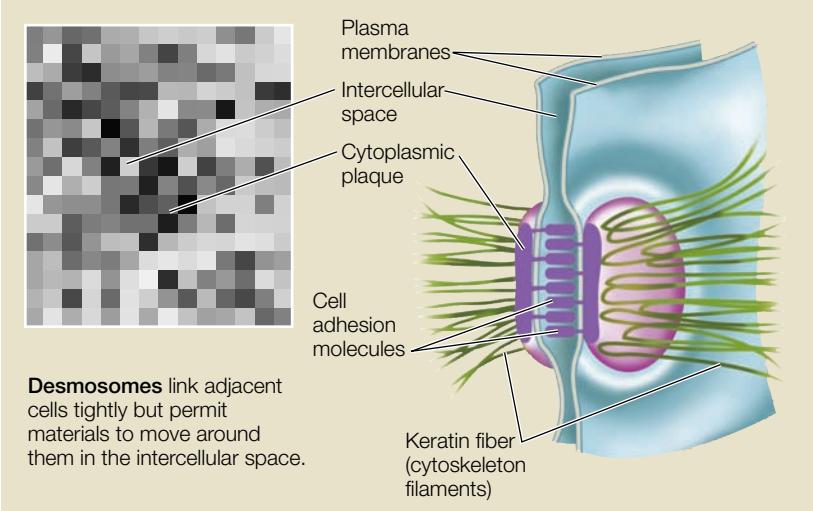
### Three types of cell junctions connect adjacent cells

In a complex multicellular organism, cell recognition proteins allow specific types of cells to bind to one another. Often, after

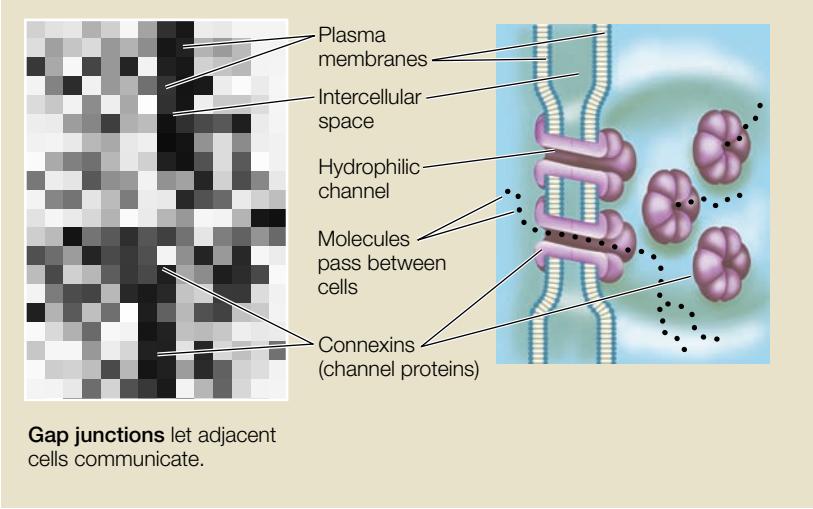
(A)



(B)



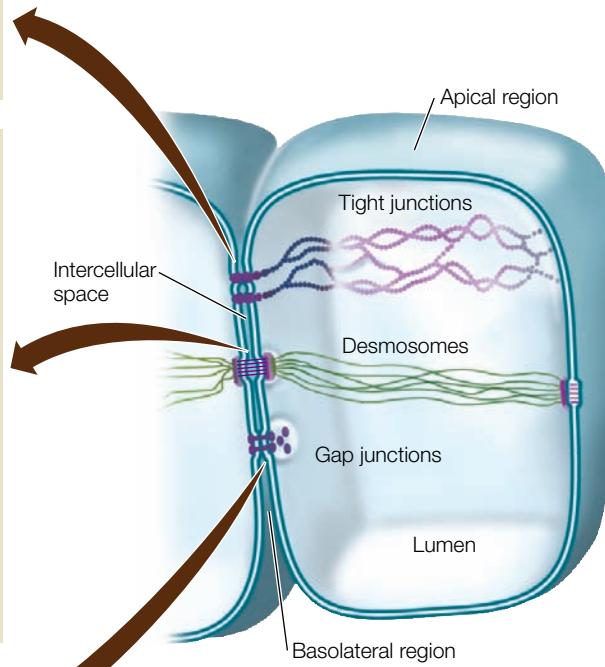
(C)



**6.7 Junctions Link Animal Cells Together** Tight junctions (A) and desmosomes (B) are abundant in epithelial tissues. Gap junctions (C) are also found in some muscle and nerve tissues, in which rapid communication between cells is important. Although all three junction types are shown in the cell at the right, all three are not necessarily seen at the same time in actual cells.

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**GO TO** Web Activity 6.2 • Animal Cell Junctions



pressure, or both, so it is particularly important that their cells adhere tightly. We will examine three types of cell junctions that enable animal cells to seal intercellular spaces, reinforce attachments to one another, and communicate with each other. Tight junctions, desmosomes, and gap junctions, respectively, perform these three functions.

**TIGHT JUNCTIONS SEAL TISSUES** **Tight junctions** are specialized structures that link adjacent epithelial cells, and they result from the mutual binding of specific proteins in the plasma membranes of the cells. These proteins are arrayed in bands so that they form a series of joints encircling each cell (**Figure 6.7A**). Tight junctions are found in the lining of lumens (cavities) in organs such as the stomach and intestine. They have two major functions:

- They prevent substances from moving from the lumen through the spaces between cells. For example, the presence of tight junctions means that substances must pass through, rather than between, the epithelial cells that form

the initial binding, both cells contribute material to form additional membrane structures that connect them to one another. These specialized structures, called **cell junctions**, are most evident in electron micrographs of *epithelial* tissues, which are layers of cells that line body cavities or cover body surfaces. These surfaces often receive stresses, or must retain contents under

the lining of the digestive tract. In another example, the cells lining the bladder have tight junctions so urine cannot leak out into the body cavity. Thus, tight junctions help to establish cellular control over what enters and leaves the body.

- They define specific functional regions of membranes by restricting the migration of membrane proteins and phospholipids from one region of the cell to another. Thus the membrane proteins and phospholipids in the apical (“tip”) region of an intestinal epithelial cell (facing the lumen) are different from those in the basolateral (*basal*, “bottom”; *lateral*, “side”) regions of the cell (facing the body cavity or blood capillary outside the lumen).

By forcing materials to enter certain cells, and by allowing different areas of the same cell to have different membrane proteins with different functions, tight junctions in the digestive tract help ensure the directional movement of materials into the body.

**DESMOSOMES HOLD CELLS TOGETHER** Desmosomes connect adjacent plasma membranes. Desmosomes hold neighboring cells firmly together, acting like spot welds or rivets (Figure 6.7B). Each desmosome has a dense structure called a plaque on the cytoplasmic side of the plasma membrane. To this plaque are attached special cell adhesion molecules that stretch from the plaque through the plasma membrane of one cell, across the intercellular space, and through the plasma membrane of the adjacent cell, where they bind to the plaque proteins in that adjacent cell.

The plaque is also attached to fibers in the cytoplasm. These fibers, which are intermediate filaments of the cytoskeleton (see Figure 5.18), are made of a protein called keratin. They stretch from one cytoplasmic plaque across the cell to another plaque on the other side of the cell. Anchored thus on both sides of the cell, these extremely strong fibers provide great mechanical stability to epithelial tissues. This stability is needed for these tissues, which often receive rough wear while protecting the integrity of the organism’s body surface, or the surface of an organ.

**GAP JUNCTIONS ARE A MEANS OF COMMUNICATION** Whereas tight junctions and desmosomes have mechanical roles, gap junctions facilitate communication between cells. Each gap junction is made up of specialized channel proteins, called *connexins*, which interact to form a structure (called a *connexon*) that spans the plasma membranes of adjacent cells and the intercellular space between them (Figure 6.7C). Water, dissolved small molecules, and ions can pass from cell to cell through these junctions. This allows groups of cells to coordinate their activities. In Chapter 7 we discuss cell communication and signaling, and in that chapter we describe in more detail the roles of gap junctions and plasmodesmata, which perform a similar role in plants.

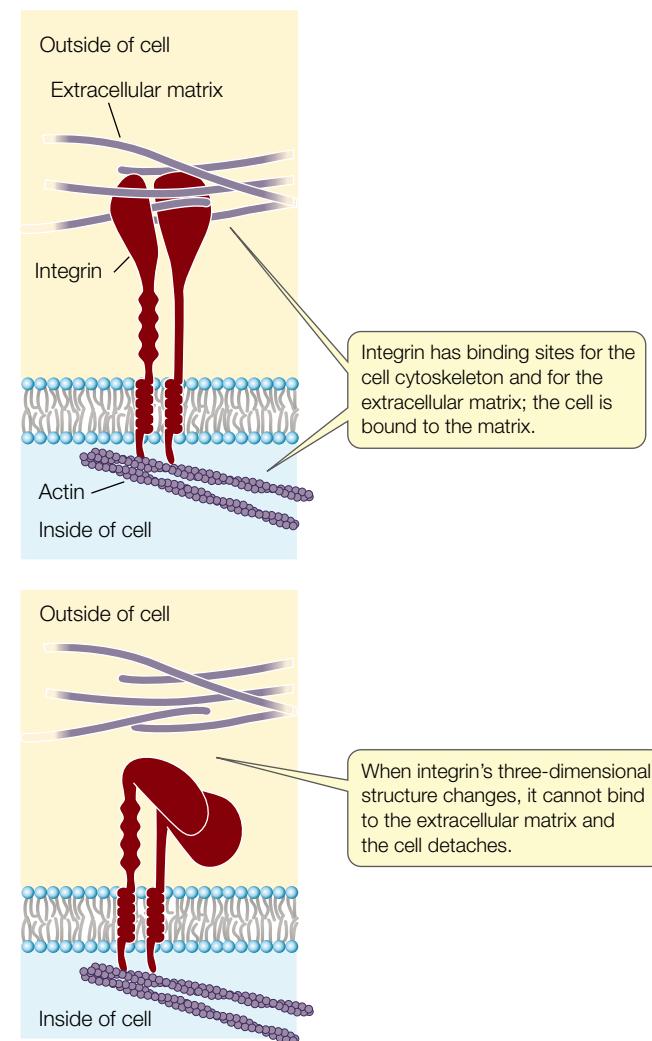
### Cell membranes adhere to the extracellular matrix

In Section 5.4 we describe the extracellular matrix of animal cells, which is composed of collagen protein arranged in fibers

in a gelatinous matrix of proteoglycans. The attachment of a cell to the extracellular matrix is important in maintaining the integrity of a tissue. In addition, some cells can detach from their neighbors, move, and attach to other cells; this is often mediated by interactions with the extracellular matrix.

A transmembrane protein called **integrin** often mediates the attachment of epithelial cells to the extracellular matrix (Figure 6.8). More than 24 different integrins have been described in human cells. All of them bind to a protein in the extracellular matrix on the outside of the cell, and to actin filaments, which are part of the cytoskeleton, on the inside of the cell. So, in addition to adhesion, integrin has a role in maintaining cell structure via its interaction with the cytoskeleton.

The binding of integrin to the extracellular matrix is noncovalent and reversible. When a cell moves its location within a tissue or organism, the first step is detachment of the cell’s integrin from the matrix. The integrin protein changes its three-dimensional structure and no longer maintains its link to the matrix. These events are important for cell movement within the developing embryo, and for the spread of cancer cells.



**6.8 Integrins Mediate the Attachment of Animal Cells to the Extracellular Matrix**

## 6.2 RECAP

In multicellular organisms, cells arrange themselves in groups by two processes: cell recognition and cell adhesion. Both processes are mediated by integral proteins in the plasma membrane. Cell membrane proteins also interact with the extracellular matrix.

- Describe the difference between cell recognition and cell adhesion. **See p. 111**
- How do the three types of cell junctions regulate the passage of materials between cells and through the intercellular space? **See pp. 111–113 and Figure 6.7**

We have just examined how the plasma membrane structure accommodates the binding and maintenance of cell adhesion. We turn now to another major function of membranes: regulating the substances that enter or leave a cell or organelle.

## 6.3 What Are the Passive Processes of Membrane Transport?

As you have already learned, biological membranes have many functions, and control of the cell's internal composition is one of the most significant. Biological membranes allow some substances, but not others, to pass through them. This characteristic of membranes is called **selective permeability**. Selective permeability allows the membrane to determine what substances enter or leave a cell or organelle.

There are two fundamentally different processes by which substances cross biological membranes:

- The processes of **passive transport** do not require any input of outside energy to drive them (no metabolic energy).
- The processes of **active transport** require the input of chemical energy from an outside source (metabolic energy).

This section focuses on the passive processes by which substances cross membranes. The energy for the passive transport of a substance is found in the difference between its concentration on one side of the membrane and its concentration on the other. Passive transport processes include two types of diffusion: simple diffusion through the phospholipid bilayer, and facilitated diffusion through *channel proteins* or by means of *carrier proteins*.

### Diffusion is the process of random movement toward a state of equilibrium

Nothing in this world is ever absolutely at rest. Everything is in motion, although the motions may be very small. An important consequence of all this random vibration, rotation and translocation (moving from one location to another) of molecules is that all the components of a solution tend eventually to become evenly distributed. For example, if a drop of ink is allowed to

fall into a container of water, the pigment molecules of the ink are initially very concentrated. Without human intervention, such as stirring, the pigment molecules move about at random, spreading slowly through the water until eventually the concentration of pigment—and thus the intensity of color—is exactly the same in every drop of liquid in the container.

A solution in which the solute particles are uniformly distributed is said to be at *equilibrium* because there will be no future net change in their concentration. Equilibrium does not mean that the particles have stopped moving; it just means that they are moving in such a way that their overall distribution does not change.

**Diffusion** is the process of random movement toward a state of equilibrium. Although the motion of each individual particle is absolutely random, the net movement of particles is directional until equilibrium is reached. Diffusion is thus a net movement from regions of greater concentration to regions of lesser concentration (**Figure 6.9**).

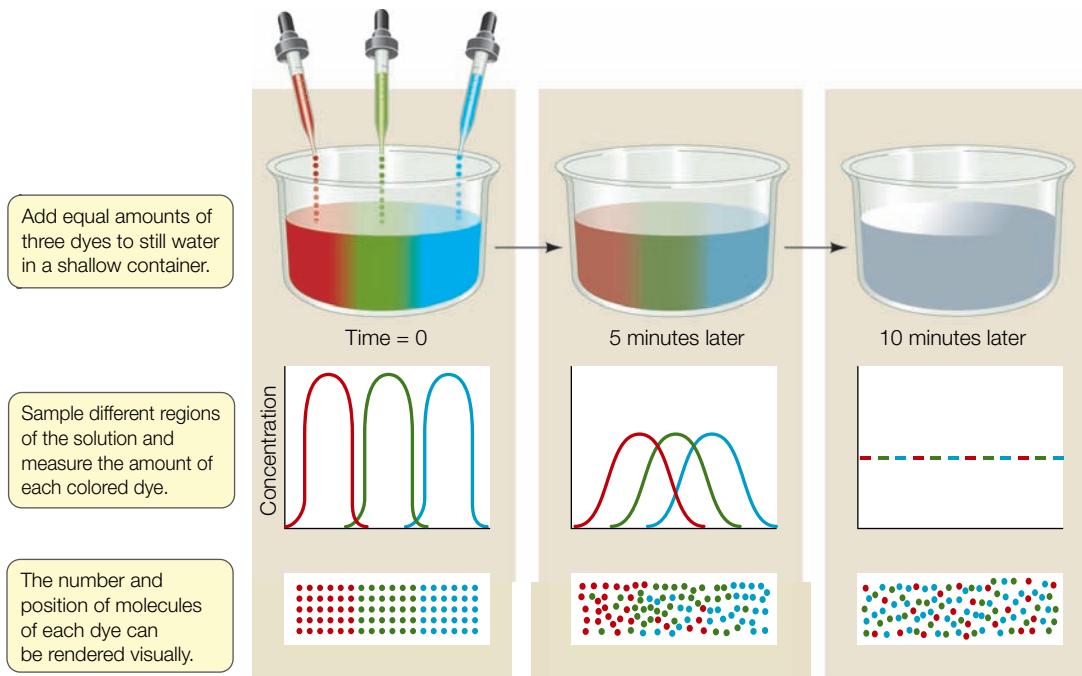
In a complex solution (one with many different solutes), the diffusion of each solute is independent of those of the others. How fast a substance diffuses depends on three factors:

- The *diameter* of the molecules or ions: smaller molecules diffuse faster.
- The *temperature* of the solution: higher temperatures lead to faster diffusion because ions or molecules have more energy, and thus move more rapidly, at higher temperatures.
- The *concentration gradient* in the system—that is, the change in solute concentration with distance in a given direction: the greater the concentration gradient, the more rapidly a substance diffuses.

We'll see how these factors influence membrane transport in the detailed discussions that follow.

**DIFFUSION WITHIN CELLS AND TISSUES** Within cells, or wherever distances are very short, solutes distribute themselves rapidly by diffusion. Small molecules and ions may move from one end of an organelle to another in a millisecond ( $10^{-3}$  s, or one-thousandth of a second). However, the usefulness of diffusion as a transport mechanism declines drastically as distances become greater. In the absence of mechanical stirring, diffusion across more than a centimeter may take an hour or more, and diffusion across meters may take years! Diffusion would not be adequate to distribute materials over the length of a human body, much less that of a larger organism. But within our cells or across layers of one or two cells, diffusion is rapid enough to distribute small molecules and ions almost instantaneously.

**DIFFUSION ACROSS MEMBRANES** In a solution without barriers, all the solutes diffuse at rates determined by temperature, their physical properties, and their concentration gradients. If a biological membrane divides the solution into separate compartments, then the movement of the different solutes can be affected by the properties of the membrane. The membrane is said to be *permeable* to solutes that can cross it more or less easily, but *impermeable* to substances that cannot move across it.



### 6.9 Diffusion Leads to Uniform Distribution of Solutes

A simple experiment demonstrates that solutes move from regions of greater concentration to regions of lesser concentration until equilibrium is reached.

Molecules to which the membrane is impermeable remain in separate compartments, and their concentrations may be different on the two sides of the membrane. Molecules to which the membrane is permeable diffuse from one compartment to the other until their concentrations are equal on both sides of the membrane. When the concentrations of a diffusing substance on the two sides of the permeable membrane are identical, equilibrium is reached. Individual molecules continue to pass through the membrane after equilibrium is established, but equal numbers of molecules move in each direction, so *at equilibrium there is no net change in concentration*.

#### Simple diffusion takes place through the phospholipid bilayer

In **simple diffusion**, small molecules pass through the phospholipid bilayer of the membrane. A molecule that is itself hydrophobic, and is therefore soluble in lipids, enters the membrane readily and is able to pass through it. The more lipid-soluble the molecule is, the more rapidly it diffuses through the membrane bilayer. This statement holds true over a wide range of molecular weights.

On the other hand, electrically charged or polar molecules, such as amino acids, sugars, and ions, do not pass readily through a membrane for two reasons. First, such charged or polar molecules are not very soluble in the hydrophobic interior of the bilayer. Second, such charged and polar substances form many hydrogen bonds with water and ions in the aqueous environment, be it the cytoplasm or the cell exterior. The multiplicity of these hydrogen bonds prevent the substances from moving into the hydrophobic interior of the membrane.

Consider two molecules: a small protein made up of a few polar amino acids, and a cholesterol-based steroid of equivalent size. If a membrane separates high and low concentrations of these substances, the protein, being polar, will diffuse only very

slowly through the membrane, while the nonpolar steroid will diffuse through it readily.

#### Osmosis is the diffusion of water across membranes

Water molecules pass through specialized channels in membranes (see below) by a diffusion process called **osmosis**. This completely passive process uses no metabolic energy and can be understood in terms of solute concentrations. Recall that a solute dissolves in a solvent and the solute's constituents are dispersed throughout the solution. Osmosis depends on the *number* of solute particles present, not on the *kinds* of particles. We will describe osmosis using red blood cells and plant cells as examples. In these examples, the plasma membranes are considered to be permeable to water and impermeable to most solutes.

Red blood cells are normally suspended in a fluid called plasma, which contains salts, proteins, and other solutes. Examining a drop of blood under the light microscope reveals that these red cells have a characteristic flattened disk shape with a depressed center, sometimes called "biconcave." If pure water is added to the drop of blood, drastically reducing the solute concentration of the plasma, the red cells quickly swell and burst. Similarly, if slightly wilted lettuce is placed in pure water, it soon becomes crisp; by weighing it before and after, we can show that it has taken up water. If, on the other hand, red blood cells or crisp lettuce leaves are placed in a relatively concentrated solution of salt or sugar, the leaves become limp (they wilt), and the red blood cells pucker and shrink.

From such observations we know that the difference in solute concentration between a cell and its surrounding environment determines whether water will move from the environment into the cell or out of the cell into the environment. Other things being equal, if two different solutions are separated by a membrane that allows water, *but not solutes*, to pass through, water molecules will move across the membrane toward the solu-

tion with a higher solute concentration. In other words, water will diffuse from a region of its higher concentration (with a lower concentration of solutes) to a region of its lower concentration (with a higher concentration of solutes).

Three terms are used to compare the solute concentrations of two solutions separated by a membrane:

- A **hypertonic** solution has a higher solute concentration than the other solution with which it is being compared (**Figure 6.10A**).
- **Isotonic** solutions have equal solute concentrations (**Figure 6.10B**).
- A **hypotonic** solution has a lower solute concentration than the other solution with which it is being compared (**Figure 6.10C**).

Water moves from a hypotonic solution across a membrane to a hypertonic solution.

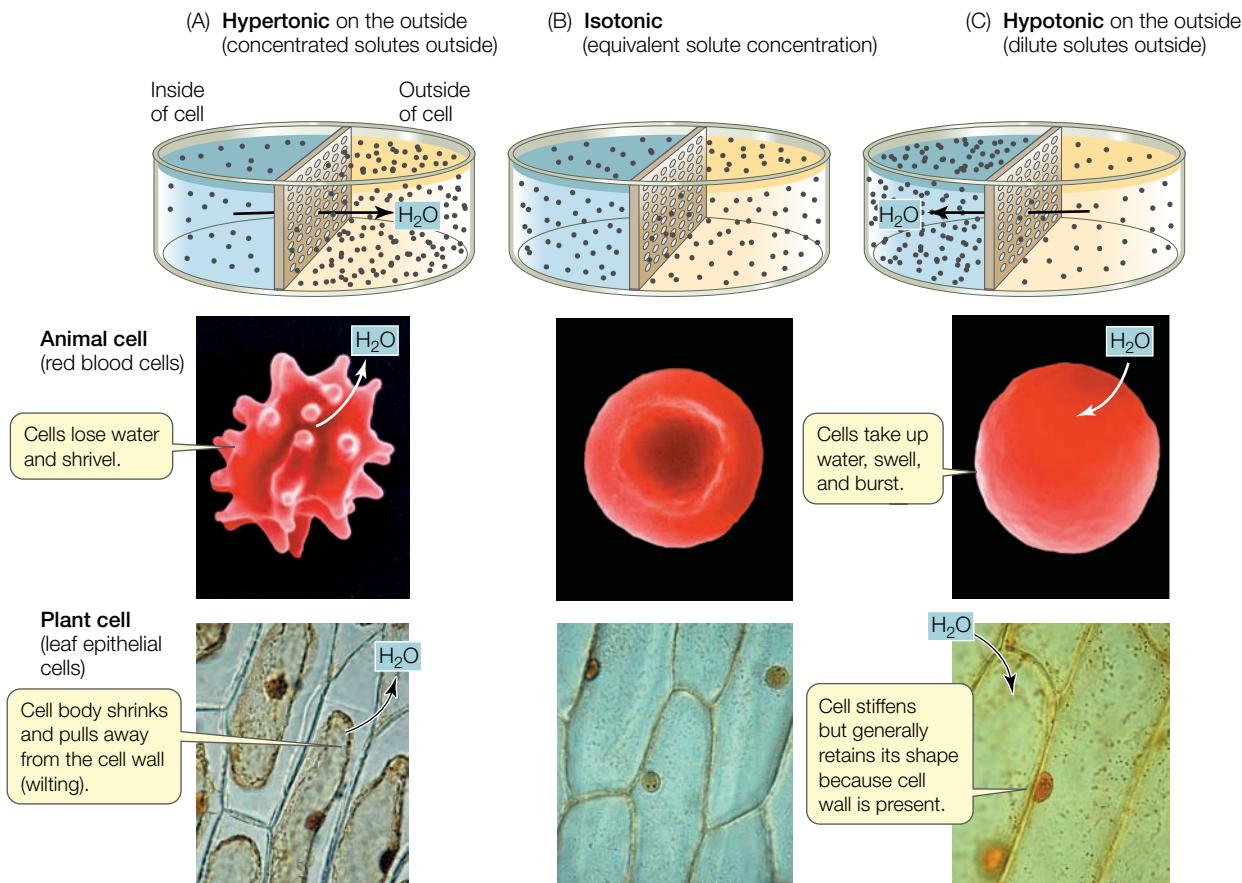
When we say that “water moves,” bear in mind that we are referring to the net movement of water. Since it is so abundant, water is constantly moving through protein channels across the plasma membrane into and out of cells. What concerns us here is whether the overall movement is greater in one direction or the other.

The concentration of solutes in the environment determines the direction of osmosis in all animal cells. A red blood cell takes up water from a solution that is hypotonic to the cell’s contents.

The cell bursts because its plasma membrane cannot withstand the pressure created by the water entry and the resultant swelling. The integrity of red blood cells (and other blood cells) is absolutely dependent on the maintenance of a constant solute concentration in the blood plasma: the plasma must be isotonic to the blood cells if the cells are not to burst or shrink. Regulation of the solute concentration of body fluids is thus an important process for organisms without cell walls.

In contrast to animal cells, the cells of plants, archaea, bacteria, fungi, and some protists have cell walls that limit their volumes and keep them from bursting. Cells with sturdy walls take up a limited amount of water, and in so doing they build up internal pressure against the cell wall, which prevents further water from entering. This pressure within the cell is called **turgor pressure**. Turgor pressure keeps plants upright (and lettuce crisp) and is the driving force for the enlargement of plant cells. It is a normal and essential component of plant growth. If enough water leaves the cells, turgor pressure drops and the plant wilts. Turgor pressure reaches about 100 pounds per square inch ( $0.7 \text{ kg/cm}^2$ )—several times greater than the pres-

**6.10 Osmosis Can Modify the Shapes of Cells** In a solution that is isotonic with the cytoplasm (center column), a plant or animal cell maintains a consistent, characteristic shape because there is no net movement of water into or out of the cell. In a solution that is hypotonic to the cytoplasm (right), water enters the cell. An environment that is hypertonic to the cytoplasm (left) draws water out of the cell.



sure in automobile tires. This pressure is so great that the cells would change shape and detach from one another, were it not for adhesive molecules in the plant cell wall.

### Diffusion may be aided by channel proteins

As we saw earlier, polar or charged substances such as water, amino acids, sugars and ions do not readily diffuse across membranes. But they can cross the hydrophobic phospholipid bilayer passively (that is, without the input of energy) in one of two ways, depending on the substance:

- **Channel proteins** are integral membrane proteins that form channels across the membrane through which certain substances can pass.
- Some substances can bind to membrane proteins called **carrier proteins** that speed up their diffusion through the phospholipid bilayer.

Both of these processes are forms of **facilitated diffusion**. That is, the substances diffuse according to their concentration gradients, but their diffusion is facilitated by protein channels or carriers.

**ION CHANNELS** The best-studied channel proteins are the **ion channels**. As you will see in later chapters, the movement of ions across membranes is important in many biological processes, ranging from respiration within the mitochondria, to the electrical activity of the nervous system and the opening of the pores in leaves that allow gas exchange with the environment. Several types of ion channels have been identified, each of them specific for a particular ion. All of them show the same basic structure of a hydrophilic pore that allows a particular ion to move through it (**Figure 6.11**).

Just as a fence may have a gate that can be opened or closed, most ion channels are gated: they can be opened or closed to ion passage. A **gated channel** opens when a stimulus causes a change in the three-dimensional shape of the channel. In some cases, this stimulus is the binding of a chemical signal, or **ligand** (see Figure 6.11). Channels controlled in this way are called *ligand-gated channels*. In contrast, a *voltage-gated channel* is stimulated to open or close by a change in the voltage (electrical charge difference) across the membrane.

**THE MEMBRANE POTENTIAL** All living cells maintain an imbalance of ion concentrations across the plasma membrane, and consequently a small voltage or **membrane potential** exists across that membrane. When a gated ion

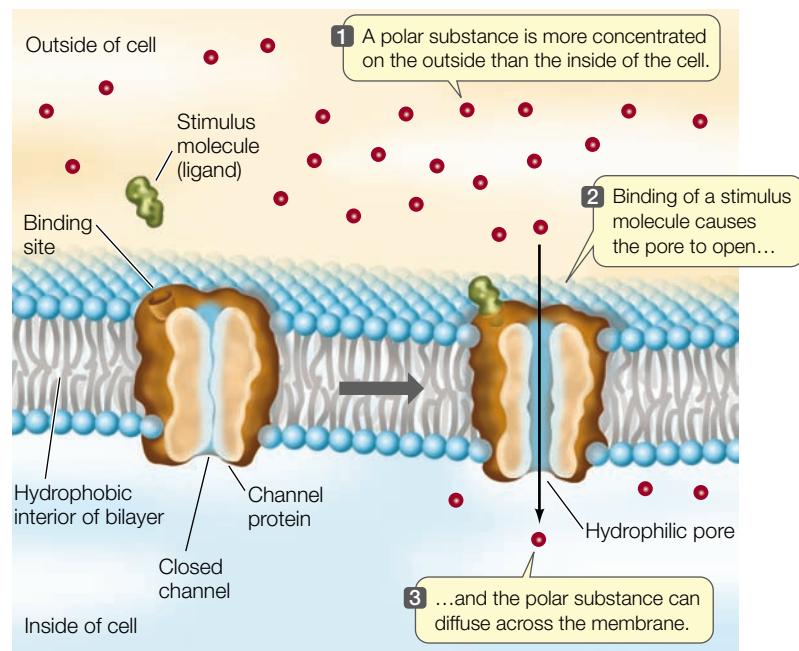
#### 6.11 A Gated Channel Protein Opens in Response to a Stimulus

The channel protein has a pore of polar amino acids and water. It is anchored in the hydrophobic bilayer interior by its outer coating of nonpolar R groups of its amino acids. The protein changes its three-dimensional shape when a stimulus molecule (ligand) binds to it, opening the pore so that hydrophilic polar substances can pass through. Other gated channels open in response to an electrical potential (voltage).

channel opens, millions of ions can rush through it per second. How fast the ions move, and in which direction (into or out of the cell), depends on two factors, the concentration gradient and the magnitude of the voltage. Let's consider how these factors affect the concentration of potassium ions ( $K^+$ ) inside an animal cell:

- **The concentration gradient:** Because of active transport (discussed below), the concentration of  $K^+$  is usually much higher inside the cell than outside, so  $K^+$  will tend to diffuse out of the cell through an open potassium channel.
- **The distribution of electrical charge:** As  $K^+$  diffuses out of the cell it leaves behind an excess of chloride ( $Cl^-$ ) and other negatively charged ions. These negatively charged substances cannot readily diffuse through the plasma membrane to follow  $K^+$  out of the cell, and this results in a charge difference (negative inside) across the membrane.  $K^+$  is attracted to the negative charge inside the cell, creating a tendency for  $K^+$  to stay inside the cell, even though it is more concentrated there than outside.

Now, consider what happens when the  $K^+$  channel is opened. Two forces are at work: diffusion draws  $K^+$  out of the cell through the channel, and electrical attraction keeps  $K^+$  inside the cell. The system exists in a state of equilibrium, in which the ion's rate of diffusion out through the channel is balanced by the rate of movement in through the channel due to electrical attraction. Obviously, the concentrations of  $K^+$  on each side of the membrane will not be equal, as we would expect if diffusion were the only force involved. Instead, the attraction of electrical charges keeps some extra  $K^+$  inside the cell. This imbalance in  $K^+$  is a major factor in generating a voltage across the plasma membrane called the *membrane potential*.



The membrane potential is related to the concentration imbalance of K<sup>+</sup> by the Nernst equation:

$$E_K = 2.3 \frac{RT}{zF} \log \left[ \frac{[K]_o}{[K]_i} \right]$$

where  $R$  is the gas constant,  $F$  is the Faraday constant (both familiar to chemistry students),  $T$  is the temperature, and  $z$  is the charge on the ion (+1). Solving for 2.3  $RT/zF$  at 20°C ("room temperature"), the equation becomes much simpler:

$$E_K = 58 \log \left[ \frac{[K]_o}{[K]_i} \right]$$

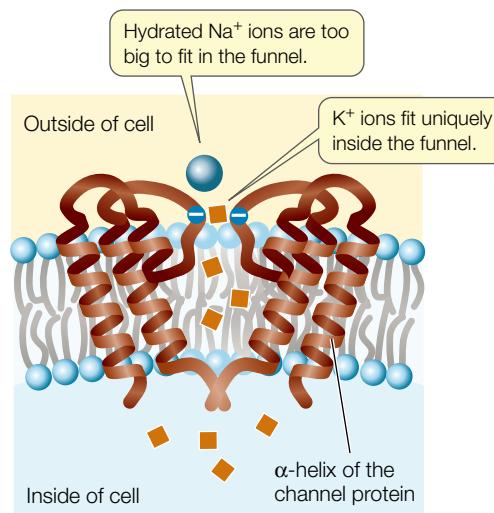
where  $E_K$  is the membrane potential (in millivolts, mV) that results from the ratio of K<sup>+</sup> concentrations outside the cell [K]<sub>o</sub> and inside the cell [K]<sub>i</sub>.

What does this equation tell us about cells? It shows that a small change in K<sup>+</sup> concentration, due to the opening of a ligand-gated K<sup>+</sup> channel, for example, can have a large effect on the electrical potential ( $E$ ) across the membrane. This change in potential might be enough to cause other proteins in the membrane, such as voltage-gated channels, to change configuration. As we discuss in Chapter 45, this is exactly what happens in the nervous system. Many drugs that act on electrically sensitive tissues work as ligands that open ion channels and thereby affect membrane potential. And as you will see shortly, membrane potential drives secondary active transport.

Actual measurements from animal cells give a total membrane potential between -60 and -70 mV across the membrane, where the inside is negative with respect to the outside (see Figure 45.5). Cells have a tremendous amount of potential energy stored in their membrane potentials. In fact, the brain cells you are using to read this book have more potential energy—about 200,000 volts per centimeter—than the high-voltage electric lines powering your reading light, which carry about 2 volts per centimeter.

**THE SPECIFICITY OF ION CHANNELS** How does an ion channel allow one ion, but not another, to pass through? It is not simply a matter of charge and size of the ion. For example, a sodium ion (Na<sup>+</sup>), with a radius of 0.095 nanometers, is smaller than K<sup>+</sup> (0.130 nm), and both carry the same positive charge. Yet the potassium channel lets only K<sup>+</sup> pass through the membrane, and not the smaller Na<sup>+</sup>. Nobel Laureate Roderick MacKinnon at The Rockefeller University found an elegant explanation for this when he deciphered the structure of a potassium channel from a bacterium (Figure 6.12).

Being charged, both Na<sup>+</sup> and K<sup>+</sup> are attracted to water molecules. They are surrounded by water "shells" in solution, held by the attraction of their positive charges to the negatively charged oxygen atoms on the water molecules (see Figure 2.10). The potassium channel contains highly polar oxygen atoms at its opening. The gap enclosed by these atoms is exactly the right size so that when a K<sup>+</sup> ion approaches the opening, it is more strongly attracted to the oxygen atoms there than to those of the



**6.12 The Potassium Channel** The positively charged potassium ions are attracted by the polar (negatively charged) oxygen atoms in the R groups (side chains) of the channel protein, and the ions funnel through the channel. This channel is a "custom fit" for K<sup>+</sup>; other ions do not pass through.

water molecules in its shell. It sheds its water shell and passes through the channel. The smaller Na<sup>+</sup> ion, on the other hand, is kept a bit more distant from the oxygen atoms at the opening of the channel because extra water molecules can fit between the ion (with its shell) and the oxygen atoms at the opening. So Na<sup>+</sup> does not enter the potassium channel. The gate that opens or closes the channel appears to be an interaction between positively charged arginine residues on the protein and negative charges on membrane phospholipids. This is an example of the functional interactions between membrane proteins and lipids.

**AQUAPORINS FOR WATER** Water crosses membranes at a much faster rate than would be expected for simple diffusion through the hydrophobic phospholipid bilayer. One way that water can do this is by "hitchhiking" with some ions, such as Na<sup>+</sup>, as they pass through ion channels. Up to 12 water molecules may coat an ion as it traverses a channel. But there is an even faster way to get water across membranes. Plant cells and some animal cells, such as red blood cells and kidney cells, have membrane channels called **aquaporins**. These channels function as a cellular plumbing system for moving water. Like the K<sup>+</sup> channel, the aquaporin channel is highly specific. Water molecules move in single file through the channel, which excludes ions so that the electrical properties of the cell are maintained.

Aquaporins were first identified by Peter Agre at Duke University, who shared the Nobel Prize with Rod MacKinnon (see above). Agre noticed a membrane protein that was present in red blood cells, kidney cells, and plant cells but did not know its function. A colleague suggested that it might be a water channel, because these cell types show rapid diffusion of water across their membranes. Agre inserted the protein into the membrane of an oocyte, which normally does not permit much diffusion of water. He injected the oocyte with mRNA for aquaporin, from which the protein was produced and inserted into

the membrane. Remarkably, the oocyte began swelling immediately after being transferred to a hypotonic solution, indicating rapid diffusion of water into the cell (**Figure 6.13**).

### Carrier proteins aid diffusion by binding substances

As we described earlier, another kind of facilitated diffusion involves not just the opening of a channel, but also the actual binding of the transported substance to a membrane protein called a carrier protein. Like channel proteins, carrier proteins allow diffusion both into and out of the cell or organelle. In other words, carrier proteins operate in both directions. Carrier proteins transport polar molecules such as sugars and amino acids.

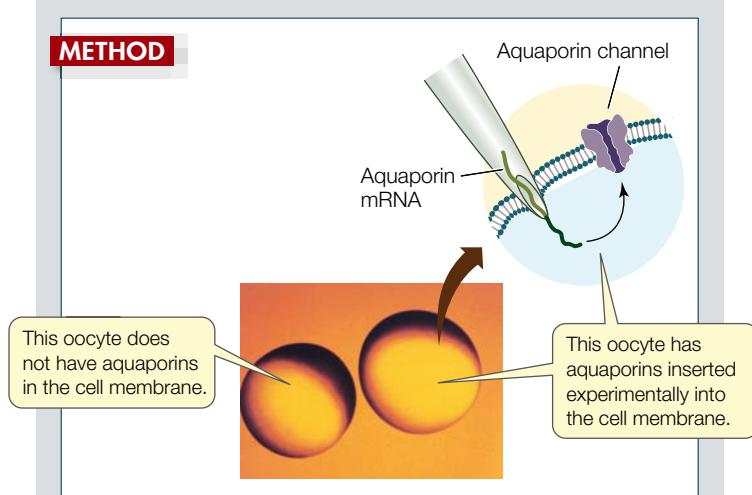
## INVESTIGATING LIFE

### 6.13 Aquaporin Increases Membrane Permeability to Water

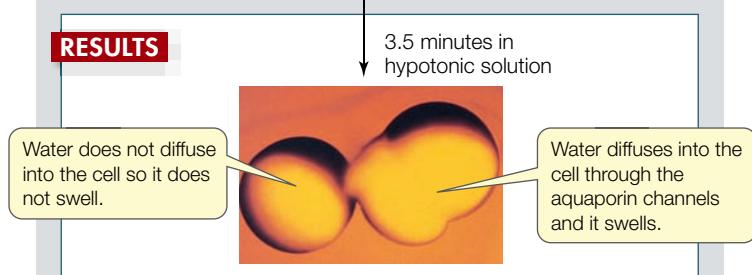
A protein was isolated from the membranes of cells in which water diffuses rapidly across the membranes. When the protein was inserted into oocytes, which do not normally have it, the water permeability of the oocytes was greatly increased.

**HYPOTHESIS** | Aquaporin increases membrane permeability to water.

#### METHOD



#### RESULTS



**CONCLUSION** | Aquaporin increases the rate of water diffusion across the cell membrane.

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Glucose is the major energy source for most mammalian cells, and they require a great deal of it. Their membranes contain a carrier protein—the glucose transporter—that facilitates glucose uptake into the cell. Binding of glucose to a specific three-dimensional site on one side of the transporter protein causes the protein to change its shape and release glucose on the other side of the membrane (**Figure 6.14A**). Since glucose is broken down almost as soon as it enters a cell, there is almost always a strong concentration gradient favoring glucose entry (that is, a higher concentration outside the cell than inside). The transporter allows glucose molecules to cross the membrane and enter the cell much faster than they would by simple diffusion through the bilayer. This rapid entry is necessary to ensure that the cell receives enough glucose for its energy needs.

Transport by carrier proteins is different from simple diffusion. In both processes, the rate of movement depends on the concentration gradient across the membrane. However, in carrier-mediated transport, a point is reached at which increases in the concentration gradient are not accompanied by an increased rate of diffusion. At this point, the facilitated diffusion system is said to be *saturated* (**Figure 6.14B**). Because there are only a limited number of carrier protein molecules per unit of membrane area, the rate of diffusion reaches a maximum when all the carrier molecules are fully loaded with solute molecules. Think of waiting for the elevator on the ground floor of a hotel with 50 other people. They can't all get in the elevator (carrier) at once, so the rate of transport (say 10 people at a time) is saturated.

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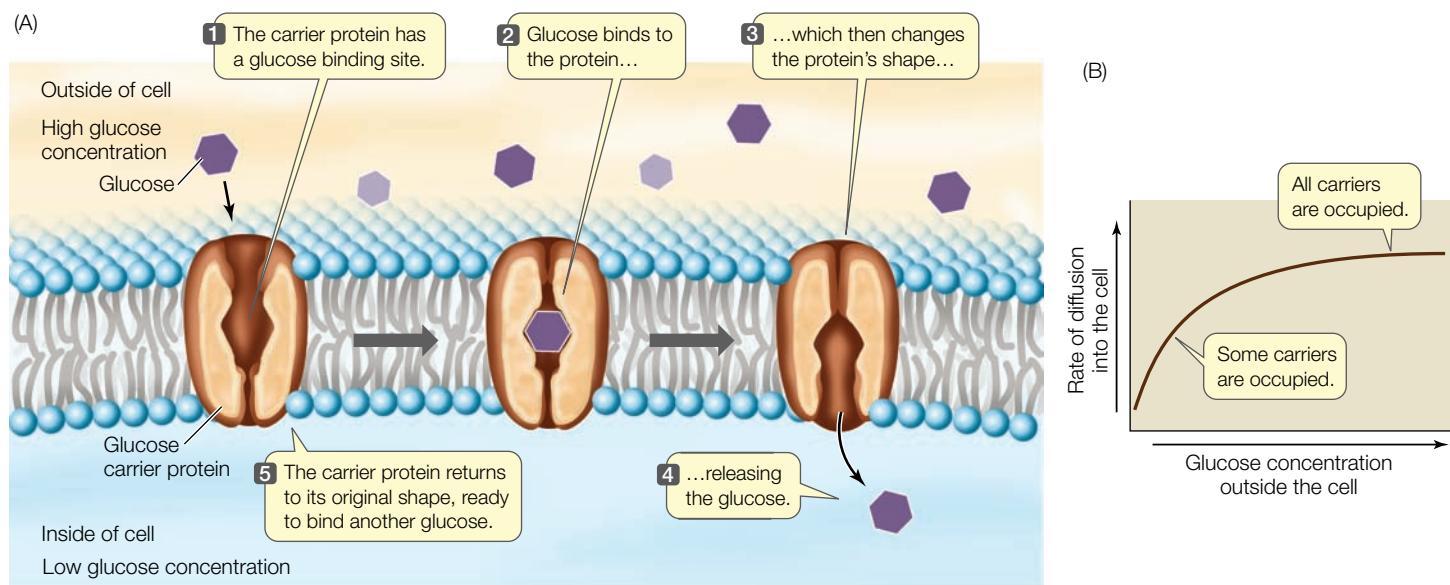
GO TO [Animated Tutorial 6.1 • Passive Transport](#)

## 6.3 RECAP

Diffusion is the movement of ions or molecules from a region of greater concentration to a region of lesser concentration. Water can diffuse through cell membranes by a process called osmosis. Channel proteins, which can be open or closed, and carrier proteins facilitate diffusion of charged and polar substances, including water. The diffusion of ions across cell membranes sets up an electrochemical potential gradient across the membranes.

- What properties of a substance determine whether, and how fast, it will diffuse across a membrane?  
**See p. 114**
- Describe osmosis and explain the terms hypertonic, hypotonic, and isotonic. **See p. 116 and Figure 6.10**
- How does a channel protein facilitate diffusion?  
**See p. 118 and Figures 6.11 and 6.12**

The process of diffusion tends to equalize the concentrations of substances outside and inside cells. However, one hallmark of



**6.14 A Carrier Protein Facilitates Diffusion** The glucose transporter is a carrier protein that allows glucose to enter the cell at a faster rate than would be possible by simple diffusion. (A) The transporter binds to glucose, brings it into the membrane interior, then changes shape, releasing glucose into the cell cytoplasm. (B) The graph shows the rate of glucose entry via a carrier versus the concentration of glucose outside the cell. As the glucose concentration increases, the rate of diffusion increases until the point at which all the available transporters are being used (the system is saturated).

a living thing is that it can have an internal composition quite different from that of its environment. To achieve this it must sometimes move substances in opposite directions from the ones in which they would naturally tend to diffuse. That is, substances must sometimes be moved against concentration gradients and/or against the cell's membrane potential (electrical gradient). This process requires work—the input of energy—and is known as *active transport*.

## 6.4 What are the Active Processes of Membrane Transport?

In many biological situations, there is a different concentration of a particular ion or small molecule inside compared with outside a cell. In these cases, the imbalance is maintained by a pro-

tein in the plasma membrane that moves the substance against its concentration and/or electrical gradient. This is called *active transport*, and because it is acting “against the normal flow,” it requires the expenditure of energy. Often the energy source is adenosine triphosphate (ATP). In eukaryotes, ATP is produced in the mitochondria and has chemical energy stored in its terminal phosphate bond. This energy is released when ATP is converted to adenosine diphosphate (ADP) in a hydrolysis reaction that breaks the terminal phosphate bond. This is one source of energy for active transport. (We give the details of how ATP provides energy to cells in Section 8.2.)

The differences between diffusion and active transport are summarized in **Table 6.1**.

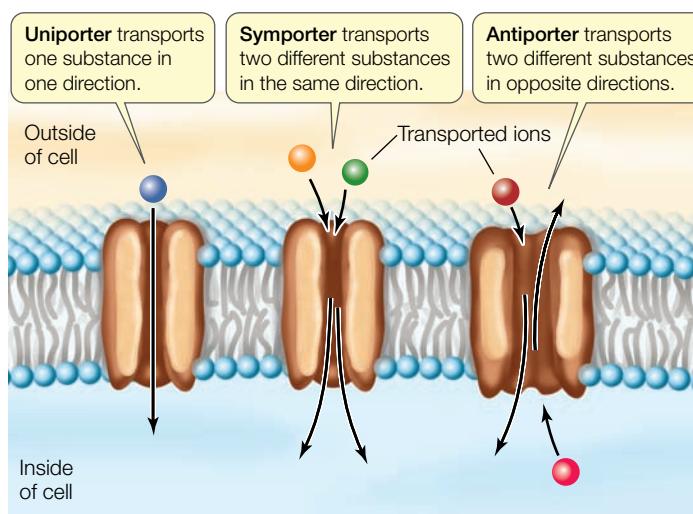
### Active transport is directional

Simple and facilitated diffusion follow concentration gradients and can occur in both directions across a membrane. In contrast, active transport is directional, and moves a substance either into or out of the cell or organelle, depending on need. There are three types of active transport, each involving its own type of membrane protein (**Figure 6.15**):

- A **uniporter** moves a single substance in one direction. For example, a calcium-binding protein found in the plasma

TABLE 6.1  
Membrane Transport Mechanisms

	SIMPLE DIFFUSION	DIFFUSION THROUGH CHANNEL	FACILITATED DIFFUSION	ACTIVE TRANSPORT
Cellular energy required?	No	No	No	Yes
Driving force	Concentration gradient	Concentration gradient	Concentration gradient	ATP hydrolysis (against concentration gradient)
Membrane protein required?	No	Yes	Yes	Yes
Specificity	No	Yes	Yes	Yes



**6.15 Three Types of Proteins for Active Transport** Note that in each of the three cases, transport is directional. Symporters and antiporters are examples of coupled transporters. All three types of transporters are coupled to energy sources in order to move substances against their concentration gradients.

membrane and endoplasmic reticulum of many cells actively transports  $\text{Ca}^{2+}$  to locations where it is more highly concentrated, either outside the cell or inside the ER.

- A **symporter** moves two substances in the same direction. For example, a symporter in the cells that line the intestine must bind  $\text{Na}^+$  in addition to an amino acid in order to absorb amino acids from the intestine.

- An **antiporter** moves two substances in opposite directions, one into the cell (or organelle) and the other out of the cell (or organelle). For example, many cells have a sodium-potassium pump that moves  $\text{Na}^+$  out of the cell and  $\text{K}^+$  into the cell.

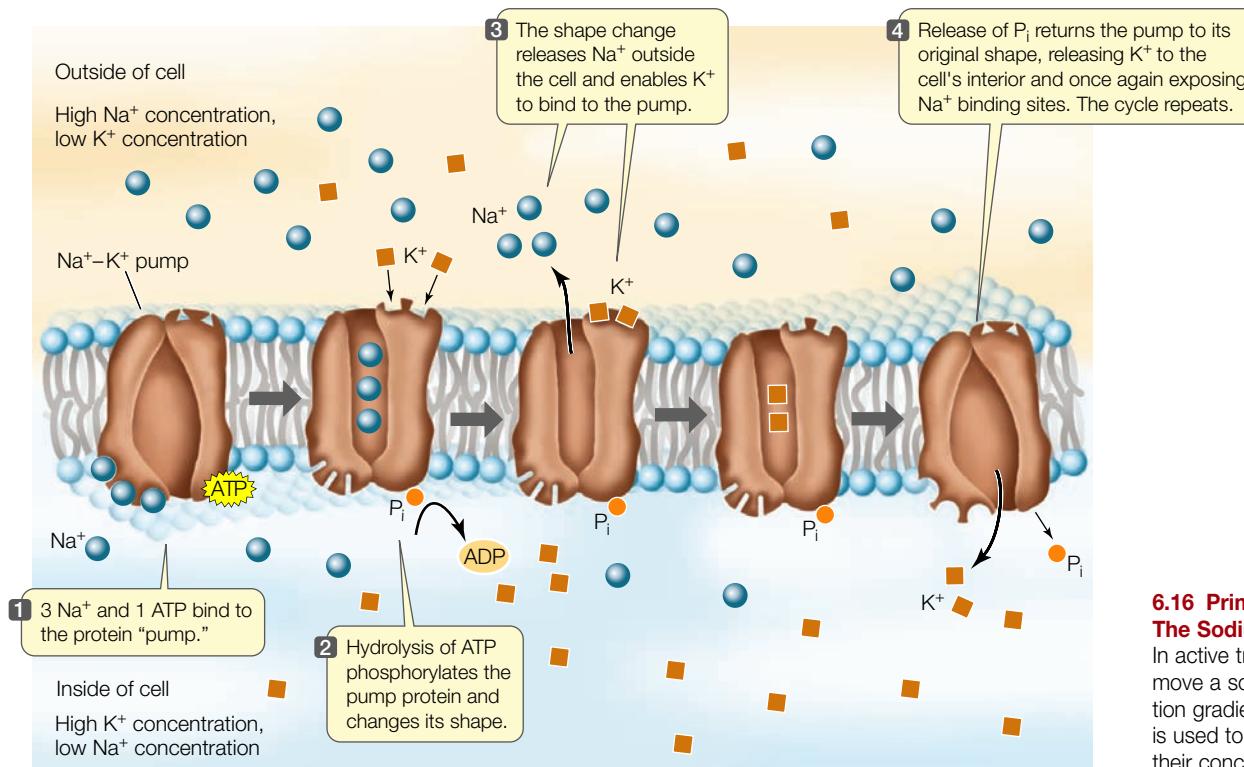
Symporters and antiporters are also known as *coupled transporters* because they move two substances at once.

### Different energy sources distinguish different active transport systems

There are two basic types of active transport:

- **Primary active transport** involves the direct hydrolysis of ATP, which provides the energy required for transport.
- **Secondary active transport** does not use ATP directly. Instead, its energy is supplied by an ion concentration and electrical gradient established by primary active transport. This transport system uses the energy of ATP indirectly to set up the gradient.

In primary active transport, energy released by the hydrolysis of ATP drives the movement of specific ions against their concentration gradients. For example, we mentioned earlier that concentrations of potassium ions ( $\text{K}^+$ ) inside a cell are often much higher than in the fluid bathing the cell. On the other hand, the concentration of sodium ions ( $\text{Na}^+$ ) is often much higher outside the cell. A protein in the plasma membrane pumps  $\text{Na}^+$  out of the cell and  $\text{K}^+$  into the cell against these concentration and electrochemical gradients, ensuring that the gradients are maintained (Figure 6.16). This **sodium-potassium ( $\text{Na}^+-\text{K}^+$ ) pump** is



### 6.16 Primary Active Transport: The Sodium-Potassium Pump

In active transport, energy is used to move a solute against its concentration gradient. Here, energy from ATP is used to move  $\text{Na}^+$  and  $\text{K}^+$  against their concentration gradients.

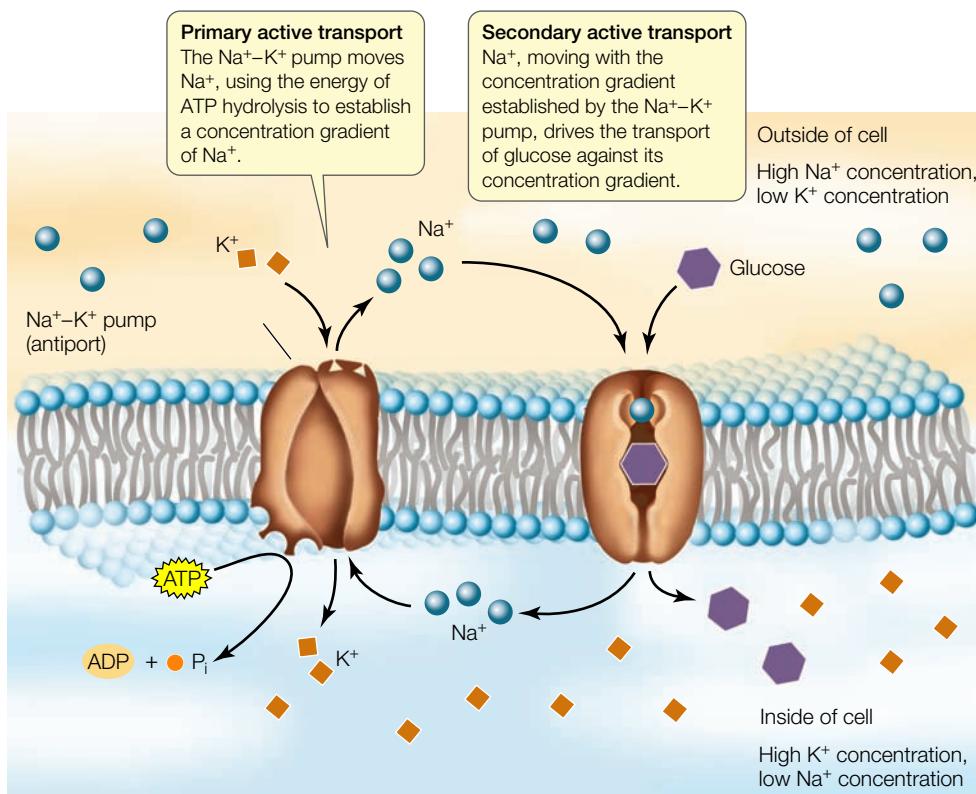
**6.17 Secondary Active Transport** The  $\text{Na}^+$  concentration gradient established by primary active transport (left) powers the secondary active transport of glucose (right). A symporter protein couples the movement of glucose across the membrane against its concentration gradient to the passive movement of  $\text{Na}^+$  into the cell.

found in all animal cells. The pump is an integral membrane glycoprotein. It breaks down a molecule of ATP to ADP and a free phosphate ion ( $\text{P}_i$ ) and uses the energy released to bring two  $\text{K}^+$  ions into the cell and export three  $\text{Na}^+$  ions. The  $\text{Na}^+-\text{K}^+$  pump is thus an antiporter because it moves two substances in different directions.

In secondary active transport, the movement of a substance against its concentration gradient is accomplished using energy “regained” by letting ions move across the membrane with their electrochemical and concentration gradients. For example, once the sodium–potassium pump establishes a concentration gradient of sodium ions, the passive diffusion of some  $\text{Na}^+$  back into the cell can provide energy for the secondary active transport of glucose into the cell (Figure 6.17). This occurs when glucose is absorbed into the bloodstream from the digestive tract. Secondary active transport aids in the uptake of amino acids and sugars, which are essential raw materials for cell maintenance and growth. Both types of coupled transport proteins—symporters and antiporters—are used for secondary active transport.

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GO TO Animated Tutorial 6.2 • Active Transport



We have examined a number of passive and active ways in which ions and small molecules can enter and leave cells. But what about large molecules such as proteins? Many proteins are so large that they diffuse very slowly, and their bulk makes it difficult for them to pass through the phospholipid bilayer. It takes a completely different mechanism to move intact large molecules across membranes.

## 6.5 How Do Large Molecules Enter and Leave a Cell?

Macromolecules such as proteins, polysaccharides, and nucleic acids are simply too large and too charged or polar to pass through biological membranes. This is actually a fortunate property—think of the consequences if such molecules diffused out of cells. A red blood cell would not retain its hemoglobin! Indeed, as we discuss in Chapter 5, the development of a selectively permeable membrane was essential for the functioning of the first cells when life on Earth began. The interior of a cell can be maintained as a separate compartment with a different composition from that of the exterior environment, which is subject to abrupt changes. On the other hand, cells must sometimes take up or secrete (release to the external environment) intact large molecules. In Section 5.3 we describe phagocytosis, the mechanism by which solid particles can be brought into the cell by means of vesicles that pinch off from the plasma membrane. The general terms for the mechanisms by which substances enter and leave the cell via membrane vesicles are *endocytosis* and *exocytosis*.

## 6.4 RECAP

Active transport across a membrane is directional and requires an input of energy to move substances against their concentration gradients. Active transport allows a cell to maintain small molecules and ions at concentrations very different from those in the surrounding environment.

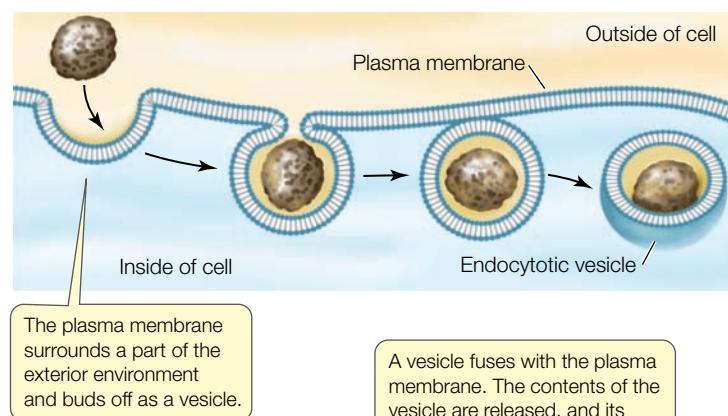
- Why is energy required for active transport? See p. 120
- Explain the difference between primary active transport and secondary active transport. See p. 121
- Why is the sodium–potassium ( $\text{Na}^+-\text{K}^+$ ) pump classified as an antiporter? See p. 122 and Figure 6.16

### Macromolecules and particles enter the cell by endocytosis

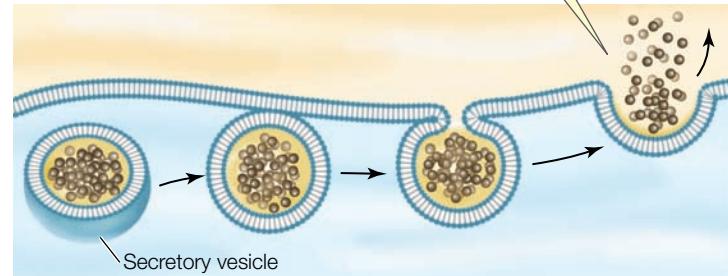
**Endocytosis** is a general term for a group of processes that bring small molecules, macromolecules, large particles, and even small cells into the eukaryotic cell (**Figure 6.18A**). There are three types of endocytosis: phagocytosis, pinocytosis, and receptor-mediated endocytosis. In all three, the plasma membrane invaginates (folds inward), forming a small pocket around materials from the environment. The pocket deepens, forming a vesicle. This vesicle separates from the plasma membrane and migrates with its contents to the cell's interior.

- In **phagocytosis** ("cellular eating"), part of the plasma membrane engulfs large particles or even entire cells. Unicellular protists use phagocytosis for feeding, and some white blood cells use phagocytosis to defend the body by engulfing foreign cells and substances. The food vacuole or phagosome that forms usually fuses with a lysosome, where its contents are digested (see Figure 5.11).
- In **pinocytosis** ("cellular drinking"), vesicles also form. However, these vesicles are smaller, and the process operates to bring dissolved substances, including proteins or fluids, into the cell. Like phagocytosis, pinocytosis can be relatively nonspecific regarding what it brings into the cell. For example, pinocytosis goes on constantly in the endothelium, the single layer of cells that separates a tiny blood capillary from the surrounding tissue. Pinocytosis allows cells of the endothelium to rapidly acquire fluids and dissolved solutes from the blood.

#### (A) Endocytosis



#### (B) Exocytosis



- In **receptor-mediated endocytosis**, molecules at the cell surface recognize and trigger the uptake of specific materials. Let's take a closer look at this last process.

### Receptor-mediated endocytosis is highly specific

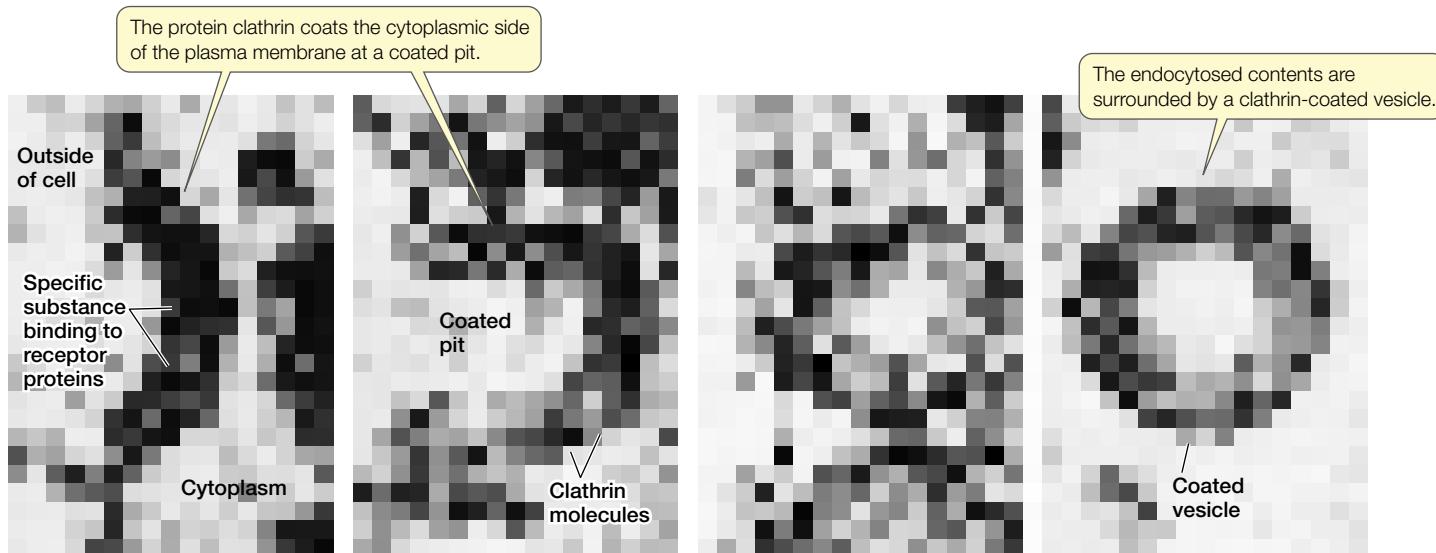
Receptor-mediated endocytosis is used by animal cells to capture specific macromolecules from the cell's environment. This process depends on **receptor proteins**, which are proteins that can bind to specific molecules within the cell or in the cell's external environment. In receptor-mediated endocytosis, the receptors are integral membrane proteins located at particular regions on the extracellular surface of the plasma membrane. These membrane regions are called *coated pits* because they form slight depressions in the plasma membrane and their cytoplasmic surfaces are coated by other proteins, such as clathrin. The uptake process is similar to that in phagocytosis.

When a receptor protein binds to its specific ligand (in this case, the macromolecule to be taken into the cell), its coated pit invaginates and forms a coated vesicle around the bound macromolecule. The clathrin molecules strengthen and stabilize the vesicle, which carries the macromolecule away from the plasma membrane and into the cytoplasm (**Figure 6.19**). Once inside, the vesicle loses its clathrin coat and may fuse with a lysosome, where the engulfed material is digested (by the hydrolysis of polymers to monomers) and the products released into the cytoplasm. Because of its specificity for particular macromolecules, receptor-mediated endocytosis is an efficient method of taking up substances that may exist at low concentrations in the cell's environment.

Receptor-mediated endocytosis is the method by which cholesterol is taken up by most mammalian cells. Water-insoluble cholesterol and triglycerides are packaged by liver cells into lipoprotein particles. Most of the cholesterol is packaged into a type of lipoprotein particle called *low-density lipoprotein*, or LDL, which is circulated via the bloodstream. When a particular cell requires cholesterol, it produces specific LDL receptors, which are inserted into the plasma membrane in clathrin-coated pits. Binding of LDLs to the receptor proteins triggers the uptake of the LDLs via receptor-mediated endocytosis. Within the resulting vesicle, the LDL particles are freed from the receptors. The receptors segregate to a region that buds off and forms a new vesicle, which is recycled to the plasma membrane. The freed LDL particles remain in the original vesicle, which fuses with a lysosome. There, the LDLs are digested and the cholesterol made available for cell use.

In healthy individuals, the liver takes up unused LDLs for recycling. People with the inherited disease *familial hypercholesterolemia* have a deficient LDL receptor in their livers. This prevents receptor-mediated endocytosis of LDLs, resulting in

**6.18 Endocytosis and Exocytosis** Endocytosis (A) and exocytosis (B) are used by eukaryotic cells to take up and release large molecules and particles, and small cells.



dangerously high levels of cholesterol in the blood. The cholesterol builds up in the arteries that nourish the heart and causes heart attacks. In extreme cases where only the deficient receptor is present, children and teenagers can have severe cardiovascular disease.

### Exocytosis moves materials out of the cell

**Exocytosis** is the process by which materials packaged in vesicles are secreted from a cell when the vesicle membrane fuses with the plasma membrane (see Figure 6.18B). This fusing makes an opening to the outside of the cell. The contents of the vesicle are released into the environment, and the vesicle membrane is smoothly incorporated into the plasma membrane.

In Chapter 5 we encounter exocytosis as the last step in the processing of material engulfed by phagocytosis—the release of undigested materials back to the extracellular environment. Exocytosis is also important in the secretion of many different substances, including digestive enzymes from the pancreas, neurotransmitters from neurons, and materials for the construction of the plant cell wall. You will encounter these processes in later chapters.

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GO TO Animated Tutorial 6.3 • Endocytosis and Exocytosis

### 6.5 RECAP

Endocytosis and exocytosis are the processes by which large particles and molecules are transported into and out of the cell. Endocytosis may be mediated by a receptor protein in the plasma membrane.

- Explain the difference between phagocytosis and pinocytosis. See p. 123
- Describe an example of receptor-mediated endocytosis. See p. 123 and Figure 6.19

**6.19 Receptor-Mediated Endocytosis** The receptor proteins in a coated pit bind specific macromolecules, which are then carried into the cell by a coated vesicle.

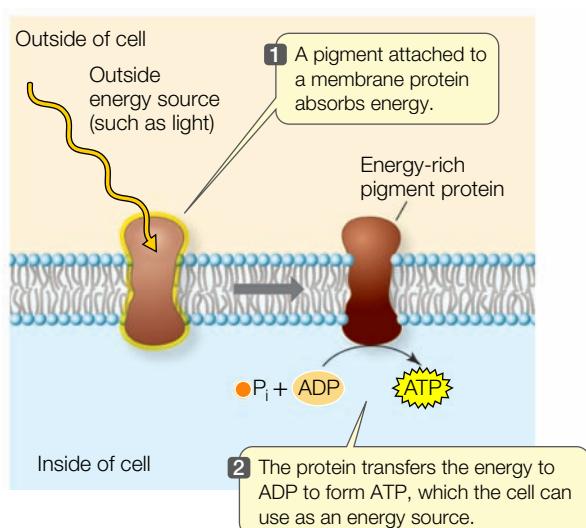
We have now examined the structures and some of the functions of biological membranes. We have seen how macromolecules on the plasma membrane surface allow cells to recognize and adhere to each other, so that tissues and organs can form. We have also seen how membranes selectively regulate the traffic of small and large molecules, and how large particles such as LDLs can be taken up by cells. These are crucial functions, but they are not the only functions of biological membranes.

### 6.6 What Are Some Other Functions of Membranes?

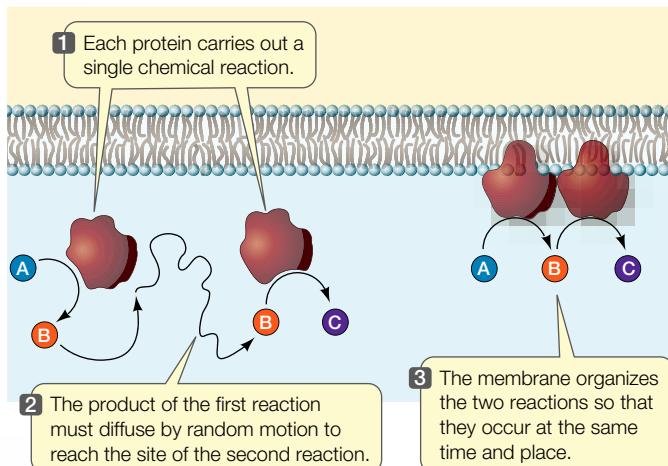
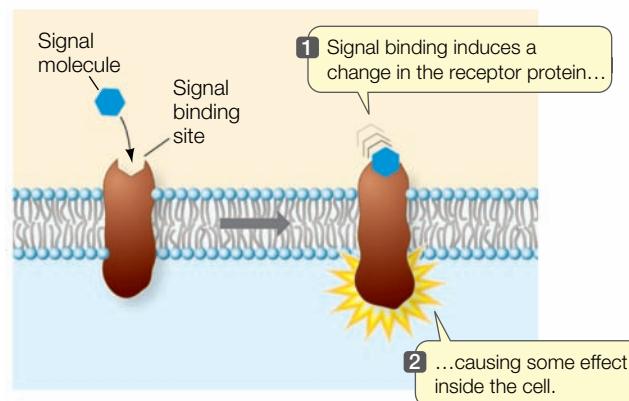
The plasma membranes of certain types of cells, such as neurons and muscle cells, respond to the electric charges carried by ions. These membranes are thus electrically excitable, which gives them important properties. For example, in neurons, the plasma membrane conducts nerve impulses from one end of the cell to the other. In muscle cells, electrical excitation results in muscle contraction.

Other biological activities and properties associated with membranes are discussed in the chapters that follow. Throughout evolution, these activities have been essential for the specialization of cells, tissues, and organisms. Three of these activities are especially important:

- *Some organelle membranes help transform energy (Figure 6.20A).* For example, the inner mitochondrial membrane helps convert the energy of fuel molecules to the energy of phosphate bonds in ATP. The thylakoid membranes of chloroplasts participate in the conversion of light energy to the energy of chemical bonds. These important processes, vital to the life of most eukaryotic organisms, are discussed in detail in Chapters 9 and 10.
- *Some membrane proteins organize chemical reactions.* Often a cellular process depends on a series of enzyme-catalyzed

**(A) Energy transformation**

**6.20 Other Membrane Functions** The compartmentation afforded by a lipid bilayer or protein membrane was a key event in the emergence of cells. Functions such as energy transformation (A), organization of chemical reactions (B), and signaling (C) probably evolved later and conferred a selective advantage on cells and organisms that had them.

**(B) Organizing chemical reactions****(C) Information processing**

reactions, in which the products of one reaction serve as reactants in the next. For such a series of reactions to occur, all the necessary molecules must come together. In a solution, reactant and enzyme molecules are randomly distributed and collisions among them are random. Because these collisions are necessary for chemical reactions to occur, a complete series of chemical reactions may occur only very slowly in a solution. However, if the different enzymes are

bound to a membrane in sequential order, the product of one reaction can be released close to the enzyme for the next reaction. Such an “assembly line” allows reactions to proceed rapidly and efficiently (Figure 6.20B).

- Some membrane proteins process information. As we have seen, biological membranes may have integral membrane proteins or attached carbohydrates that can bind to specific substances in the environment. Without entering a cell, a specific ligand can bind to a receptor and serve as a signal to initiate, modify, or turn off a cell function (Figure 6.20C). In this type of information processing, specificity in binding is essential.

We have seen the informational role of the LDL receptor protein in the recognition and endocytosis of LDL, with its cargo of cholesterol. Another example is the binding of a hormone such as insulin to specific receptors on a target cell. When insulin binds to receptors on a liver cell, it elicits the uptake of glucose. In Chapter 7 there are many other examples of the role of membrane proteins in information processing.

## CHAPTER SUMMARY

### 6.1 What Is the Structure of a Biological Membrane?

- Biological membranes consist of lipids, proteins, and carbohydrates. The **fluid mosaic model** of membrane structure describes a phospholipid bilayer in which proteins can move about within the plane of the membrane. SEE WEB ACTIVITY 6.1
- The two leaflets of a membrane may have different properties because of their different phospholipid compositions, exposed

domains of **integral membrane proteins**, and **peripheral membrane proteins**. Some proteins, called **transmembrane proteins**, span the membrane. Review Figure 6.1

- Carbohydrates, attached to proteins in **glycoproteins** or to phospholipids in **glycolipids**, project from the external surface of the plasma membrane and function as recognition signals.
- Membranes are not static structures, but are constantly forming, exchanging, and breaking down.

## 6.2 How Is the Plasma Membrane Involved in Cell Adhesion and Recognition?

- In order for cells to assemble into tissues they must recognize and adhere to one another. **Cell recognition** and **cell adhesion** depend on integral membrane proteins that protrude from the cell surface. Binding can be between the same proteins from two cells (**homotypic**) or different proteins (**heterotypic**).

**Review Figure 6.6**

- Cell junctions connect adjacent cells. **Tight junctions** prevent the passage of molecules through the intercellular spaces between cells, and they restrict the migration of membrane proteins over the cell surface. **Desmosomes** cause cells to adhere firmly to one another. **Gap junctions** provide channels for communication between adjacent cells. **Review Figure 6.7.**

**WEB ACTIVITY 6.2**

- Integrins** mediate the attachment of animal cells to the extracellular matrix. **Review Figure 6.8**

## 6.3 What Are the Passive Processes of Membrane Transport?

**SEE ANIMATED TUTORIAL 6.1**

- Membranes exhibit **selective permeability**, regulating which substances pass through them.
- A substance can diffuse passively across a membrane by one of two processes: **simple diffusion** through the phospholipid bilayer or **facilitated diffusion** either through a **channel** or by means of a **carrier protein**.
- A solute diffuses across a membrane from a region with a greater concentration of that solute to a region with a lesser concentration of that solute. Equilibrium is reached when the solute concentrations on both sides of the membrane show no net change over time. **Review Figure 6.9**
- In **osmosis**, water diffuses from a region of higher water concentration to a region of lower water concentration.
- Most cells are in an **isotonic** environment, where total solute concentrations on both sides of the plasma membrane are equal. If the solution surrounding a cell is **hypotonic** to the cell interior, more water enters the cell than leaves it. In plant cells, this leads to **turgor pressure**. In a **hypertonic** solution, more water leaves the cell than enters it. **Review Figure 6.10**
- Ion channels** are membrane proteins that allow the rapid facilitated diffusion of ions through membranes. **Gated channels** can be opened or closed by certain conditions or chemicals. The

opening or closing of channels, as well as an asymmetric distribution of charged molecules, sets up an **electrochemical gradient** on different sides of a membrane. **Review Figure 6.11**

- Aquaporins** are water channels. **Review Figure 6.13**
- Carrier proteins** bind to polar molecules such as sugars and amino acids and transport them across the membrane. The maximum rate of this type of facilitated diffusion is limited by the number of carrier (transporter) proteins in the membrane. **Review Figure 6.14**

## 6.4 What Are the Active Processes of Membrane Transport?

**SEE ANIMATED TUTORIAL 6.2**

- Active transport** requires the use of chemical energy to move substances across membranes against their concentration gradients. Active transport proteins may be **uniporters**, **symporters**, or **antiporters**. **Review Figure 6.15**
- In **primary active transport**, energy from the hydrolysis of ATP is used to move ions into or out of cells. The **sodium-potassium pump** is an important example. **Review Figure 6.16**
- Secondary active transport** couples the passive movement of one substance down its concentration gradient to the movement of another substance against its concentration gradient. Energy from ATP is used indirectly to establish the concentration gradient that results in the movement of the first substance. **Review Figure 6.17**

## 6.5 How Do Large Molecules Enter and Leave a Cell?

**SEE ANIMATED TUTORIAL 6.3**

- Endocytosis** is the transport of macromolecules, large particles, and small cells into eukaryotic cells via the invagination of the plasma membrane and the formation of vesicles. **Phagocytosis** and **pinocytosis** are types of endocytosis. **Review Figure 6.18A**
- In **receptor-mediated endocytosis**, a specific **receptor protein** on the plasma membrane binds to a particular macromolecule.
- In **exocytosis**, materials in vesicles are secreted from the cell when the vesicles fuse with the plasma membrane. **Review Figure 6.18B**

## 6.6 What Are Some Other Functions of Membranes?

- Membranes function as sites for energy transformations, for organizing chemical reactions, and for recognition and initial processing of extracellular signals. **Review Figure 6.20**

### SELF-QUIZ

- Which statement about membrane phospholipids is *not* true?
  - They associate to form bilayers.
  - They have hydrophobic “tails.”
  - They have hydrophilic “heads.”
  - They give the membrane fluidity.
  - They flip-flop readily from one side of the membrane to the other.
- When a hormone molecule binds to a specific protein on the plasma membrane, the protein it binds to is called a
  - ligand.
  - clathrin.
  - receptor protein.
  - hydrophobic protein.
  - cell adhesion molecule.
- Which statement about membrane proteins is *not* true?
  - They all extend from one side of the membrane to the other.
  - Some serve as channels for ions to cross the membrane.
  - Many are free to migrate laterally within the membrane.
  - Their position in the membrane is determined by their tertiary structure.
  - Some play roles in photosynthesis.

4. Which statement about membrane carbohydrates is *not* true?
    - a. Some are bound to proteins.
    - b. Some are bound to lipids.
    - c. They are added to proteins in the Golgi apparatus.
    - d. They show little diversity.
    - e. They are important in recognition reactions at the cell surface.
  5. Which statement about animal cell junctions is *not* true?
    - a. Tight junctions are barriers to the passage of molecules between cells.
    - b. Desmosomes allow cells to adhere firmly to one another.
    - c. Gap junctions block communication between adjacent cells.
    - d. Connexons are made of protein.
    - e. The fibers associated with desmosomes are made of protein.
  6. You are studying how the protein transferrin enters cells. When you examine cells that have taken up transferrin, you find it inside clathrin-coated vesicles. Therefore, the most likely mechanism for uptake of transferrin is
    - a. facilitated diffusion.
    - b. an antiporter.
    - c. receptor-mediated endocytosis.
    - d. gap junctions.
    - e. ion channels.
7. Which statement about ion channels is *not* true?
    - a. They form pores in the membrane.
    - b. They are proteins.
    - c. All ions pass through the same type of channel.
    - d. Movement through them is from regions of high concentration to regions of low concentration.
    - e. Movement through them is by simple diffusion.
  8. Facilitated diffusion and active transport both
    - a. require ATP.
    - b. require the use of proteins as carriers or channels.
    - c. carry solutes in only one direction.
    - d. increase without limit as the concentration gradient increases.
    - e. depend on the solubility of the solute in lipids.
  9. Primary and secondary active transport both
    - a. generate ATP.
    - b. are based on passive movement of  $\text{Na}^+$  ions.
    - c. include the passive movement of glucose molecules.
    - d. use ATP directly.
    - e. can move solutes against their concentration gradients.
  10. Which statement about osmosis is *not* true?
    - a. It obeys the laws of diffusion.
    - b. In animal tissues, water moves into cells if they are hypertonic to their environment.
    - c. Red blood cells must be kept in a plasma that is hypotonic to the cells.
    - d. Two cells with identical solute concentrations are isotonic to each other.
    - e. Solute concentration is the principal factor in osmosis.

## FOR DISCUSSION

1. Muscle function requires calcium ions ( $\text{Ca}^{2+}$ ) to be pumped into a subcellular compartment against a concentration gradient. What types of molecules are required for this to happen?
2. Section 27.5 describes the diatoms, which are protists that have complex glassy structures in their cell walls (see Figure 27.7B). These structures form within the Golgi apparatus. How do these structures reach the cell wall without having to pass through a membrane?
3. Organisms that live in fresh water are almost always hypertonic to their environment. In what way is this a serious problem? How do some organisms cope with this problem?
4. Contrast nonspecific endocytosis and receptor-mediated endocytosis.
5. The emergence of the phospholipid membrane was important to the origin of cells. Describe the properties of membranes that might have allowed cells to thrive in comparison with molecular aggregates without membranes.

## ADDITIONAL INVESTIGATION

When a normal lung cell becomes a lung cancer cell, there are several important changes in plasma membrane properties. How would you investigate the following phenomena? (a) The cancer cell membrane is more fluid, with more rapid diffusion

in the plane of the membrane of both lipids and proteins. (b) The cancer cell has altered cell adhesion properties, binding to other tissues in addition to lung cells.

## WORKING WITH DATA (GO TO [yourBioPortal.com](http://yourBioPortal.com))

**Aquaporin Increases Membrane Permeability to Water** In this hands-on exercise based on Figure 6.13, you will investigate how Agre and colleagues used an egg cell to show that expression of aquaporin results in rapid water uptake when

the cell is placed in a hypotonic medium. Analyzing their experimental design and data, you will see how this model cell system and control experiments confirmed the important role of aquaporin as a water channel.

## 7

# Cell Signaling and Communication

## Love signals

Prairie voles (*Microtus ochrogaster*) are small rodents that live in temperate climates, where they dig tunnels in fields. When a male prairie vole encounters a female, mating often ensues. After mating (which can take as long as a day), the couple stays together, building a nest and raising their pups together. The two voles bond so tightly that they stay together for life. Contrast this behavior with that of the montane vole (*M. montanus*), which is closely related to the prairie vole and lives in the hills not far away. In this species, mating is quick, and afterwards the couple separates. The male looks for new mates and the female abandons her young soon after they are born.

The explanation for these dramatic behavioral differences lies in the brains of these two species. Neuroscientist Thomas Insel and his colleagues found that when prairie voles mate for all those hours, their brains release a

9-amino-acid peptide. In females, this peptide is oxytocin; in males, it is vasopressin. The peptide is circulated in the bloodstream and reaches all tissues in the body, but it binds to only a few cell types. These cells have surface proteins, called receptors, that specifically bind the peptide, like a key inserting into a lock.

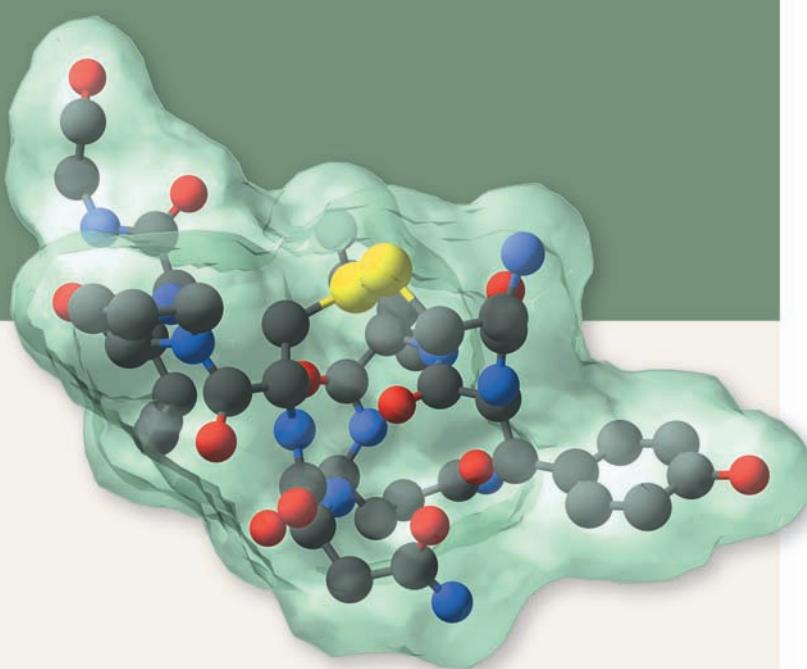
The interaction of peptide and receptor causes the receptor, which extends across the plasma membrane, to change shape. Within the cytoplasm, this change sets off a series of events called a signal transduction pathway. Such a pathway can cause many different cellular responses, but in this case, the notable changes are in behavior. The receptors for oxytocin and vasopressin in prairie voles are most concentrated in the regions of the brain that are responsible for behaviors such as bonding and caring for the young. In montane voles, there are far fewer receptors and

as a result, fewer postmating behaviors.

These cause-and-effect relationships between peptides, receptors, and behavior have been established through experiments. For example, a female prairie vole that is injected before mating with a molecule that blocks oxytocin does not bond with the male. Also, a female injected with oxytocin will bond with a male even without mating. Experiments with vasopressin in males give similar results. Furthermore, promiscuous vole males that were genetically manipulated to express prairie vole amounts of the vasopressin receptor grew up to behave more like prairie vole males. These experiments show that oxytocin and



**Voles** Prairie voles display extensive bonding behaviors after mating. These behaviors are mediated by peptides acting as intercellular signals.



**Oxytocin** This peptide with 9 amino acids acts as a signal for postmaturing behaviors.

vasopressin are signals that induce bonding and caring behaviors in voles. Could this also be true of humans?

Neuroeconomist Paul Zaks thinks so. He has done experiments with human volunteers, who were asked to “invest” funds with a stranger. A group of investors that was given a nasal spray containing oxytocin was more trusting of the stranger (and invested more funds) than a group that got an inert spray. So the oxytocin signaling pathway is important in human behavior too.

A cell’s response to any signal molecule takes place in three sequential steps. First, the signal binds to a receptor in the cell, often on the outside surface of the plasma membrane. Second, signal binding conveys a message to the cell. Third, the cell changes its activity in response to the signal. And in a multicellular organism, this leads to changes in that organism’s functioning.

**IN THIS CHAPTER** we first describe the types of signals that affect cells. These include chemicals produced by other cells and substances from outside the body, as well as physical and environmental factors such as light. Then we show how a signal affects only those cells that have the specific receptor to recognize that signal. Next, we describe the steps of signal transduction in which the receptor communicates to the cell that a signal has been received, thus causing a change in cell function.

## CHAPTER OUTLINE

- 7.1 What Are Signals, and How Do Cells Respond to Them?
- 7.2 How Do Signal Receptors Initiate a Cellular Response?
- 7.3 How Is the Response to a Signal Transduced through the Cell?
- 7.4 How Do Cells Change in Response to Signals?
- 7.5 How Do Cells Communicate Directly?

### 7.1 What Are Signals, and How Do Cells Respond to Them?

Both prokaryotic and eukaryotic cells process information from their environments. This information can be in the form of a physical stimulus, such as the light reaching your eyes as you read this book, or chemicals that bathe a cell, such as lactose in a bacterial growth medium. It may come from outside the organism, such as the scent of a female moth seeking a mate in the dark, or from a neighboring cell within the organism, such as in the heart, where thousands of muscle cells contract in unison by transmitting signals to one another.

Of course, the mere presence of a signal does not mean that a cell will respond to it, just as you do not pay close attention to every image in your environment as you study. To respond to a signal, the cell must have a specific receptor that can detect it. This section provides examples of some types of cellular signals and one model of *signal transduction*. A **signal transduction pathway** is a sequence of molecular events and chemical reactions that lead to a cell’s response to a signal. After discussing signals in this section, we will consider their receptors in Section 7.2.

#### Cells receive signals from the physical environment and from other cells

The physical environment is full of signals. Our sense organs allow us to respond to light, odors and tastes (chemical signals), temperature, touch, and sound. Bacteria and protists can respond to minute chemical changes in their environments. Plants respond to light as a signal as well as an energy source. The amount and wavelengths of light reaching a plant’s surface differ from day to night and in direct sunlight versus shade. These variations act as signals that affect plant growth and reproduction. Some plants also respond to temperature: when the weather gets cold, they may respond either by becoming tolerant to cold or by accelerating flowering.

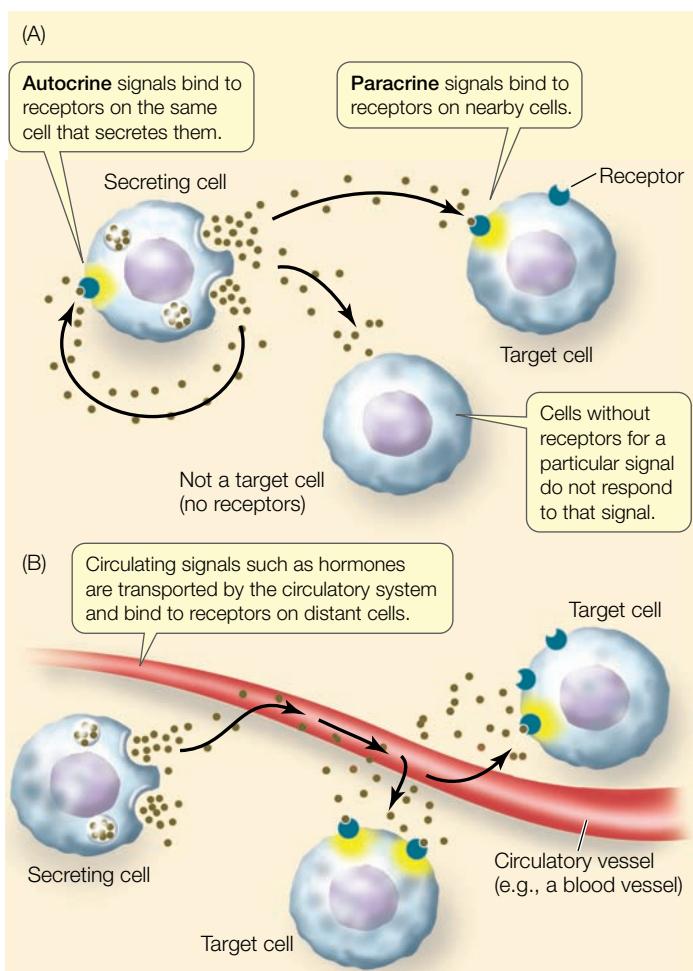
A cell deep inside a large multicellular organism is far away from the exterior environment. Such a cell’s environment consists of other cells and extracellular fluids. Cells receive their nutrients from, and pass their wastes into, extracellular fluids. Cells also receive signals—mostly chemical signals—from their extracellular fluid environment. Most of these chemical signals come from other cells, but they can also come from the environment via the digestive and respiratory systems. And cells can respond to changes in the extracellular concentrations of cer-

tain chemicals, such as  $\text{CO}_2$  and  $\text{H}^+$ , which are affected by the metabolic activities of other cells.

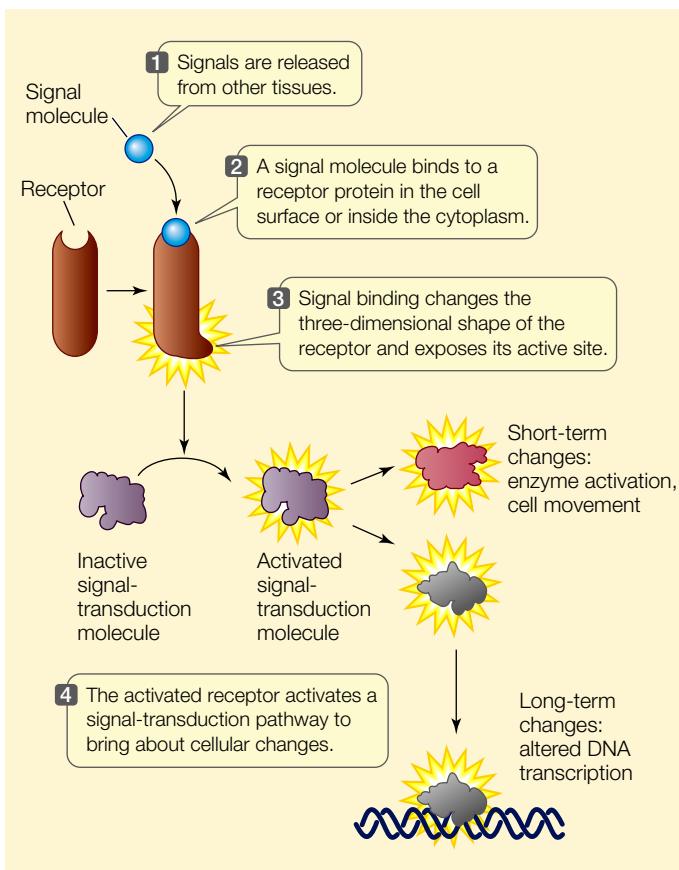
Inside a large multicellular organism, chemical signals made by the body itself reach a target cell by local diffusion or by circulation within the blood. These signals are usually in tiny concentrations (as low as  $10^{-10} \text{ M}$ ) (see Chapter 2 for an explanation of *molar* concentrations). **Autocrine** signals diffuse to and affect the cells that make them; for example, part of the reason many tumor cells reproduce uncontrollably is because they self-stimulate cell division by making their own division signals. **Paracrine** signals diffuse to and affect nearby cells; an example is a neurotransmitter made by one nerve cell that diffuses to an adjacent cell and stimulates it. (**Figure 7.1A**). Signals to distant cells called hormones travel through the circulatory system (**Figure 7.1B**).

### A signal transduction pathway involves a signal, a receptor, and responses

For the information from a signal to be transmitted to a cell, the target cell must be able to receive or sense the signal and respond to it, and the response must have some effect on the func-



**7.1 Chemical Signaling Systems** (A) A signal molecule can diffuse to act on the cell that produces it, or on a nearby cell. (B) Many signals act on distant cells and must be transported by the organism's circulatory system.



**7.2 A Signal Transduction Pathway** This general pathway is common to many cells and situations. The ultimate effects on the cell are either short-term or long-term molecular changes, or both.

tion of the cell. In a multicellular organism, all cells may receive chemical signals that are circulated in the blood, such as the peptides oxytocin and vasopressin that are released following mating in voles (see the opening of this chapter), but most body cells are not capable of responding to the signals. Only the cells with the necessary receptors can respond.

The kinds of responses vary greatly depending on the signal and the target cell. Just a few examples are: a skin cell initiating cell division to heal a wound; a cell moving to a new location in the embryo to form a tissue; a cell releasing enzymes to digest food; a plant cell loosening bonds that hold its cell wall polymers together so that it can expand; and a cell in the eye sending messages to the brain about the book you are reading. A signal transduction pathway involves a signal, a receptor, and a response (**Figure 7.2**).

Let's look at an example of such a pathway in the bacterium *Escherichia coli* (*E. coli*). Follow the features of this pathway in general (see Figure 7.2) and in particular (**Figure 7.3**).

**SIGNAL** As a prokaryotic cell, a bacterium is very sensitive to changes in its environment. One thing that can change is the total solute concentration (osmotic concentration—see Section 6.3) in the environment surrounding the cell. In the mammalian intestine where *E. coli* lives, the solute concentration around

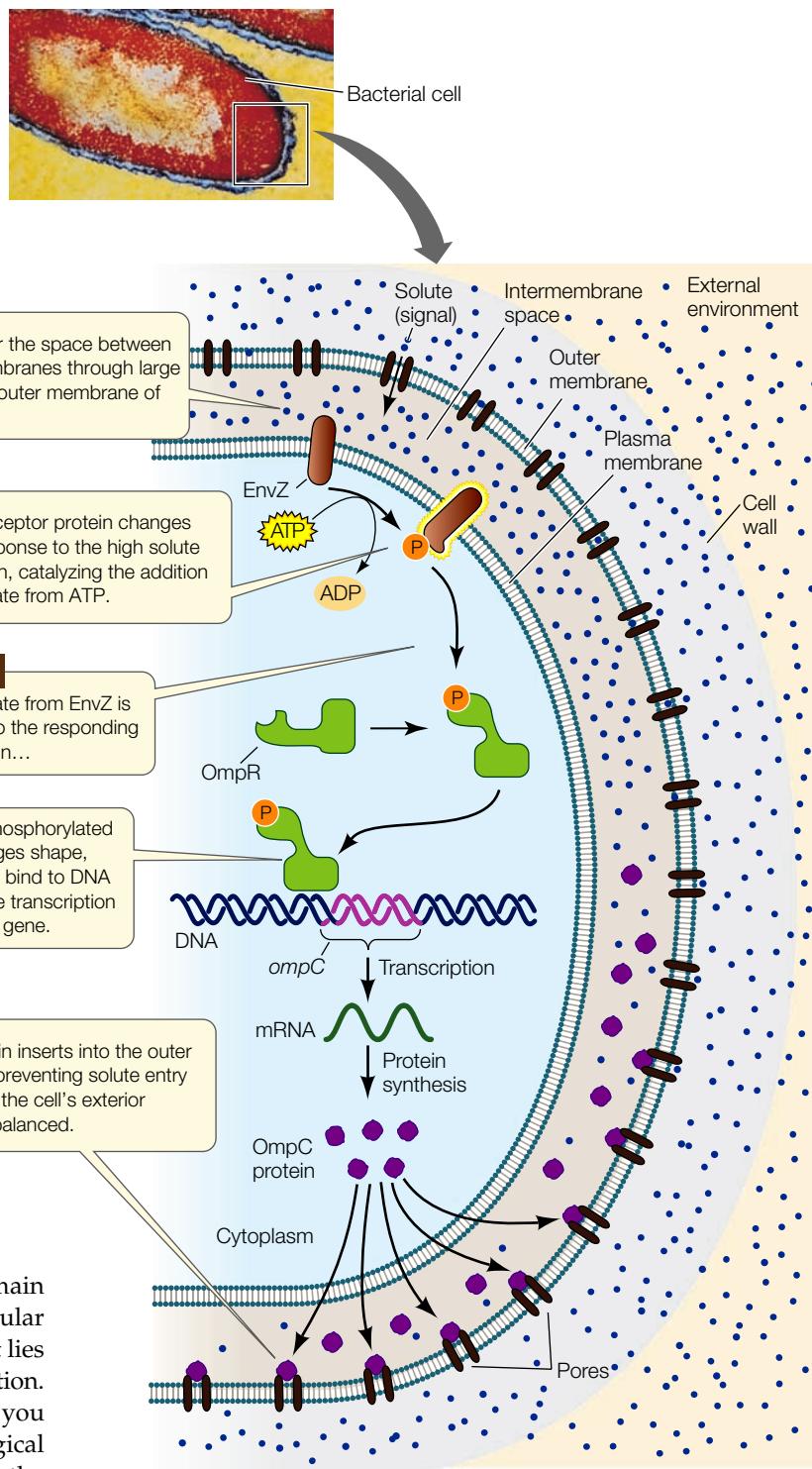
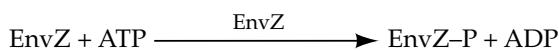
**7.3 A Model Signal Transduction Pathway** *E. coli* responds to the signal of an increase in solute concentration in its environment. The basic steps of such a signal transduction pathway occur in all living organisms.

**yourBioPortal.com**  
GO TO Web Activity 7.1 • Signal Transduction

the bacterium often rises far above the solute concentration inside the cell. A fundamental characteristic of all living cells is that they maintain a constant internal environment, or homeostasis. To do this, the bacterium must perceive and quickly respond to this environmental signal (Figure 7.3, step 1). The cell does this by a signal transduction pathway involving two major components: a receptor and a responder.

**RECEPTOR** The *E. coli* receptor protein for changes in solute concentration is called EnvZ. EnvZ is a transmembrane protein that extends across the bacterium's plasma membrane into the space between the plasma membrane and the highly porous outer membrane, which forms a complex with the cell wall. When the solute concentration of the extracellular environment rises, so does the solute concentration in the space between the two membranes. This change in the aqueous solution causes the part of the receptor protein that sticks out into the intermembrane space to undergo a change in conformation (its three-dimensional shape).

The conformational change in the intermembrane domain (*a domain* is a sequence of amino acids folded into a particular shape) causes a conformational change in the domain that lies in the cytoplasm and initiates the events of signal transduction. The cytoplasmic domain of EnvZ can act as an *enzyme*. As you will see in more detail in Chapter 8, an enzyme is a biological catalyst that greatly speeds up a chemical reaction, and the active site is the region where the reaction actually takes place. The conformational change in EnvZ exposes an active site that was previously buried within the protein, so that EnvZ becomes a **protein kinase**—an enzyme that catalyzes the transfer of a phosphate group from ATP to another molecule. EnvZ transfers the phosphate group to one of its own histidine amino acids. In other words, EnvZ *phosphorylates* itself (Figure 7.3, step 2).



What does phosphorylation do to a protein? As discussed in Section 3.2, proteins can have both hydrophilic regions (which tend to interact with water on the outside of the protein macromolecule) and hydrophobic regions (which tend to interact with one another on the inside of the macromolecule). These regions are important in giving a protein its three-dimensional shape. Phosphate groups are charged, so an amino acid with such a group tends to be on the outside of the protein. Thus

phosphorylation leads to a change in the shape and function of a protein by changing its charge.

**RESPONDER** A **responder** is the second component of a signal transduction pathway. The charged phosphate group added to the histidine of the EnvZ protein causes its cytoplasmic domain to change its shape again. It now binds to a second protein, OmpR, and transfers the phosphate to it. In turn, this phosphorylation changes the shape of OmpR (**Figure 7.3, step 3**). The change in the responder is a key event in signaling, for three reasons:

- The signal on the outside of the cell has now been *transduced* to a protein that lies totally within the cell's cytoplasm.
- The altered responder can *do something*. In the case of the phosphorylated OmpR, that "something" is to bind to DNA to alter the expression of many genes; in particular, it increases the expression of the protein OmpC. This binding begins the final phase of the signaling pathway: the effect of the signal, which is an alteration in cell function.
- The signal has been *amplified*. Because a single enzyme can catalyze the conversion of many substrate molecules, one EnvZ molecule alters the structure of many OmpR molecules.

Phosphorylated OmpR has the correct three-dimensional structure to bind to the *ompC* DNA, resulting in an increase in the transcription of that gene. This results in the production of OmpC protein, which enables the cell to respond to the increase in osmotic concentration in its environment (**Figure 7.3, step 4**). The OmpC protein is inserted into the outer membrane of the cell, where it blocks pores and prevents solutes from entering the intermembrane space. As a result, the solute concentration in the intermembrane space is lowered, and homeostasis is restored. Thus the EnvZ-OmpR signal transduction pathway allows the *E. coli* cell to function just as if the external environment had a normal solute concentration.

Many of the elements that we have highlighted in this prokaryotic signal transduction pathway also exist in the signal transduction pathways of eukaryotic organisms. A typical eukaryotic signal transduction pathway has the following general steps:

- A receptor protein changes its conformation upon interaction with a signal. This receptor protein may or may not be in a membrane.
- A conformational change in the receptor protein activates its protein kinase activity, resulting in the transfer of a phosphate group from ATP to a target protein.
- This phosphorylation alters the function of a responder protein.
- The signal is amplified.
- A protein that binds to DNA is activated.
- The expression of one or more specific genes is turned on or off.
- Cell activity is altered.

## 7.1 RECAP

Cells are constantly exposed to molecular signals that can come from the external environment or from within the body of a multicellular organism. To respond to a signal, the cell must have a specific receptor that detects the signal and activates some cellular response.

- What are the differences between an autocrine signal, a paracrine signal, and a hormone? See p. 130 and **Figure 7.1**
- Describe the three components in a cell's response to a signal. See pp. 130–132 and **Figure 7.2**
- What are the elements of signal transduction that are described at the close of this section?

The general features of signal transduction pathways described in this section will recur in more detail throughout the chapter. First let's consider more closely the nature of the receptors that bind signal molecules.

## 7.2 How Do Signal Receptors Initiate a Cellular Response?

Any given cell in a multicellular organism is bombarded with many signals. However, it responds to only some of them, because no cell makes receptors for all signals. A receptor protein that binds to a chemical signal does so very specifically, in much the same way that a membrane transport protein binds to the substance it transports. This *specificity* of binding ensures that only those cells that make a specific receptor will respond to a given signal.

### Receptors have specific binding sites for their signals

A specific chemical signal molecule fits into a three-dimensional site on its protein receptor (**Figure 7.4A**). A molecule that binds to a receptor site on another molecule in this way is called a **ligand**. Binding of the signaling ligand causes the receptor protein to change its three-dimensional shape, and that conformational change initiates a cellular response. The ligand does not contribute further to this response. In fact, the ligand is usually not metabolized into a useful product; its role is purely to "knock on the door." (This is in sharp contrast to the enzyme–substrate interaction, which is described in Chapter 8. The whole purpose of that interaction is to change the substrate into a useful product.)

Receptors bind to their ligands according to chemistry's *law of mass action*:



This means that the binding is reversible, although for most ligand–receptor complexes, the equilibrium point is far to the right—that is, binding is favored. Reversibility is important, however, because if the ligand were never released, the receptor would be continuously stimulated.

**7.4 A Signal and Its Receptor** (A) The adenosine 2A receptor occurs in the human brain, where it is involved in inhibiting arousal. (B) Adenosine is the normal ligand for the receptor. Caffeine has a similar structure to that of adenosine and can act as an antagonist that binds the receptor and prevents its normal functioning.

An inhibitor (or *antagonist*) can also bind to a receptor protein, instead of the normal ligand. There are both natural and artificial antagonists of receptor binding. For example, many substances that alter human behavior bind to specific receptors in the brain, and prevent the binding of the receptors' specific ligands. An example is caffeine, which is probably the world's most widely consumed stimulant. In the brain, the nucleoside adenosine acts as a ligand that binds to a receptor on nerve cells, initiating a signal transduction pathway that reduces brain activity, especially arousal. Because caffeine has a similar molecular structure to that of adenosine, it also binds to the adenosine receptor (**Figure 7.4B**). But in this case binding does not initiate a signal transduction pathway. Rather, it "ties up" the receptor, preventing adenosine binding and thereby allowing nerve cell activity and arousal.

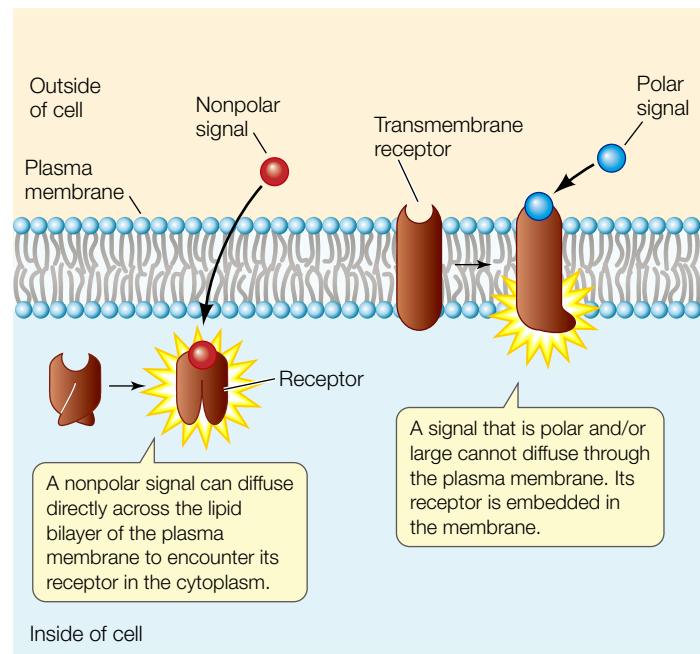
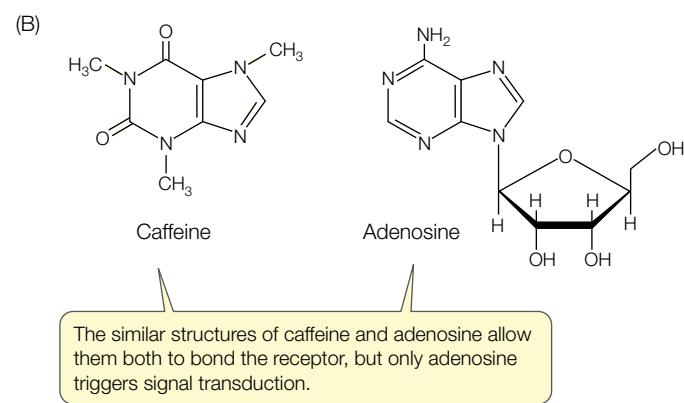
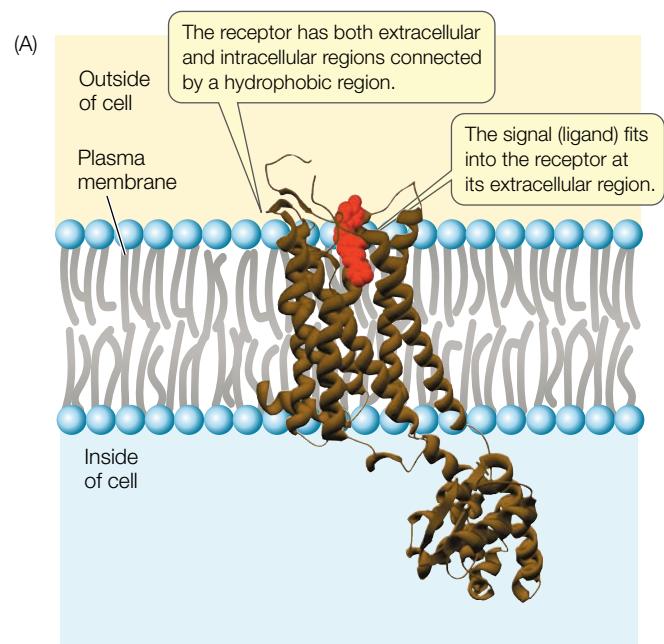
### Receptors can be classified by location and function

The chemistry of ligand signals is quite variable, but they can be divided into two groups, based on whether or not they can diffuse through membranes. Correspondingly, a receptor can be classified by its location in the cell, which largely depends on the nature of its ligand (**Figure 7.5**):

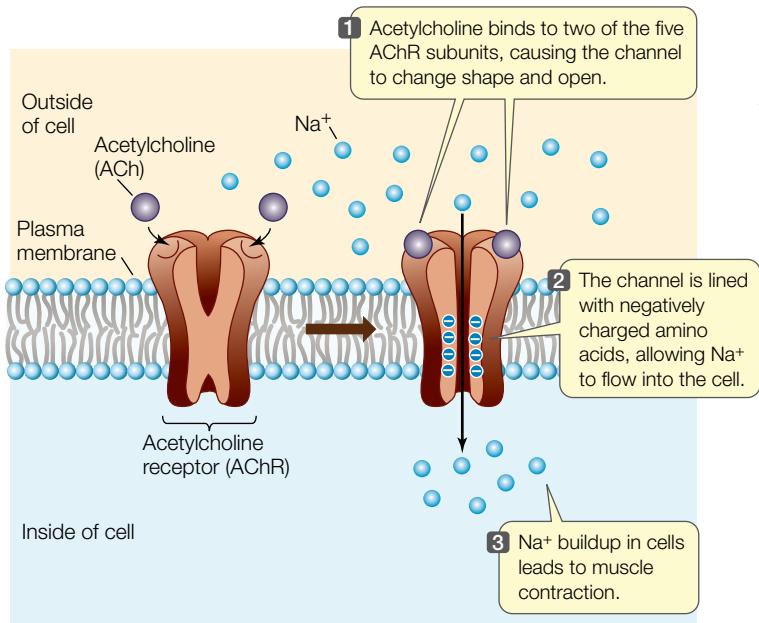
- **Cytoplasmic receptors:** Small or nonpolar ligands can diffuse across the nonpolar phospholipid bilayer of the plasma membrane and enter the cell. Estrogen, for example, is a lipid-soluble steroid hormone that can easily diffuse across the plasma membrane; it binds to a receptor in the cytoplasm.
- **Membrane receptors:** Large or polar ligands cannot cross the lipid bilayer. Insulin, for example, is a protein hormone that cannot diffuse through the plasma membrane; instead, it binds to a transmembrane receptor with an extracellular binding domain.

In complex eukaryotes such as mammals and higher plants, there are three well-studied categories of plasma membrane receptors that are grouped according to their functions: ion channels, protein kinase receptors, and G protein-linked receptors.

**ION CHANNEL RECEPTORS** As described in Section 6.3, the plasma membranes of many types of cells contain gated **ion channels** for ions such as  $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Ca}^{2+}$ , or  $\text{Cl}^-$  to enter or leave the cell (see Figure 6.11). The gate-opening mechanism is an alteration in the three-dimensional shape of the channel protein upon ligand binding; thus these proteins function as receptors. Each type of ion channel has its own signal, and these include sensory stimuli such as light, sound, and electric charge

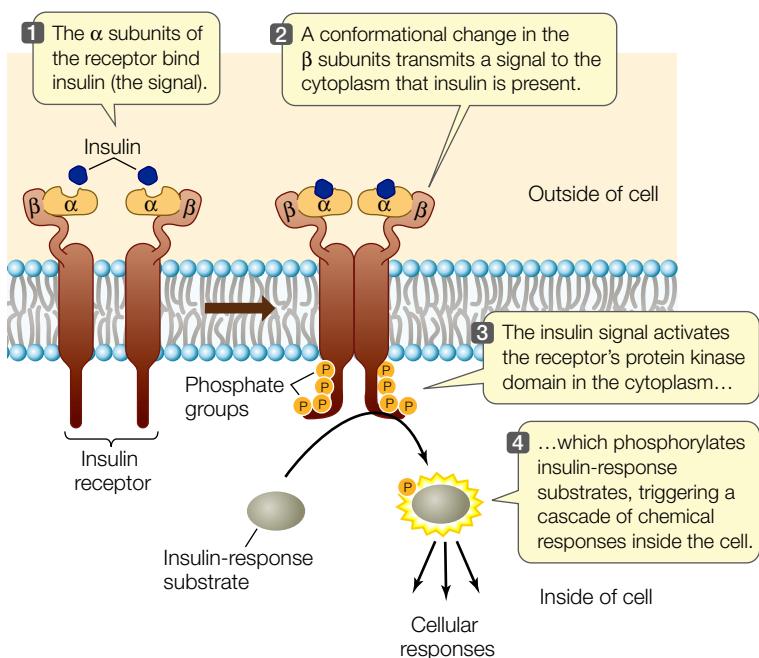


**7.5 Two Locations for Receptors** Receptors can be located in the cytoplasm or in the plasma membrane of the cell.



differences across the plasma membrane, as well as chemical ligands such as hormones and neurotransmitters.

The *acetylcholine receptor*, which is located in the plasma membrane of skeletal muscle cells, is an example of a gated ion channel. This receptor protein is a sodium channel that binds the ligand acetylcholine, which is a neurotransmitter—a chemical signal released from neurons (nerve cells) (Figure 7.6). When two molecules of acetylcholine bind to the receptor, it opens for about a thousandth of a second. That is enough time for  $\text{Na}^+$ , which is more concentrated outside the cell than inside, to rush into the cell, moving in response to both concentration and electrical potential gradients. The change in  $\text{Na}^+$  concentration in the cell initiates a series of events that result in muscle contraction.



**7.6 A Gated Ion Channel** The acetylcholine receptor (AChR) is a ligand-gated ion channel for sodium ions. It is made up of five polypeptide subunits. When acetylcholine molecules (ACh) bind to two of the subunits, the gate opens and  $\text{Na}^+$  flows into the cell. This channel helps regulate membrane polarity (see Chapter 6).

**PROTEIN KINASE RECEPTORS** Like the EnvZ receptor of *E. coli*, some eukaryotic receptor proteins become protein kinases when they are activated. They catalyze the phosphorylation of themselves and/or other proteins, thus changing their shapes and therefore their functions.

The receptor for insulin is an example of a protein kinase receptor. Insulin is a protein hormone made by the mammalian pancreas. Its receptor has two copies each of two different polypeptide subunits (Figure 7.7). When insulin binds to the receptor, the receptor becomes activated and able to phosphorylate itself and certain cytoplasmic proteins that are appropriately called *insulin response substrates*. These proteins then initiate many cellular responses, including the insertion of glucose transporters (see Figure 6.14) into the plasma membrane.

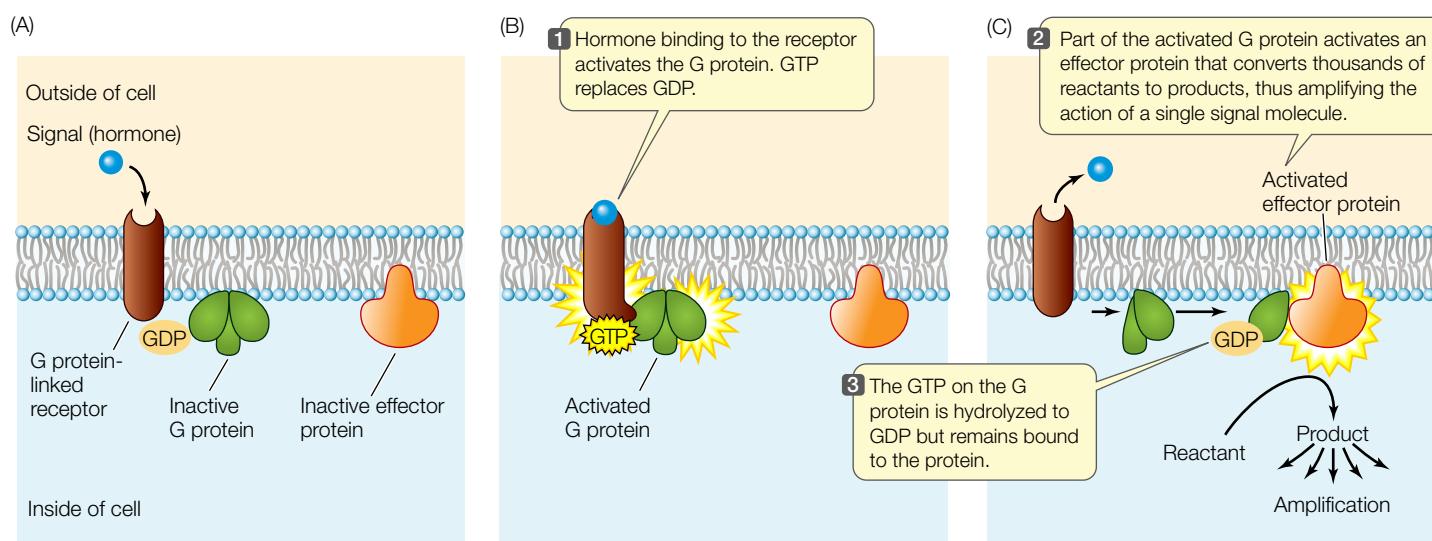
**G PROTEIN-LINKED RECEPTORS** A third category of eukaryotic plasma membrane receptors is the G protein-linked receptors, also referred to as the seven transmembrane domain receptors. This descriptive name identifies a fascinating group of receptors, each of which is composed of a single protein with seven transmembrane domains. These seven domains pass through the phospholipid bilayer and are separated by short loops that extend either outside or inside the cell. Ligand binding on the extracellular side of the receptor changes the shape of its cytoplasmic region, exposing a site that binds to a mobile membrane protein called a **G protein**. The G protein is partially inserted into the lipid bilayer and partially exposed on the cytoplasmic surface of the membrane.

Many G proteins have three polypeptide subunits and can bind three different molecules (Figure 7.8A):

- The receptor
- GDP and GTP (guanosine diphosphate and triphosphate, respectively; these are nucleoside phosphates like ADP and ATP)
- An effector protein

When the G protein binds to an activated receptor protein, GDP is exchanged for GTP (Figure 7.8B). At the same time, the ligand is usually released from the extracellular side of the receptor. GTP binding causes a conformational change in the G protein. The GTP-bound subunit then separates from the rest of the protein, diffusing in the plane of the phospholipid bilayer until it encounters an **effector protein** to which it can bind. An effector protein is just what its name implies: it causes an effect in the cell. The binding of the GTP-bearing G protein

**7.7 A Protein Kinase Receptor** The mammalian hormone insulin binds to a receptor on the outside surface of the cell and initiates a response.



**7.8 A G Protein-Linked Receptor** The G protein is an intermediary between the receptor and an effector.

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subunit activates the effector—which may be an enzyme or an ion channel—thereby causing changes in cell function (**Figure 7.8C**).

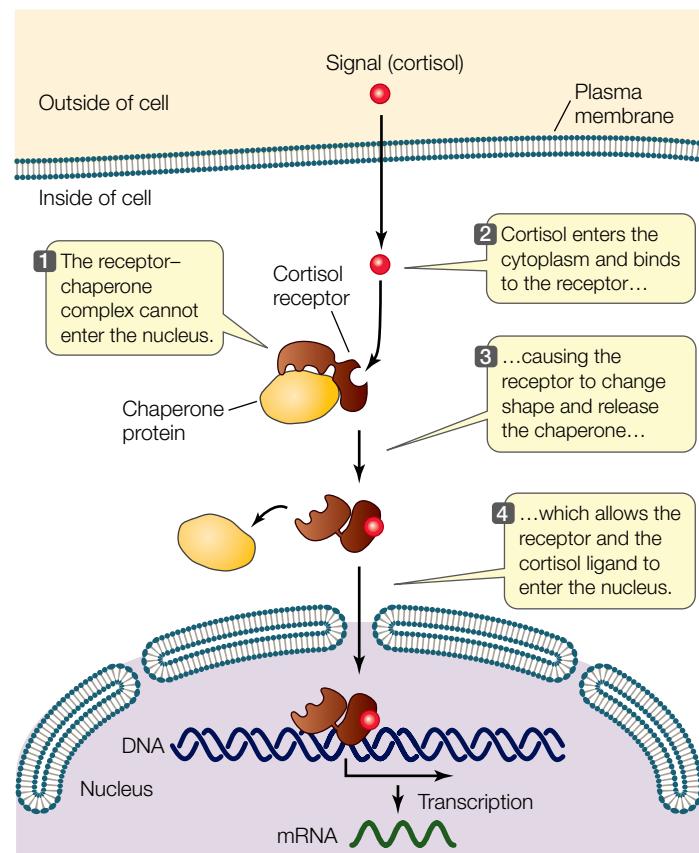
After activation of the effector protein, the GTP on the G protein is hydrolyzed to GDP. The now inactive G protein subunit separates from the effector protein and diffuses in the membrane to collide with and bind to the other two G protein subunits. When the three components of the G protein are reassembled, the protein is capable of binding again to an activated receptor. After binding, the activated receptor exchanges the GDP on the G protein for a GTP, and the cycle begins again.

There are variations in all three G protein subunits, giving different G protein complexes different functions. A G protein can either activate or inhibit an effector protein. An example in humans of an *activating* response involves the receptor for epinephrine (adrenaline), which is a hormone made by the adrenal gland in response to stress or heavy exercise. In heart muscle, this hormone binds to its G protein-linked receptor, activating a G protein. The GTP-bound subunit then activates a membrane-bound enzyme to produce a small molecule, cyclic adenosine monophosphate (cAMP). This molecule, in turn, has many effects on the cell (as we will see below), including the mobilization of glucose for energy and muscle contraction.

G protein-mediated *inhibition* occurs when the same hormone, epinephrine, binds to its receptor in the smooth muscle cells surrounding blood vessels lining the digestive tract. Again, the epinephrine-bound receptor changes its shape and activates a G protein, and the GTP-bound subunit binds to a target enzyme. But in this case, the enzyme is inhibited instead of being activated. As a result, the muscles relax and the blood vessel diameter increases, allowing more nutrients to be carried away from the digestive system to the rest of the body. Thus the same signal and signaling mechanism can have different consequences in different cells, depending on the presence of specific receptor and effector molecules.

**CYTOPLASMIC RECEPTORS** **Cytoplasmic receptors** are located inside the cell and bind to signals that can diffuse across the

plasma membrane. Binding to the signaling ligand causes the receptor to change its shape so that it can enter the cell nucleus, where it affects expression of specific genes. But this general view is somewhat simplified. The receptor for the steroid hormone cortisol, for example, is normally bound to a chaperone protein, which blocks it from entering the nucleus. Binding of the hormone causes the receptor to change its shape so that the chaperone is released (**Figure 7.9**). This release allows the



**7.9 A Cytoplasmic Receptor** The receptor for cortisol is bound to a chaperone protein. Binding of the signal to the receptor releases the chaperone and allows the ligand–receptor complex to enter the cell's nucleus, where it binds to DNA. Changes in DNA transcription are long-term in comparison to the more immediate changes in enzyme activity observed in other pathways (see Figure 7.20).

receptor to fold into an appropriate conformation for entering the nucleus and initiating DNA transcription.

## 7.2 RECAP

Receptors are proteins that bind, or are changed by, specific signals or ligands; the changed receptor initiates a response in the cell. These receptors may be at the plasma membrane or inside the cell.

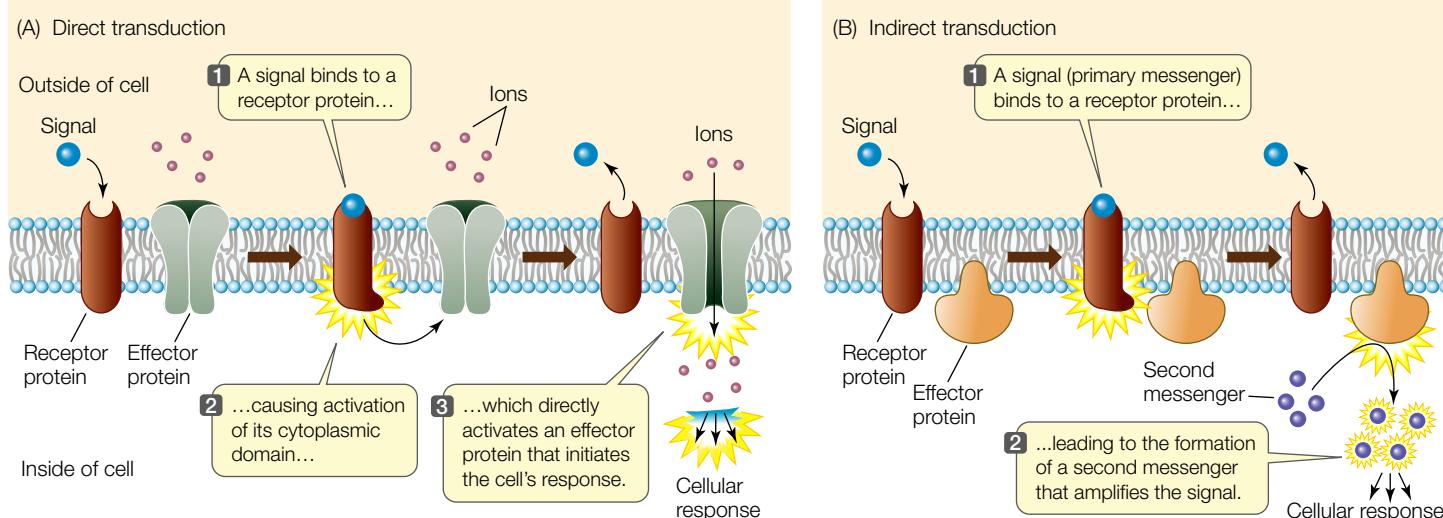
- What are the nature and importance of specificity in the binding of receptors to their particular ligands? **See pp. 132–133**
- What are three important categories of plasma membrane receptors seen in complex eukaryotes? **See pp. 133–134 and Figures 7.6, 7.7, and 7.8**

Now that we have discussed signals and receptors, let's examine the characteristics of the molecules (*transducers*) that mediate between the receptor and the cellular response.

## 7.3 How Is the Response to a Signal Transduced through the Cell?

As we have just seen with epinephrine, the same signal may produce different responses in different tissues. These different responses to the same signal–receptor complex are mediated by the components of different signal transduction pathways. Signal transduction may be either direct or indirect:

- **Direct transduction** is a function of the receptor itself and occurs at the plasma membrane. The interaction between the signal (primary messenger) and receptor results in the cellular response. (Figure 7.10A).
- In **indirect transduction**, which is more common, another molecule termed a **second messenger** diffuses into the cytoplasm and mediates additional steps in the signal transduction pathway (Figure 7.10B).



In both cases, the signal can initiate a *cascade* of events, in which proteins interact with other proteins until the final responses are achieved. Through such a cascade, an initial signal can be both amplified and distributed to cause several different responses in the target cell.

### A protein kinase cascade amplifies a response to ligand binding

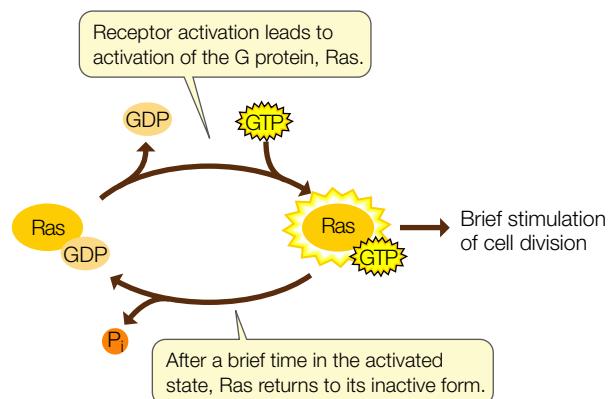
We have seen that when a signal binds to a protein kinase receptor, the receptor's conformation changes, exposing a protein kinase active site on the receptor's cytoplasmic domain. The protein kinase then catalyzes the phosphorylation of target proteins. This process is an example of direct signal transduction, because the amplifying enzyme is the receptor itself. Protein kinase receptors are important in binding signals called growth factors that stimulate cell division in both plants and animals.

A complete signal transduction pathway that occurs after a protein kinase receptor binds a growth factor was discovered in studies on a cell that went wrong. Many human bladder cancers contain an abnormal form of a protein called Ras (so named because a similar protein was previously isolated from a *rat* sarcoma tumor). Investigations of these bladder cancers showed that Ras was a G protein, and the abnormal form was always active because it was permanently bound to GTP, and thus caused continuous cell division (Figure 7.11). If this abnormal form of Ras was inhibited, the cells stopped dividing. This discovery has led to a major effort to develop specific Ras inhibitors for cancer treatment.

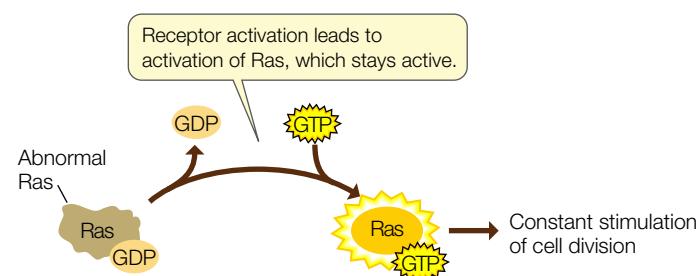
Other cancers have abnormalities in different aspects of signal transduction. Biologists have compared the defects in these cells with the normal signaling process in non-cancerous cells, and thus worked out the entire signaling pathway. It is an ex-

**7.10 Direct and Indirect Signal Transduction** (A) All the events of direct transduction occur at or near the receptor (in this case, at the plasma membrane). (B) In indirect transduction, a second messenger mediates the events inside the cell. The signal is considered to be the first messenger.

## (A) Normal cell



## (B) Cancer cell



**7.11 Signal Transduction and Cancer** (A) Ras is a G protein that regulates cell division. (B) In some tumors, the Ras protein is permanently active, resulting in uncontrolled cell division.

ample of a more general phenomenon, called a **protein kinase cascade**, where one protein kinase activates the next, and so on (Figure 7.12). Such cascades are key to the external regulation of many cellular activities. Indeed, the eukaryotic genome codes for hundreds, even thousands, of such kinases.

Protein kinase cascades are useful signal transducers for four reasons:

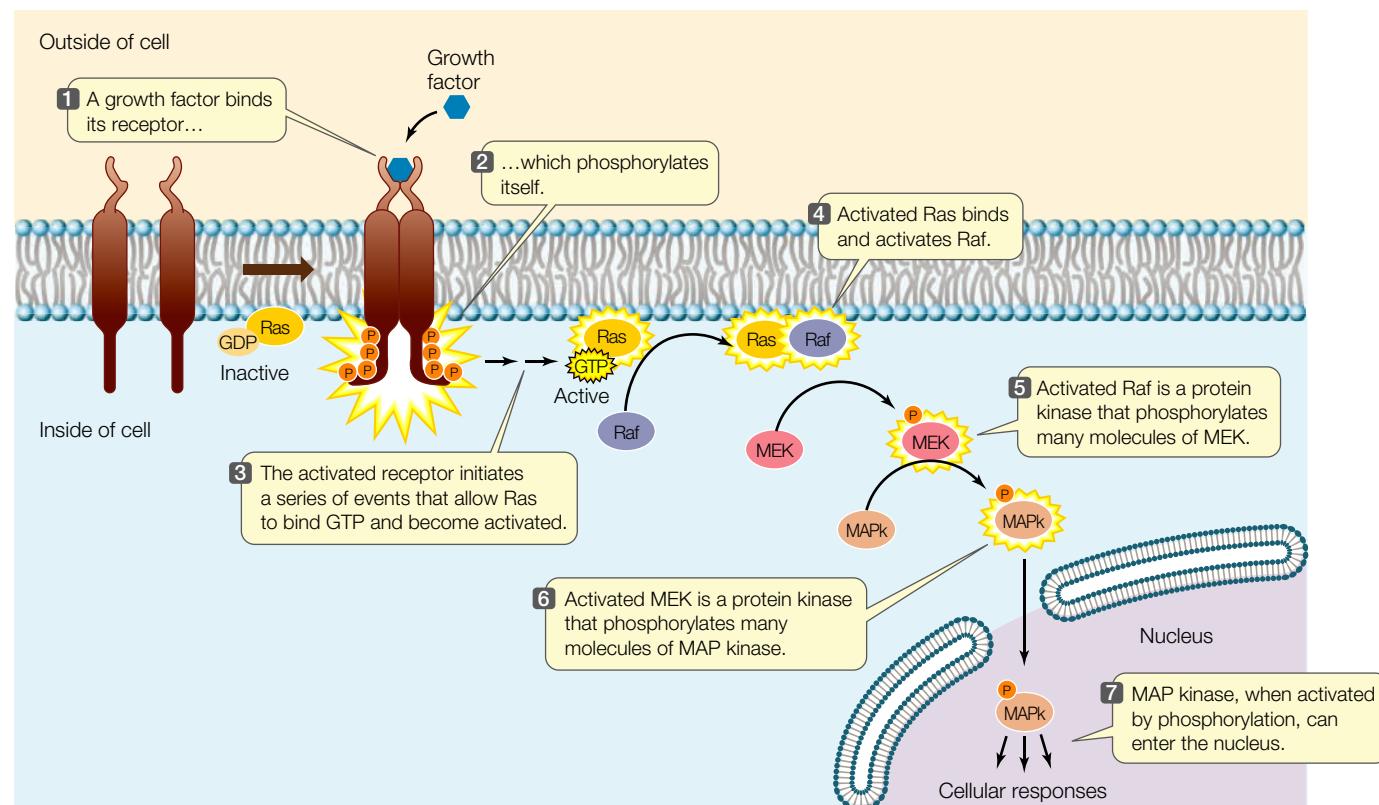
- At each step in the cascade of events, the signal is *amplified*, because each newly activated protein kinase is an enzyme that can catalyze the phosphorylation of many target proteins.
- The information from a signal that originally arrived at the plasma membrane is *communicated* to the nucleus.
- The multitude of steps provides some *specificity* to the process.
- Different target proteins at each step in the cascade can provide *variation* in the response.

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### Second messengers can stimulate protein kinase cascades

As we have just seen, protein kinase receptors initiate protein kinase cascades right at the plasma membrane. However, the stimulation of events in the cell is more often indirect. In a series of clever experiments, Earl Sutherland and his colleagues at Case Western Reserve University discovered that a small water-solu-



**7.12 A Protein Kinase Cascade** In a protein kinase cascade, a series of proteins are sequentially activated.

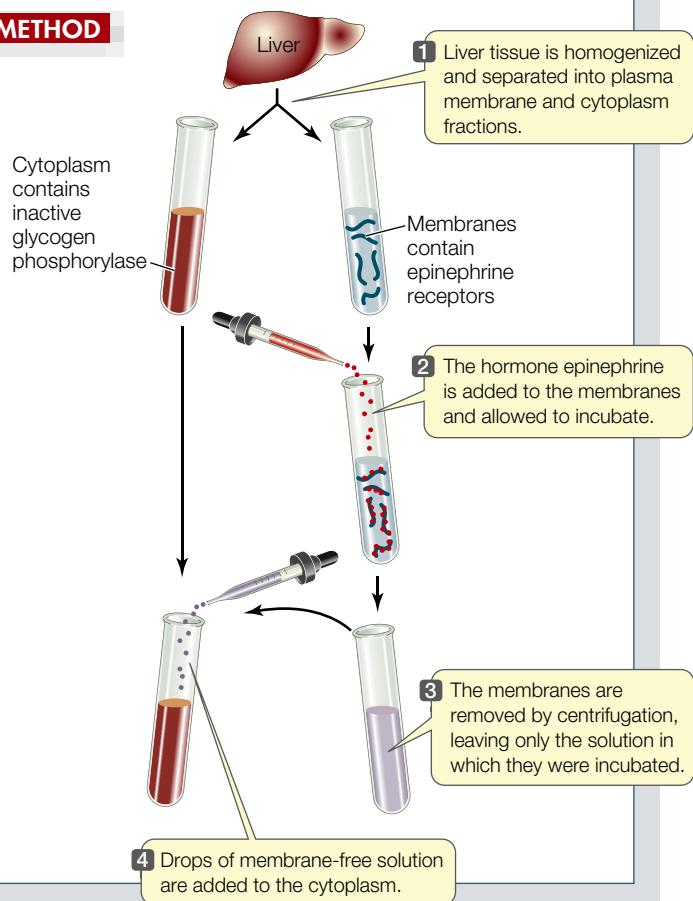
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## 7.13 The Discovery of a Second Messenger

Glycogen phosphorylase is activated in liver cells after epinephrine binds to a membrane receptor. Sutherland and his colleagues observed that this activation could occur *in vivo* only if fragments of the plasma membrane were present. They designed experiments to show that a second messenger caused the activation of glycogen phosphorylase.

**HYPOTHESIS** A second messenger mediates between receptor activation at the plasma membrane and enzyme activation in the cytoplasm.

### METHOD



### RESULTS

Active glycogen phosphorylase is present in the cytoplasm.

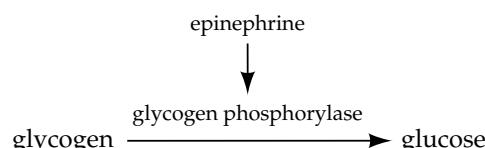
### CONCLUSION

A soluble second messenger, produced by hormone-activated membranes, is present in the solution and activates enzymes in the cytoplasm.

**FURTHER INVESTIGATION:** The soluble molecule produced in this experiment was later identified as cAMP. How would you show that cAMP, and not ATP, is the second messenger in this system?

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ble chemical messenger mediates the cytoplasmic events initiated by a plasma membrane receptor. These researchers were investigating the activation of the liver enzyme glycogen phosphorylase by the hormone epinephrine. The enzyme is released when an animal faces life-threatening conditions and needs energy fast for the fight-or-flight response. Glycogen phosphorylase catalyzes the breakdown of glycogen stored in the liver so that the resulting glucose molecules can be released to the blood. The enzyme is present in the liver cell cytoplasm, but is inactive except in the presence of epinephrine.

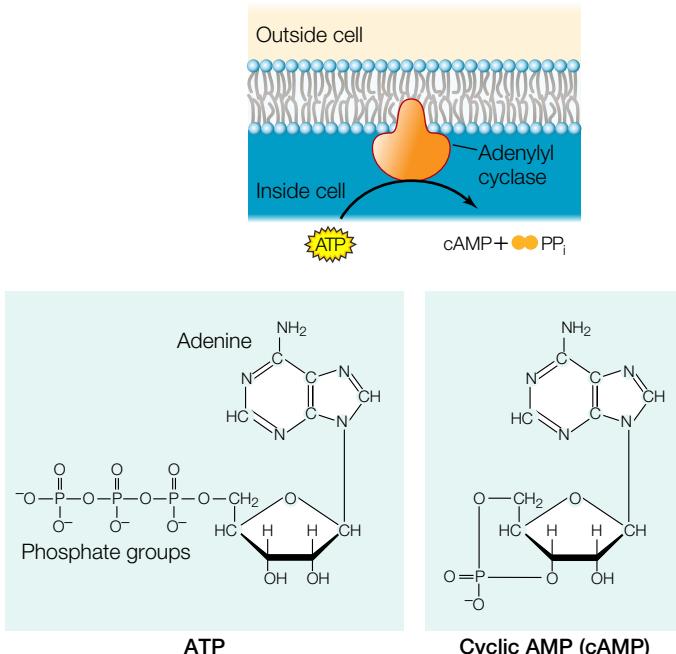


The researchers found that epinephrine could activate glycogen phosphorylase in liver cells that had been broken open, but only if the entire cell contents, including plasma membrane fragments, were present. Under these circumstances epinephrine bound to the plasma membranes, but the active phosphorylase was present in the solution. The researchers hypothesized that there must be a second “messenger” that transmits the signal of epinephrine (the “first messenger,” which binds to a receptor at the plasma membrane) to the phosphorylase (in the cytoplasm). To investigate the production of this messenger, they separated plasma membrane fragments from the cytoplasms of broken liver cells and followed the sequence of steps described in **Figure 7.13**. This experiment confirmed their hypothesis that hormone binding to the membrane receptor causes the production of a small, water-soluble molecule that diffuses into the cytoplasm and activates the enzyme. Later, this second messenger was identified as **cyclic AMP (cAMP)**. (We will describe the signal transduction pathway leading to the fight-or-flight response in more detail in Section 7.4.) Second messengers do not have enzymatic activity; rather, they act to regulate target enzymes (see Chapter 8).

A second messenger is a small molecule that mediates later steps in a signal transduction pathway after the first messenger—the signal or ligand—binds to its receptor. In contrast to the specificity of receptor binding, second messengers allow a cell to respond to a single event at the plasma membrane with *many events inside the cell*. Thus, second messengers serve to amplify the signal—for example, binding of a single epinephrine molecule leads to the production of many molecules of cAMP, which then activate many enzyme targets by binding to them noncovalently. In the case of epinephrine and the liver cell, glycogen phosphorylase is just one of several enzymes that are activated.

Cyclic AMP is a second messenger in a wide variety of signal transduction pathways. An effector protein, adenylyl cyclase, catalyzes the formation of cAMP from ATP. Adenylyl cyclase is located on the cytoplasmic surface of the plasma membrane of target cells (**Figure 7.14**). Usually a G protein activates the enzyme after it has itself been activated by a receptor.

Cyclic AMP has two major kinds of targets—ion channels and protein kinases. In many sensory cells, cAMP binds to ion channels and thus opens them. Cyclic AMP may also bind to a



**7.14 The Formation of Cyclic AMP** The formation of cAMP from ATP is catalyzed by adenyl cyclase, an enzyme that is activated by G proteins.

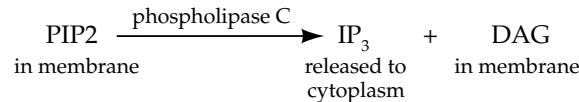
protein kinase in the cytoplasm, activating its catalytic function. A protein kinase cascade (see Figure 7.12) ensues, leading to the final effects in the cell.

### Second messengers can be derived from lipids

In addition to their role as structural components of the plasma membrane, phospholipids are also involved in signal transduction. When certain phospholipids are hydrolyzed into their component parts by enzymes called **phospholipases**, second messengers are formed.

The best-studied examples of lipid-derived second messengers come from the hydrolysis of the phospholipid **phosphatidyl inositol-bisphosphate (PIP2)**. Like all phospholipids, PIP2 has a hydrophobic portion embedded in the plasma membrane: two fatty acid tails attached to a molecule of glycerol, which together form **diacylglycerol**, or **DAG**. The hydrophilic portion of PIP2 is **inositol trisphosphate**, or **IP<sub>3</sub>**, which projects into the cytoplasm.

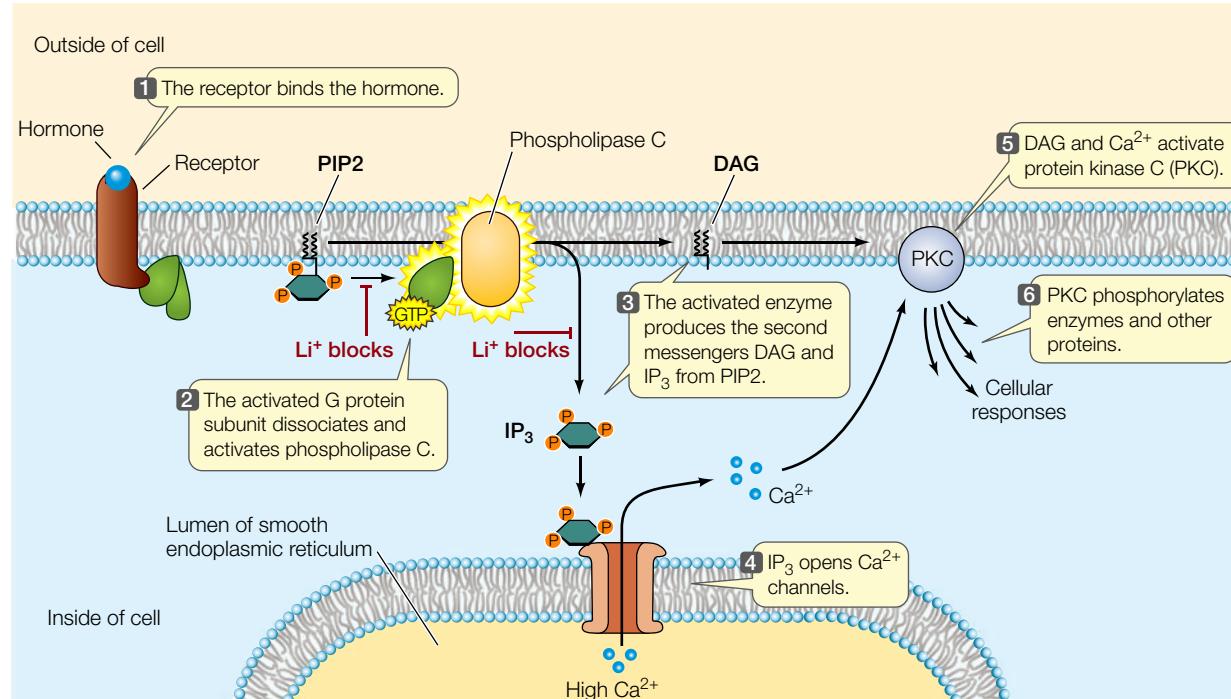
As with cAMP, the receptors involved in this second-messenger system are often G protein-linked receptors. A G protein subunit is activated by the receptor, then diffuses within the plasma membrane and activates phospholipase C, an enzyme that is also located in the membrane. This enzyme cleaves off the IP<sub>3</sub> from PIP2, leaving the diacylglycerol (DAG) in the phospholipid bilayer:



IP<sub>3</sub> and DAG, both second messengers, have different modes of action that build on each other, activating protein kinase C (PKC) (Figure 7.15). PKC refers to a family of protein kinases that can phosphorylate a wide variety of target proteins, leading to a multiplicity of cellular responses that vary depending on the tissue or cell type.

The IP<sub>3</sub>/DAG pathway is apparently a target for the ion lithium (Li<sup>+</sup>), which was used for many years as a psychoactive drug to treat bipolar (manic-depressive) disorder. This serious illness occurs in about 1 in every 100 people. In these patients, an overactive IP<sub>3</sub>/DAG signal transduction pathway in the

**7.15 The IP<sub>3</sub>/DAG Second-Messenger System** Phospholipase C hydrolyzes the phospholipid PIP2 into its components, IP<sub>3</sub> and DAG, both of which are second messengers. Lithium ions (Li<sup>+</sup>) block this pathway and are used to treat bipolar disorder (red type).



brain leads to excessive brain activity in certain regions. Lithium “tones down” this pathway in two ways, as indicated by the red notations in Figure 7.15. It inhibits G protein activation of phospholipase C, and also inhibits the synthesis of IP<sub>3</sub>. The overall result is that brain activity returns to normal.

### Calcium ions are involved in many signal transduction pathways

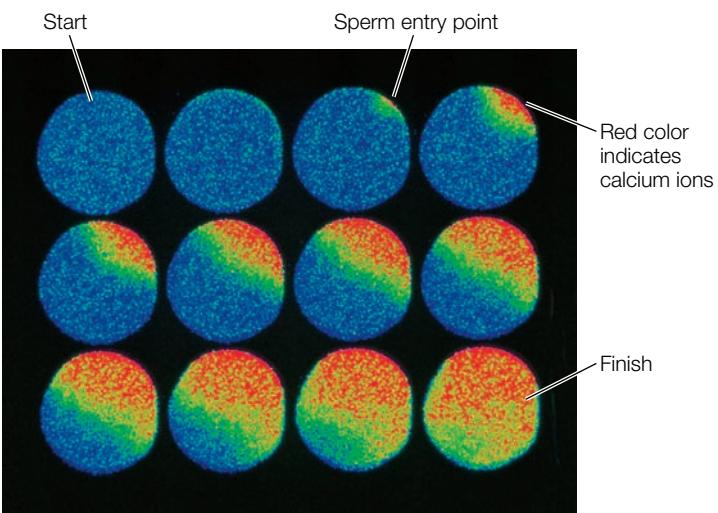
Calcium ions (Ca<sup>2+</sup>) are scarce inside most cells, which have cytosolic Ca<sup>2+</sup> concentrations of only about 0.1 mM. Ca<sup>2+</sup> concentrations outside cells and within the endoplasmic reticulum are usually much higher. Active transport proteins in the plasma and ER membranes maintain this concentration difference by pumping Ca<sup>2+</sup> out of the cytosol. In contrast to cAMP and the lipid-derived second messengers, Ca<sup>2+</sup> cannot be made in order to increase the intracellular Ca<sup>2+</sup> concentration. Instead, Ca<sup>2+</sup> ion levels are regulated via the opening and closing of ion channels, and the action of membrane pumps.

There are many signals that can cause calcium channels to open, including IP<sub>3</sub> (see Figure 7.15). The entry of a sperm into an egg is a very important signal that causes a massive opening of calcium channels, resulting in numerous and dramatic changes that prepare the now fertilized egg for cell divisions and development (Figure 7.16). Whatever the initial signal that causes the calcium channels to open, their opening results in a dramatic increase in cytosolic Ca<sup>2+</sup> concentration, which can increase up to one hundredfold within a fraction of a second. As we saw earlier, this increase activates protein kinase C. In addition, Ca<sup>2+</sup> controls other ion channels and stimulates secretion by exocytosis in many cell types.

### Nitric oxide can act in signal transduction

Most signaling molecules and second messengers are solutes that remain dissolved in either the aqueous or hydrophobic components of cells. It was a great surprise to find that a gas could also be active in signal transduction. Pharmacologist Robert Furchtgott, at the State University of New York in Brooklyn, was investigating the mechanisms that cause the smooth muscles lining blood vessels in mammals to relax, thus allowing more blood to flow to certain organs. The neurotransmitter acetylcholine (see Section 7.2) appeared to stimulate the IP<sub>3</sub>/DAG signal transduction pathway to produce an influx of Ca<sup>2+</sup>, leading to an increase in the level of another second messenger, cyclic guanosine monophosphate (cGMP). Cyclic GMP then binds to a protein kinase, stimulating a protein kinase cascade that leads to muscle relaxation. So far, the pathway seemed to conform to what was generally understood about signal transduction in general.

While this signal transduction pathway seemed to work in intact animals, it did not work on isolated strips of artery tissue. However, when Furchtgott switched to tubular sections of artery, signal transduction did occur. What accounted for the different results between tissue strips and tubular sections? Furchtgott realized that the endothelium, the delicate inner layer of cells lining the blood vessels, was lost during preparation of

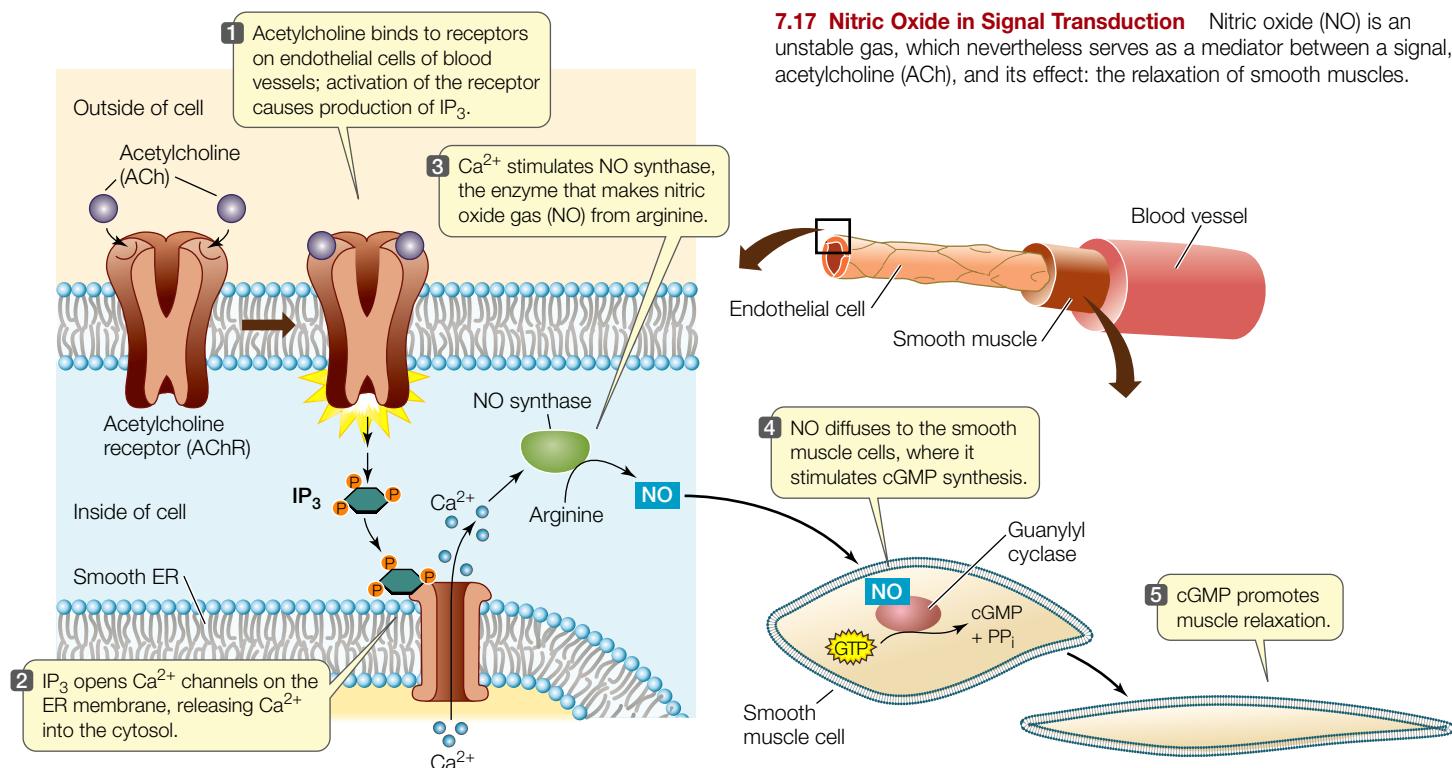


**7.16 Calcium Ions as Second Messengers** The concentration of Ca<sup>2+</sup> can be measured using a dye that fluoresces when it binds the ion. Here, fertilization in a starfish egg causes a rush of Ca<sup>2+</sup> from the environment into the cytoplasm. Areas of high calcium ion concentration are indicated by the red color and the events are photographed at 5-second intervals. Calcium signaling occurs in virtually all animal groups and triggers cell division in fertilized eggs, initiating the development of new individuals.

the tissue strips. He hypothesized that the endothelium was producing some chemical that diffused into the smooth muscle cells and was needed for their response to acetylcholine. However, the substance was not easy to isolate. It seemed to break down quickly, with a half-life (the time in which half of it disappeared) of 5 seconds in living tissue.

Furchtgott's elusive substance turned out to be a gas, **nitric oxide (NO)**, which formerly had been recognized only as a toxic air pollutant! In the body, NO is made from the amino acid arginine by the enzyme NO synthase. When the acetylcholine receptor on the surface of an endothelial cell is activated, IP<sub>3</sub> is released, causing a calcium channel on the ER membrane to open and a subsequent increase in cytosolic Ca<sup>2+</sup>. The Ca<sup>2+</sup> then activates NO synthase to produce NO. NO is chemically very unstable, readily reacting with oxygen gas as well as other small molecules. Although NO diffuses readily, it does not get far. Conveniently, the endothelial cells are close to the smooth muscle cells, where NO acts as a paracrine signal. In smooth muscle, NO activates an enzyme called guanylyl cyclase, catalyzing the formation of cGMP, which in turn relaxes the muscle cells (Figure 7.17).

The discovery of NO as a participant in signal transduction explained the action of nitroglycerin, a drug that has been used for over a century to treat angina, the chest pain caused by insufficient blood flow to the heart. Nitroglycerin releases NO, which results in relaxation of the blood vessels and increased blood flow. The drug sildenafil (Viagra) was developed to treat angina via the NO signal transduction pathway, but was only modestly useful for that purpose. However, men taking it reported more pronounced penile erections. During sexual stimulation, NO acts as a signal causing an increase in cGMP and a subsequent relaxation of the smooth muscles surrounding the arteries in the corpus cavernosum of the penis. As a result of this signal, the penis



fills with blood, producing an erection. Sildenafil acts by inhibiting an enzyme (a phosphodiesterase) that breaks down cGMP—resulting in more cGMP and better erections.

### Signal transduction is highly regulated

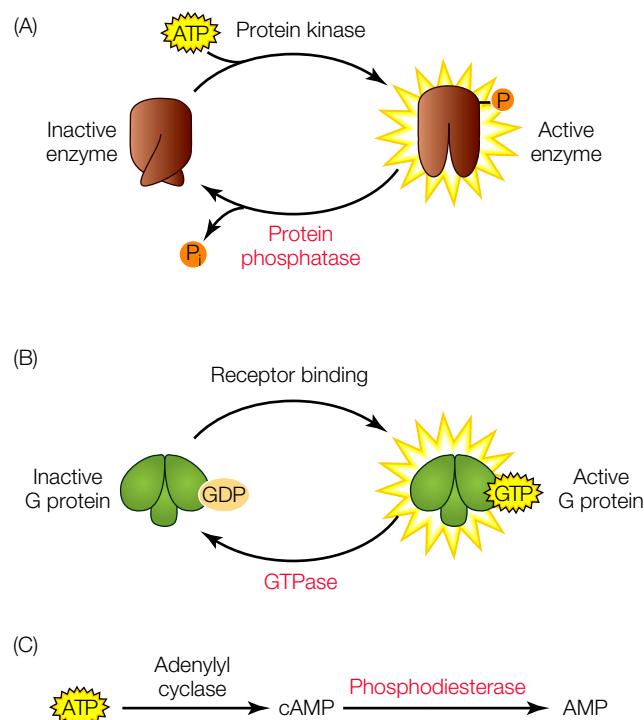
There are several ways in which cells can regulate the activity of a transducer. The concentration of NO, which breaks down quickly, can be regulated only by how much of it is made. On the other hand, membrane pumps and ion channels regulate the concentration of Ca<sup>2+</sup>, as we have seen. To regulate protein kinase cascades, G proteins, and cAMP, there are enzymes that convert the activated transducer back to its inactive precursor (**Figure 7.18**).

The balance between the activities of enzymes that activate transducers (for example, protein kinase) and enzymes that inactivate them (for example, protein phosphatase) is what determines the ultimate cellular response to a signal. Cells can alter this balance in several ways:

- **Synthesis or breakdown of the enzymes involved.** For example, synthesis of adenylyl cyclase and breakdown of phosphodiesterase (which breaks down cAMP) would tilt the balance in favor of more cAMP in the cell.
- **Activation or inhibition of the enzymes by other molecules.** Examples include the activation of a G protein-linked receptor by ligand binding, and inhibition of phosphodiesterase (which also breaks down cAMP) by sildenafil.

Because cell signaling is so important in diseases such as cancer, a search is under way for new drugs that can modulate the activities of enzymes that participate signal transduction pathways.

**7.17 Nitric Oxide in Signal Transduction** Nitric oxide (NO) is an unstable gas, which nevertheless serves as a mediator between a signal, acetylcholine (ACh), and its effect: the relaxation of smooth muscles.

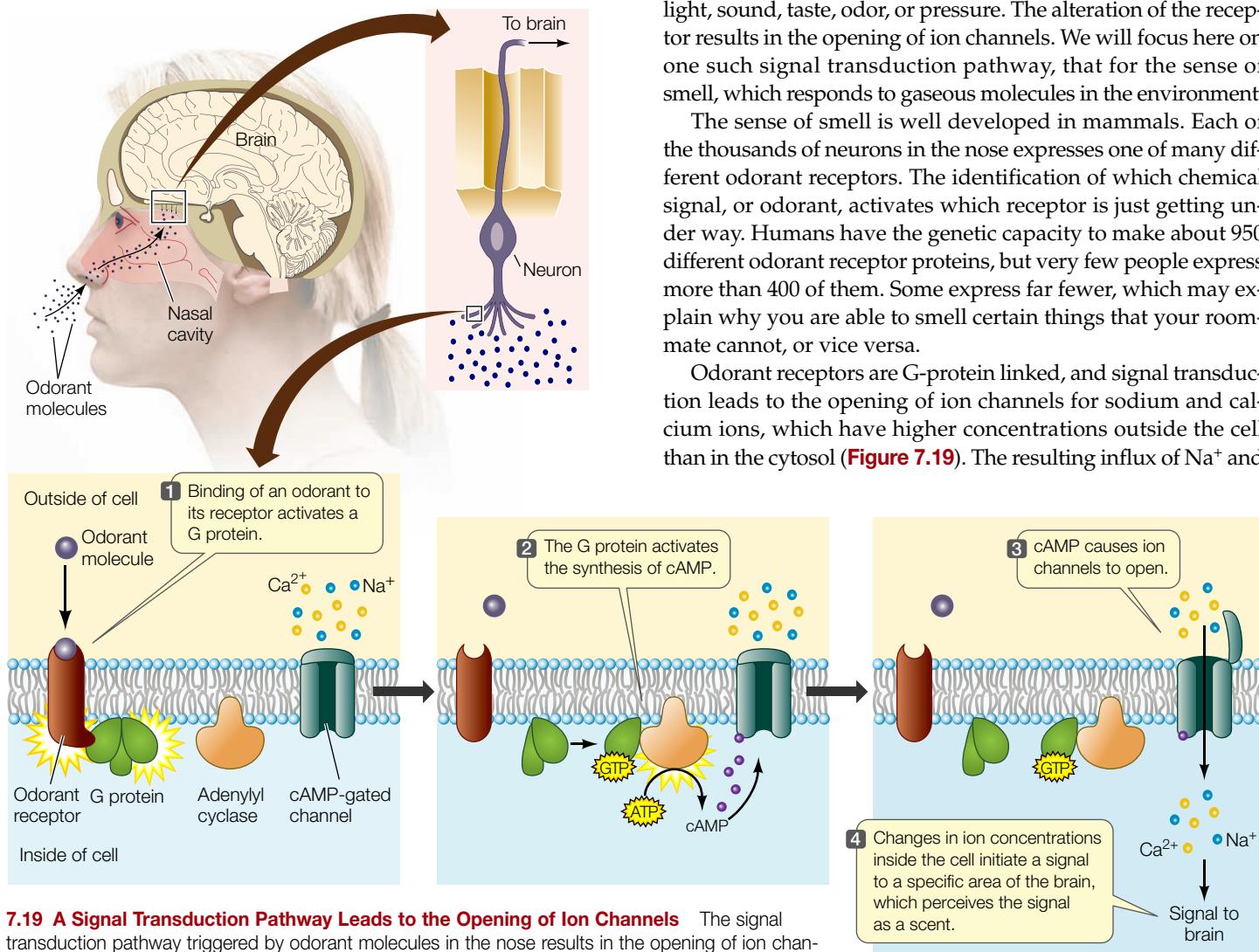


**7.18 Regulation of Signal Transduction** Some signals lead to the production of active transducers such as (A) protein kinases, (B) G proteins, and (C) cAMP. Other enzymes (red type) inactivate or remove these transducers.

## 7.3 RECAP

Signal transduction is the series of steps between the binding of a signal to a receptor and the ultimate cellular response. A receptor can activate a signal transduction pathway, such as a protein kinase cascade, directly. In many cases, a second messenger serves to amplify the signal and activate the signaling pathway indirectly. Protein kinase cascades amplify, distribute, and regulate signaling.

- How does a protein kinase cascade amplify a signal's message inside the cell? See pp. 136–137 and Figure 7.12
- What is the role of cAMP as a second messenger? See p. 138
- How are signal transduction cascades regulated? See p. 141 and Figure 7.18



**7.19 A Signal Transduction Pathway Leads to the Opening of Ion Channels** The signal transduction pathway triggered by odorant molecules in the nose results in the opening of ion channels. The resulting influx of  $\text{Na}^+$  and  $\text{Ca}^{2+}$  into the neuron cells of the nose stimulates the transmission of a scent message to a specific region of the brain.

We have seen how the binding of a signal to its receptor initiates the response of a cell to the signal, and how signal transduction pathways amplify the signal and distribute its effects to numerous targets in the cell. In the next section we will consider the third step in the signal transduction process, the actual effects of the signal on cell function.

## 7.4 How Do Cells Change in Response to Signals?

The effects of a signal on cell function take three primary forms: the opening of ion channels, changes in the activities of enzymes, or differential gene expression. These events set the cell on a path for further and sometimes dramatic changes in form and function.

### Ion channels open in response to signals

The opening of ion channels is a key step in the response of the nervous system to signals. In the sense organs, specialized cells have receptors that respond to external stimuli such as light, sound, taste, odor, or pressure. The alteration of the receptor results in the opening of ion channels. We will focus here on one such signal transduction pathway, that for the sense of smell, which responds to gaseous molecules in the environment.

The sense of smell is well developed in mammals. Each of the thousands of neurons in the nose expresses one of many different odorant receptors. The identification of which chemical signal, or odorant, activates which receptor is just getting under way. Humans have the genetic capacity to make about 950 different odorant receptor proteins, but very few people express more than 400 of them. Some express far fewer, which may explain why you are able to smell certain things that your roommate cannot, or vice versa.

Odorant receptors are G-protein linked, and signal transduction leads to the opening of ion channels for sodium and calcium ions, which have higher concentrations outside the cell than in the cytosol (Figure 7.19). The resulting influx of  $\text{Na}^+$  and

$\text{Ca}^{2+}$  causes the neuron to become stimulated so that it sends a signal to the brain that a particular odor is present.

### Enzyme activities change in response to signals

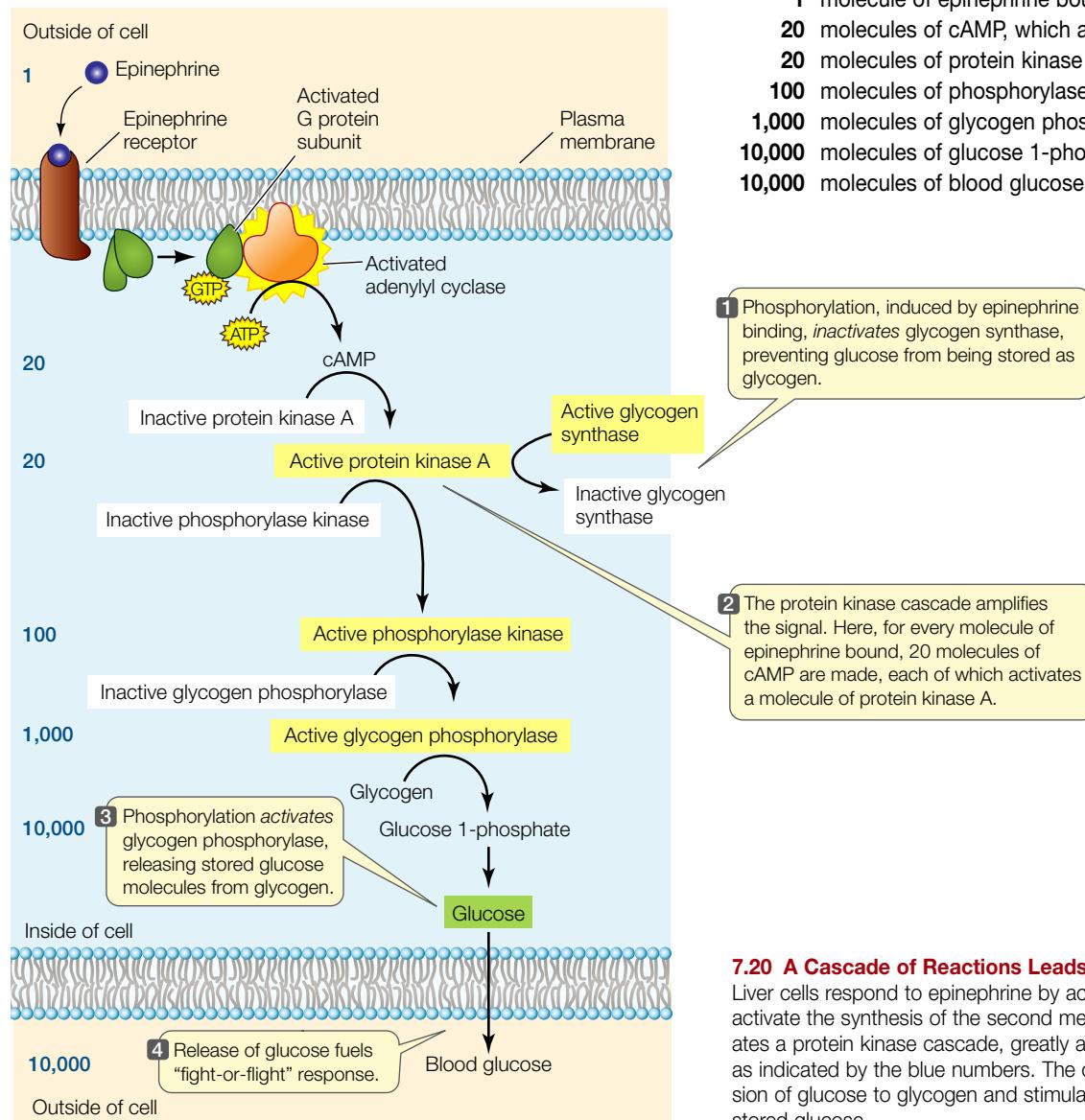
Proteins will change their shapes if they are modified either covalently or noncovalently. We have seen examples of both types of modification in our description of signal transduction. A protein kinase adds a phosphate group to a target protein, and this covalent change alters the protein's conformation and activates or inhibits a function. Cyclic AMP binds noncovalently to a target protein, and this changes the protein's shape, activating or inhibiting its function. In the case of activation, a previously inaccessible active site is exposed, and the target protein goes on to perform a new cellular role.

The G protein-mediated protein kinase cascade that is stimulated by epinephrine in liver cells results in the activation by cAMP of a key signaling molecule, protein kinase A. In turn,

protein kinase A phosphorylates two other enzymes, with opposite effects:

- **Inhibition.** Glycogen synthase, which catalyzes the joining of glucose molecules to synthesize the energy-storing molecule glycogen, is inactivated when a phosphate group is added to it by protein kinase A. Thus the epinephrine signal *prevents glucose from being stored in glycogen* (**Figure 7.20, step 1**).
- **Activation.** Phosphorylase kinase is activated when a phosphate group is added to it. It is part of a protein kinase cascade that ultimately leads to the activation of glycogen phosphorylase, another key enzyme in glucose metabolism. This enzyme results in the *liberation of glucose molecules from glycogen* (**Figure 7.20, steps 2 and 3**).

The amplification of the signal in this pathway is impressive; as detailed in Figure 7.20, each molecule of epinephrine that arrives at the plasma membrane ultimately results in 10,000 molecules of blood glucose:



### 7.20 A Cascade of Reactions Leads to Altered Enzyme Activity

Liver cells respond to epinephrine by activating G proteins, which in turn activate the synthesis of the second messenger cAMP. Cyclic AMP initiates a protein kinase cascade, greatly amplifying the epinephrine signal, as indicated by the blue numbers. The cascade both inhibits the conversion of glucose to glycogen and stimulates the release of previously stored glucose.

### Signals can initiate DNA transcription

As we introduce in Section 4.1, the genetic material, DNA, is expressed by transcription as RNA, which is then translated into a protein whose amino acid sequence is specified by the original DNA sequence. Proteins are important in all cellular functions, so a key way to regulate specific functions in a cell is to regulate which proteins are made, and therefore, which DNA sequences are transcribed.

Signal transduction plays an important role in determining which DNA sequences are transcribed. Common targets of signal transduction are proteins called transcription factors, which bind to specific DNA sequences in the cell nucleus and activate or inactivate transcription of the adjacent DNA regions. For example, the Ras signaling pathway ends in the nucleus (see Figure 7.12). The final protein kinase in the Ras signaling cascade, MAPk, enters the nucleus and phosphorylates a protein which stimulates the expression of a number of genes involved in cell proliferation.

In this chapter we have concentrated on signaling pathways that occur in animal cells. However, as you will see in Part Eight of this book, plants also have signal transduction pathways, with equally important roles.

### 7.4 RECAP

**Cells respond to signal transduction by activating enzymes, opening membrane channels, or initiating gene transcription.**

- What role does cAMP play in the sense of smell? See pp. 142–143 and Figure 7.19
- How does amplification of a signal occur and why is it important in a cell's response to changes in its environment? See p. 143 and Figure 7.20

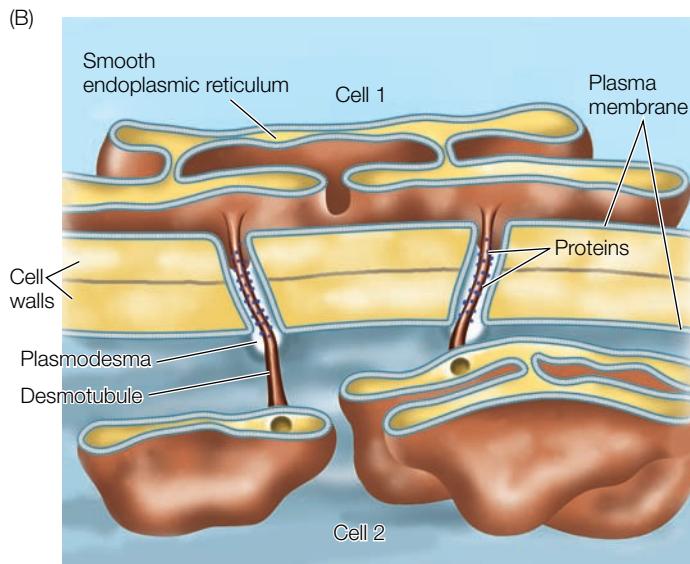
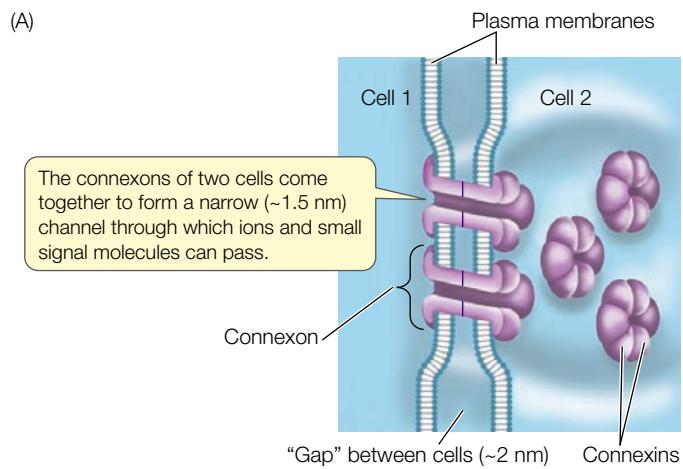
We have described how signals from a cell's environment can influence the cell. But the environment of a cell in a multicellular organism is more than the extracellular medium—it includes neighboring cells as well. In the next section we'll look at specialized junctions between cells that allow them to signal one another directly.

## 7.5 How Do Cells Communicate Directly?

Most cells are in contact with their neighbors. Section 6.2 describes various ways in which cells adhere to one another, such as via recognition proteins that protrude from the cell surface, or via tight junctions and desmosomes. But as we know from our own experience with our neighbors (and roommates), just being in proximity does not necessarily mean that there is functional communication. Neither tight junctions nor desmosomes are specialized for intercellular communication. However, many multicellular organisms have specialized cell junctions that allow their cells to communicate directly. In animals, these structures are gap junctions; in plants, they are plasmodesmata.

### Animal cells communicate by gap junctions

**Gap junctions** are channels between adjacent cells that occur in many animals, occupying up to 25 percent of the area of the plasma membrane (Figure 7.21A). Gap junctions traverse the narrow space between the plasma membranes of two cells (the “gap”) by means of channel structures called **connexons**. The walls of a connexon are composed of six subunits of the integral membrane protein connexin. In adjacent cells, two connexons come together to form a gap junction that links the cytoplasms of the two cells. There may be hundreds of these channels between a cell and its neighbors. The channel pores are about 1.5 nm in diameter—far too narrow for the passage of large molecules such as proteins. But they are wide enough to allow small mol-



**7.21 Communicating Junctions** (A) An animal cell may contain hundreds of gap junctions connecting it to neighboring cells. The pores of gap junctions allow small molecules to pass from cell to cell, assuring similar concentrations of important signaling molecules in adjacent cells so that the cells can carry out the same functions. (B) Plasmodesmata connect plant cells. The desmotubule, derived from the smooth endoplasmic reticulum, fills up most of the space inside a plasmodesma, leaving a tiny gap through which small metabolites and ions can pass.

ecules to pass between the cells. Experiments in which labeled signal molecules or ions are injected into one cell show that they can readily pass into adjacent cells if the cells are connected by gap junctions. Why is it necessary to have these linkages between the cytoplasms of adjacent cells?

Gap junctions permit *metabolic cooperation* between the linked cells. Such cooperation ensures the sharing between cells of important small molecules such as ATP, metabolic intermediates, amino acids, and coenzymes (see Section 8.4). In some tissues, metabolic cooperation is needed so that signals and metabolic products can be passed from cells at the edges of tissues to cells in the interior and vice versa. It is not clear how important this function is in many tissues, but it is known to be vital in some. For example, in the lens of the mammalian eye only the cells at the periphery are close enough to the blood supply to allow diffusion of nutrients and wastes. But because lens cells are connected by large numbers of gap junctions, material can diffuse between them rapidly and efficiently.

As mentioned above, there is evidence that signal molecules such as hormones and second messengers such as cAMP can move through gap junctions. If this is true, then only a few cells would need receptors for a signal in order for the signal to be transduced throughout the tissue. In this way, a tissue can have a coordinated response to the signal.

### Plant cells communicate by plasmodesmata

Instead of gap junctions, plants have **plasmodesmata** (singular *plasmodesma*), which are membrane-lined tunnels that traverse the thick cell walls separating plant cells from one another. A typical plant cell has several thousand plasmodesmata.

Plasmodesmata differ from gap junctions in one fundamental way: unlike gap junctions, in which the wall of the channel is made of integral proteins from the adjacent plasma membranes,

plasmodesmata are lined by the fused plasma membranes themselves. Plant biologists are so familiar with the notion of a tissue as cells interconnected in this way that they refer to these continuous cytoplasms as a *symplast* (see Figure 35.6).

The diameter of a plasmodesma is about 6 nm, far larger than a gap junction channel. But the actual space available for diffusion is about the same—1.5 nm. Examination of the interior of the plasmodesma by transmission electron microscopy reveals that a tubule called the **desmotubule**, apparently derived from the endoplasmic reticulum, fills up most of the opening of the plasmodesma (Figure 7.21B). Typically, only small metabolites and ions can move between plant cells. This fact is important in plant physiology because the bulk transport system in plants, the vascular system, lacks the tiny circulatory vessels (capillaries) that many animals have for bringing gases and nutrients to every cell. Diffusion from cell to cell across plasma membranes is probably inadequate to account for the movement of a plant hormone from the site of production to the site of action. Instead, plants rely on more rapid diffusion through plasmodesmata to ensure that all cells of a tissue respond to a signal at the same time. There are cases in which larger molecules or particles can pass between cells via plasmodesmata. For example, some viruses can move through plasmodesmata by using “movement proteins” to assist their passage.

## 7.5 RECAP

Cells can communicate with their neighbors through specialized cell junctions. In animals, these structures are gap junctions; in plants, they are plasmodesmata.

- What are the roles that gap junctions and plasmodesmata play in cell signaling?

## CHAPTER SUMMARY

### 7.1 What Are Signals, and How Do Cells Respond to Them?

- Cells receive many signals from the physical environment and from other cells. Chemical signals are often at very low concentrations. **Autocrine** signals affect the cells that make them; **paracrine** signals diffuse to and affect nearby cells. **Review Figure 7.1, WEB ACTIVITY 7.1**
- A **signal transduction pathway** involves the interaction of a signal molecule with a **receptor**; the transduction and amplification of the signal via a series of steps within the cell; and effects on the function of the cell. **Review Figure 7.2**

### 7.2 How Do Signal Receptors Initiate a Cellular Response?

- Cells respond to signals only if they have specific receptor proteins that can bind those signals. Depending on the nature of its signal or **ligand**, a receptor may be located in the plasma membrane or in the cytoplasm of the target cell. **Review Figure 7.5**
- Receptors located in the plasma membrane include **ion channels**, **protein kinases**, and **G protein-linked receptors**.

- Ion channel receptors are “gated”: the gate “opens” when the three-dimensional structure of the channel protein is altered by ligand binding. **Review Figure 7.6**

- A **G protein** has three important binding sites, which bind a G protein-linked receptor, GDP or GTP, and an **effector protein**. A G protein can either activate or inhibit an effector protein. **Review Figure 7.8, ANIMATED TUTORIAL 7.1**

- Lipid-soluble signals, such as steroid hormones, can diffuse through the plasma membrane and meet their receptors in the cytoplasm; the ligand–receptor complex may then enter the nucleus to affect gene expression. **Review Figure 7.9**

### 7.3 How Is the Response to a Signal Transduced through the Cell?

- **Direct signal transduction** is a function of the receptor itself and occurs at the plasma membrane. **Indirect transduction** involves a soluble **second messenger**. **Review Figure 7.10**
- A **protein kinase cascade** amplifies the response to receptor binding. **Review Figure 7.12, ANIMATED TUTORIAL 7.2**

- Second messengers include **cyclic AMP (cAMP)**, **inositol trisphosphate (IP<sub>3</sub>)**, **diacylglycerol (DAG)**, and **calcium ions**. IP<sub>3</sub> and DAG are derived from the phospholipid **phosphatidyl inositol-bisphosphate (PIP2)**.
- The gas **nitric oxide (NO)** is involved in signal transduction in human smooth muscle cells. **Review Figure 7.11**
- Signal transduction can be regulated in several ways. The balance between activating and inactivating the molecules involved determines the ultimate cellular response to a signal. **Review Figure 7.18**

#### 7.4 How Do Cells Change in Response to Signals?

- The cellular responses to signals may be the opening of ion channels, the alteration of enzyme activities, or changes in gene expression. **Review Figure 7.19**
- Protein kinases covalently add phosphate groups to target proteins; cAMP binds target proteins noncovalently. Both kinds of

binding change the target protein's conformation to expose or hide its active site.

- Activated enzymes may activate other enzymes in a signal transduction pathway, leading to impressive amplification of a signal. **Review Figure 7.20**

#### 7.5 How Do Cells Communicate Directly?

- Many adjacent animal cells can communicate with one another directly through small pores in their plasma membranes called **gap junctions**. Protein structures called **connexons** form thin channels between two adjacent cells through which small signal molecules and ions can pass. **Review Figure 7.21A**
- Plant cells are connected by somewhat larger pores called **plasmodesmata**, which traverse both plasma membranes and cell walls. The **desmotubule** narrows the opening of the plasmodesma. **Review Figure 7.21B**

**SEE WEB ACTIVITY 7.2 for a concept review of this chapter.**

#### SELF-QUIZ

- What is the correct order for the following events in the interaction of a cell with a signal? (1) Alteration of cell function; (2) signal binds to receptor; (3) signal released from source; (4) signal transduction.
  - 1234
  - 2314
  - 3214
  - 3241
  - 3421
- Why do some signals ("first messengers") trigger "second messengers" to activate target cells?
  - The first messenger requires activation by ATP.
  - The first messenger is not water soluble.
  - The first messenger binds to many types of cells.
  - The first messenger cannot cross the plasma membrane.
  - There are no receptors for the first messenger.
- Steroid hormones such as estrogen act on target cells by
  - initiating second messenger activity.
  - binding to membrane proteins.
  - initiating gene expression.
  - activating enzymes.
  - binding to membrane lipids.
- The major difference between a cell that responds to a signal and one that does not is the presence of a
  - DNA sequence that binds to the signal.
  - nearby blood vessel.
  - receptor.
  - second messenger.
  - transduction pathway.
- Which of the following is *not* a consequence of a signal binding to a receptor?
  - Activation of receptor enzyme activity
  - Diffusion of the receptor in the plasma membrane
  - Change in conformation of the receptor protein
  - Breakdown of the receptor to amino acids
  - Release of the signal from the receptor
- A nonpolar molecule such as a steroid hormone usually binds to a
  - cytoplasmic receptor.
  - protein kinase.
  - ion channel.
  - phospholipid.
  - second messenger.
- Which of the following is *not* a common type of receptor?
  - Ion channel
  - Protein kinase
  - G protein-linked receptor
  - Cytoplasmic receptor
  - Adenyl cyclase
- Which of the following is *not* true of a protein kinase cascade?
  - The signal is amplified.
  - A second messenger is formed.
  - Target proteins are phosphorylated.
  - The cascade ends up at the mitochondrion.
  - The cascade begins at the plasma membrane.
- Which of the following is *not* a second messenger?
  - Calcium ion
  - Inositol trisphosphate
  - ATP
  - Cyclic AMP
  - Diacylglycerol
- Plasmodesmata and gap junctions
  - allow small molecules and ions to pass rapidly between cells.
  - are both membrane-lined channels.
  - are channels about 1 mm in diameter.
  - are present only once per cell.
  - are involved in cell recognition.

## FOR DISCUSSION

- Like the Ras protein itself, the various components of the Ras signaling pathway were discovered when cancer cells showed changes (mutations) in the genes encoding one or another of the components. What might be the biochemical consequences of mutations in the genes coding for (a) Raf and (b) MAP kinase that resulted in rapid cell division?
- Cyclic AMP is a second messenger in many different responses. How can the same messenger act in different ways in different cells?
- Compare direct communication via plasmodesmata or gap junctions with receptor-mediated communication between cells. What are the advantages of one method over the other?
- The tiny invertebrate Hydra has an apical region with tentacles and a long, slender body. Hydra can reproduce asexually when cells on the body wall differentiate and form a bud, which then breaks off as a new organism. Buds form only at certain distances from the apex, leading to the idea that the apex releases a signal molecule that diffuses down the body and, at high concentrations (i.e., near the apex), inhibits bud formation. Hydra lacks a circulatory system, so this inhibitor must diffuse from cell to cell. If you had an antibody that binds to connexons and plugs up the gap junctions, how would you test the hypothesis that Hydra's inhibitory factor passes through these junctions?

## ADDITIONAL INVESTIGATION

Endosymbiotic bacteria in the marine invertebrate *Begula neritina* synthesize bryostatins, a name derived from the invertebrate's animal group Ectoprocta, once known as bryozoans ("moss animals"), and *stat* (stop). When used as drugs, bryostatins curtail

cell division in many cell types, including several cancers. It has been proposed that bryostatins inhibit protein kinase C (see Figure 7.15). How would you investigate this hypothesis, and how would you relate this inhibition to cell division?

### WORKING WITH DATA (GO TO [yourBioPortal.com](http://yourBioPortal.com))

**The Discovery of a Second Messenger** In this hands-on exercise, you will examine the experiments that Sutherland and his colleagues performed (Figure 7.13) using liver tissue to demonstrate that there can be a second, soluble chemical

messenger between a hormone binding to a receptor and its eventual effects in the cell. By analyzing their data, you will see how controls were important in their reasoning.

## Lactase deficiency

United Nations officials first noticed the problem during the 1950s when massive food relief efforts were made to alleviate famines in Asia and Africa. The conventional wisdom was that donated food should provide a balanced diet, and that an important component of the diet (one of the “four major food groups”) was dairy products. Reports started coming in of people developing bloating, nausea, and diarrhea after consuming donated dairy products.

At first, this problem was attributed to contamination by bacteria during shipping, or to errors in the preparation of powdered milk products by the recipients. It never occurred to the donors that the scientific principles of nutrition that they had so carefully developed did not apply to people everywhere. But it soon became apparent that

the donors in Europe and other wealthy countries, who were usually of European descent, were atypical of humanity in their ability to hydrolyze the disaccharide lactose, the major milk sugar, to its constituent monosaccharides, glucose and galactose. Their small intestines make a protein called lactase ( $\beta$ -galactosidase) that acts to speed up the hydrolysis reaction millions-fold. Such catalytic proteins are called enzymes, and their names often end with the suffix “ase.” Most people around the world are born with the ability to make the enzyme lactase, but soon after infancy they lose it. People of European descent are unusual in that they do not lose their lactase production after infancy.

When many non-European adults consume lactose it does not get hydrolyzed in their small intestine, because they do not produce lactase. Disaccharides such as lactose are not absorbed into the blood stream by cells lining the small intestine. So the lactose remains intact and travels onward to the colon (large intestine). Among the billions of bacteria in the colon, there are species that make lactase. But as a side product, these bacteria produce the gases that cause all the discomfort. The condition of discomfort after eating lactose is called lactose intolerance.

Why does lactase production go down after infancy in most humans? The explanation lies with diet: an infant first consumes mother’s milk, which contains abundant lactose. This stimulates the intestinal cells to make lactase. But many humans—and other mammals—consume little or no milk after weaning, and the ability to make lactase in the small intestine is not needed. So most mammals have evolved to produce lactase only during infancy. Lactose intolerance is not a problem in many human societies because the people simply don’t consume dairy products—



**A Precursor to Trouble** Many adults do not produce the enzyme lactase in their small intestines. When they consume dairy products, these people have ill effects.



**Maasai Herders** The Maasai are unusual among Africans in that they consume milk throughout their lives. They can do this because they produce lactase after weaning.

unless they are given them by well-meaning donors!  
They get their carbohydrates from other sources.

Then why are many people of European descent still able to make lactase as adults? It turns out that they carry a mutation (a change in their DNA sequence) that eliminates the shutdown in lactase production after weaning. This mutation became predominant in European (and some east African) populations after those people began to keep grazing animals and to use their milk.

Lactase activity is an example of an enzyme-catalyzed biochemical transformation. The hydrolysis of lactose is the beginning of its transformation to simpler molecules—ultimately  $\text{CO}_2$ —and this transformation releases energy.

**IN THIS CHAPTER** we begin our study of biochemical transformations, focusing on the role of energy. We first describe the physical principles that underlie energy transformations and how these principles apply to biology. Then, we go on to show how the energy carrier ATP plays an important role in the cell. Finally, we follow up on the lactase story by describing the nature, activities, and regulation of enzymes, which speed up biochemical transformations and are essential for life.

## CHAPTER OUTLINE

- 8.1 What Physical Principles Underlie Biological Energy Transformations?
- 8.2 What Is the Role of ATP in Biochemical Energetics?
- 8.3 What Are Enzymes?
- 8.4 How Do Enzymes Work?
- 8.5 How Are Enzyme Activities Regulated?

### 8.1 What Physical Principles Underlie Biological Energy Transformations?

Metabolic reactions and catalysts are essential to the biochemical transformation of energy by living things. Whether it is a plant using light energy to produce carbohydrates or a cat transforming food energy so it can leap to a countertop (where it hopes to find food so it can obtain more energy), the transformation of energy is a hallmark of life.

Physicists define energy as the capacity to do work. Work occurs when a force operates on an object over a distance. In biochemistry, it is more useful to consider energy as *the capacity for change*. In biochemical reactions these energy changes are usually associated with changes in the chemical composition and properties of molecules. No cell creates energy; all living things must obtain energy from the environment. Indeed one of the fundamental laws of physics is that energy can neither be created nor destroyed. However, energy can be transformed from one form into another, and living cells carry out many such transformations. For example, green plant cells convert light energy into chemical energy; the jumping cat transforms chemical energy into movement. Energy transformations are linked to the chemical transformations that occur in cells—the breaking and creating of chemical bonds, the movement of substances across membranes, cell reproduction, and so forth.

#### There are two basic types of energy and of metabolism

Energy comes in many forms: chemical, electrical, heat, light, and mechanical. But all forms of energy can be considered as one of two basic types:

- *Potential energy* is the energy of state or position—that is, stored energy. It can be stored in many forms: in chemical bonds, as a concentration gradient, or even as an electric charge imbalance (as in the membrane potential; see Section 6.3). Think of a crouching cat, holding still as it prepares to pounce.
- *Kinetic energy* is the energy of movement—that is, the type of energy that does work, that makes things change. Think of the cat leaping as some of the potential energy stored in its muscles is converted into the kinetic energy of muscle contractions.

Potential energy can be converted into kinetic energy and vice versa, and the form that the energy takes can also be converted. The potential energy in the cat's muscles is in covalent bonds (chemical energy), while the kinetic energy of the pouncing cat is mechanical (**Figure 8.1**). You can think of many other such



**8.1 Energy Conversions and Work** A leaping cat illustrates both the conversion between potential and kinetic energy and the conversion of energy from one form (chemical) to another (mechanical).

conversions: while reading this book, for example, light energy is converted into chemical energy in your eyes, and then is converted into electric energy in the nerve cells that carry messages to your brain. When you decide to turn a page, the electrical and chemical energy of nerve and muscle are converted into kinetic energy.

In any living organism, chemical reactions are occurring continuously. **Metabolism** is defined as the totality of these reactions. While particular cells carry out many reactions at any given instant, scientists usually focus on a few reactions at a time. Two broad categories of metabolic reactions occur in all cells of all organisms:

- **Anabolic reactions** (anabolism) link simple molecules to form more complex molecules (for example, the synthesis of a protein from amino acids). Anabolic reactions require an input of energy and capture it in the chemical bonds that are formed.
- **Catabolic reactions** (catabolism) break down complex molecules into simpler ones and release the energy stored in chemical bonds. For example, when the polysaccharide starch is hydrolyzed to simpler molecules, energy is released.

*Catabolic and anabolic reactions are often linked.* The energy released in catabolic reactions is often used to drive anabolic re-

actions—that is, to do biological work. For example, the energy released by the breakdown of glucose (catabolism) is used to drive anabolic reactions such as the synthesis of nucleic acids and proteins.

Catabolic reactions also provide energy for movement: muscle contraction is driven by the catabolism (hydrolysis) of ATP (see Section 8.2). In this case, the potential energy released by catabolism is converted to kinetic energy.

The **laws of thermodynamics** (thermo, “energy”; dynamics, “change”) were derived from studies of the fundamental physical properties of energy, and the ways it interacts with matter. The laws apply to all matter and all energy transformations in the universe. Their application to living systems helps us to understand how organisms and cells harvest and transform energy to sustain life.

### The first law of thermodynamics: Energy is neither created nor destroyed

The first law of thermodynamics states that in any conversion of energy, it is neither created nor destroyed. Another way of saying this is: in any conversion of energy, the total energy before and after the conversion is the same (**Figure 8.2A**). As you will see in the next two chapters, the potential energy present in the chemical bonds of carbohydrates and lipids can be converted to potential energy in the form of ATP. This can then be converted into kinetic energy to do mechanical work (such as in muscle contractions), or used to do biochemical work (such as protein synthesis).

### The second law of thermodynamics: Disorder tends to increase

Although energy cannot be created or destroyed, the second law of thermodynamics states that when energy is converted from one form to another, some of that energy becomes unavailable for doing work (**Figure 8.2B**). In other words, no physical process or chemical reaction is 100 percent efficient; some of the released energy is lost to a form associated with disorder. Think of disorder as a kind of randomness due to the thermal motion of particles; this energy is of such a low value and so dispersed that it is unusable. *Entropy* is a measure of the disorder in a system.

It takes energy to impose order on a system. Unless energy is applied to a system, it will be randomly arranged or disordered. The second law applies to all energy transformations, but we will focus here on chemical reactions in living systems.

**NOT ALL ENERGY CAN BE USED** In any system, the total energy includes the usable energy that can do work and the unusable energy that is lost to disorder:

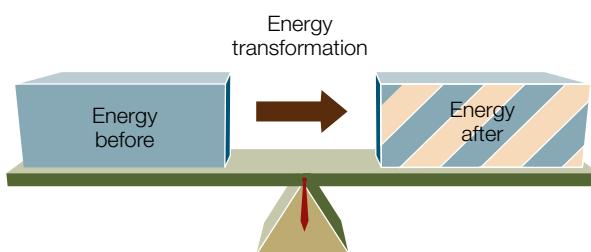
$$\text{total energy} = \text{usable energy} + \text{unusable energy}$$

In biological systems, the total energy is called **enthalpy (H)**. The usable energy that can do work is called **free energy (G)**. Free energy is what cells require for all the chemical reactions needed for growth, cell division, and maintenance. The unusable en-

(A)

**The First Law of Thermodynamics**

The total amount of energy before a transformation equals the total amount after a transformation. No new energy is created, and no energy is lost.

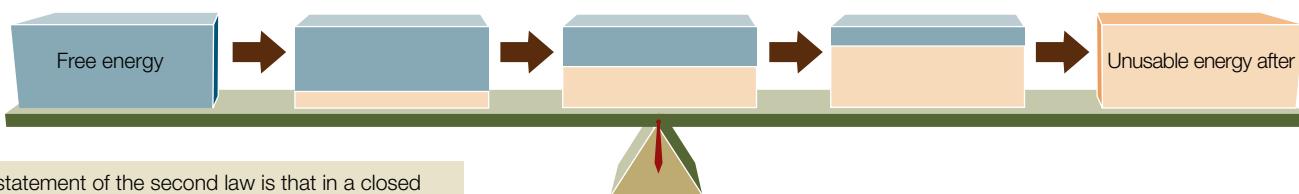
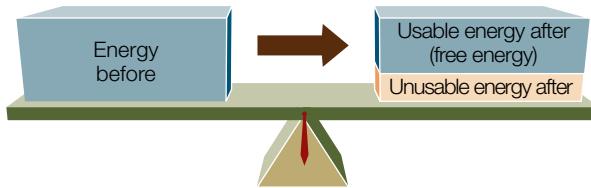
**8.2 The Laws of Thermodynamics**

(A) The first law states that energy cannot be created or destroyed. (B) The second law states that after energy transformations, some energy becomes unavailable to do work.

(B)

**The Second Law of Thermodynamics**

Although a transformation does not change the total amount of energy within a closed system (one that is not exchanging matter or energy with the surroundings), after any transformation the amount of energy available to do work is always less than the original amount of energy.



Another statement of the second law is that in a closed system, with repeated energy transformations, free energy decreases and unusable energy (disorder) increases—a phenomenon known as the increase in **entropy**.

ergy is represented by **entropy (S)** multiplied by the absolute temperature ( $T$ ). Thus we can rewrite the word equation above more precisely as:

$$H = G + TS$$

Because we are interested in usable energy, we rearrange this expression:

$$G = H - TS$$

Although we cannot measure  $G$ ,  $H$ , or  $S$  absolutely, we can determine the change in each at a constant temperature. Such energy changes are measured in calories (cal) or joules (J).\* A change in energy is represented by the Greek letter delta ( $\Delta$ ). The change in free energy ( $\Delta G$ ) of any chemical reaction is equal to the difference in free energy between the products and the reactants:

$$\Delta G_{\text{reaction}} = G_{\text{products}} - G_{\text{reactants}}$$

Such a change can be either positive or negative; that is, the free energy of the products can be more or less than the free energy of the reactants. If the products have more free energy than the reactants, then there must have been some input of energy

\*A calorie is the amount of heat energy needed to raise the temperature of 1 gram of pure water from 14.5°C to 15.5°C. In the SI system, energy is measured in joules. 1 J = 0.239 cal; conversely, 1 cal = 4.184 J. Thus, for example, 486 cal = 2,033 J, or 2.033 kJ. Although defined here in terms of heat, the calorie and the joule are measures of any form of energy—mechanical, electrical, or chemical. When you compare data on energy, always compare joules with joules and calories with calories.

into the reaction. (Remember that energy cannot be created, so some energy must have been added from an external source.) At a constant temperature,  $\Delta G$  is defined in terms of the change in total energy ( $\Delta H$ ) and the change in entropy ( $\Delta S$ ):

$$\Delta G = \Delta H - T\Delta S$$

This equation tells us whether free energy is released or consumed by a chemical reaction:

- If  $\Delta G$  is negative ( $\Delta G < 0$ ), free energy is released.
- If  $\Delta G$  is positive ( $\Delta G > 0$ ), free energy is required (consumed).

If the necessary free energy is not available, the reaction does not occur. The sign and magnitude of  $\Delta G$  depend on the two factors on the right of the equation:

- $\Delta H$ : In a chemical reaction,  $\Delta H$  is the total amount of energy added to the system ( $\Delta H > 0$ ) or released ( $\Delta H < 0$ ).
- $\Delta S$ : Depending on the sign and magnitude of  $\Delta S$ , the entire term,  $T\Delta S$ , may be negative or positive, large or small. In other words, in living systems at a constant temperature (no change in  $T$ ), the magnitude and sign of  $\Delta G$  can depend a lot on changes in entropy.

If a chemical reaction increases entropy, its products are more disordered or random than its reactants. If there are more products than reactants, as in the hydrolysis of a protein to its amino acids, the products have considerable freedom to move around. The disorder in a solution of amino acids will be large compared with that in the protein, in which peptide bonds and other forces prevent free movement. So in hydrolysis, the change in entropy ( $\Delta S$ ) will be positive. Conversely, if there are fewer products and they are more restrained in their movements than the reac-

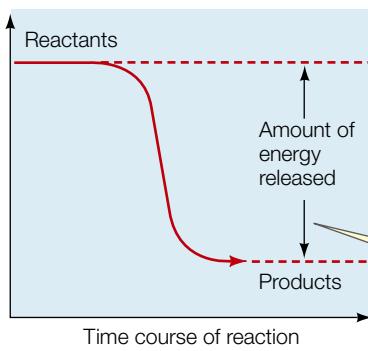
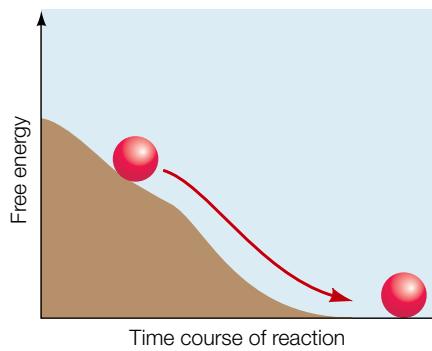
tants (as for amino acids being joined in a protein),  $\Delta S$  will be negative.

**DISORDER TENDS TO INCREASE** The second law of thermodynamics also predicts that, as a result of energy transformations, disorder tends to increase; some energy is always lost to random thermal motion (entropy). Chemical changes, physical changes, and biological processes all tend to increase entropy (see Figure 8.2B), and this tendency gives direction to these processes. It explains why some reactions proceed in one direction rather than another.

How does the second law apply to organisms? Consider the human body, with its highly organized tissues and organs composed of large, complex molecules. This level of complexity appears to be in conflict with the second law but is not for two reasons. First, the construction of complexity also generates disorder. Constructing 1 kg of a human body requires the metabolism of about 10 kg of highly ordered biological materials, which are converted into  $\text{CO}_2$ ,  $\text{H}_2\text{O}$ , and other simple molecules that move independently and randomly. So metabolism creates far more disorder (more energy is lost to entropy) than the amount of order (total energy; enthalpy) stored in 1 kg of flesh. Second, life requires a constant input of energy to maintain order. Without this energy, the complex structures of living systems would break down. Because energy is used to generate and maintain order, there is no conflict with the second law of thermodynamics.

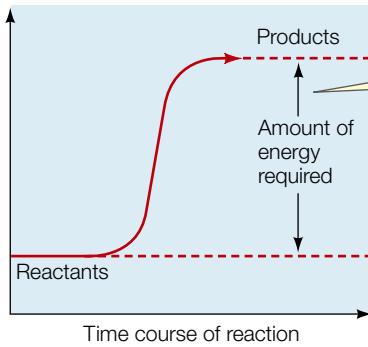
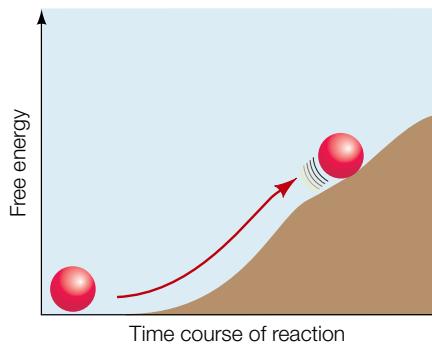
Having seen that the laws of thermodynamics apply to living things, we will now turn to a consideration of how these laws apply to biochemical reactions.

(A) Exergonic reaction



In an exergonic reaction, energy is released as the reactants form lower-energy products.  $\Delta G$  is negative.

(B) Endergonic reaction



Energy must be added for an endergonic reaction, in which reactants are converted to products with a higher energy level.  $\Delta G$  is positive.

### Chemical reactions release or consume energy

Since anabolic reactions link simple molecules to form more complex molecules, they tend to increase complexity (order) in the cell. On the other hand, catabolic reactions break down complex molecules into simpler ones, so they tend to decrease complexity (generate disorder).

- *Catabolic* reactions may break down an ordered reactant into smaller, more randomly distributed products. Reactions that release free energy ( $-\Delta G$ ) are called **exergonic** reactions (Figure 8.3A). For example:



- *Anabolic* reactions may make a single product (a highly ordered substance) out of many smaller reactants (less ordered). Reactions that require or consume free energy ( $+\Delta G$ ) are called **endergonic** reactions (Figure 8.3B).

For example:



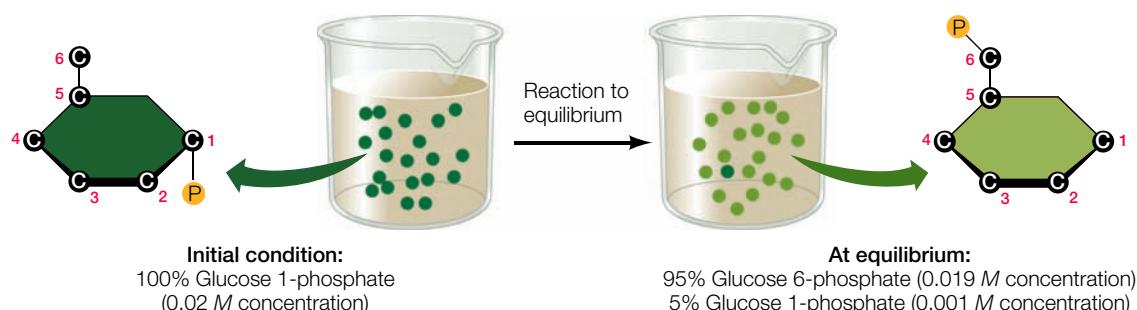
In principle, chemical reactions are reversible and can run both forward and backward. For example, if compound A can be converted into compound B ( $A \rightarrow B$ ), then B, in principle, can be converted into A ( $B \rightarrow A$ ), although *the concentrations of A and B determine which of these directions will be favored*. Think of the overall reaction as resulting from competition between forward and reverse reactions ( $A \rightleftharpoons B$ ). Increasing the concentration of A speeds up the forward reaction, and increasing the concentration of B favors the reverse reaction.

At some concentration of A and B, the forward and reverse reactions take place at the same rate. At this concentration, no further net change in the system is observable, although individual molecules are still forming and breaking apart. This balance between forward and reverse reactions is known as **chemical equilibrium**. Chemical equilibrium is a state of no net change, and a state in which  $\Delta G = 0$ .

**8.3 Exergonic and Endergonic Reactions** (A) In an exergonic reaction, the reactants behave like a ball rolling down a hill, and energy is released. (B) A ball will not roll uphill by itself. Driving an endergonic reaction, like moving a ball uphill, requires the addition of free energy.

### 8.4 Chemical Reactions Run to Equilibrium

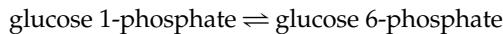
No matter what quantities of glucose 1-phosphate and glucose 6-phosphate are dissolved in water, when equilibrium is attained, there will always be 95 percent glucose 6-phosphate and 5 percent glucose 1-phosphate.



### Chemical equilibrium and free energy are related

Every chemical reaction proceeds to a certain extent, but not necessarily to completion (all reactants converted into products). Each reaction has a specific equilibrium point, which is related to the free energy released by the reaction under specified conditions. To understand the principle of equilibrium, consider the following example.

Most cells contain glucose 1-phosphate, which is converted into glucose 6-phosphate.



Imagine that we start out with an aqueous solution of glucose 1-phosphate that has a concentration of 0.02 M. (M stands for molar concentration; see Section 2.4). The solution is maintained under constant environmental conditions (25°C and pH 7). As the reaction proceeds to equilibrium, the concentration of the product, glucose 6-phosphate, rises from 0 to 0.019 M, while the concentration of the reactant, glucose 1-phosphate, falls to 0.001 M. At this point, equilibrium is reached (Figure 8.4). At equilibrium, the reverse reaction, from glucose 6-phosphate to glucose 1-phosphate, progresses at the same rate as the forward reaction.

At equilibrium, then, this reaction has a product-to-reactant ratio of 19:1 (0.019/0.001), so the forward reaction has gone 95 percent of the way to completion ("to the right," as written above). This result is obtained every time the experiment is run under the same conditions.

The change in free energy ( $\Delta G$ ) for any reaction is related directly to its point of equilibrium. The further toward completion the point of equilibrium lies, the more free energy is released. In an exergonic reaction, such as the conversion of glucose 1-phosphate to glucose 6-phosphate,  $\Delta G$  is a negative number (in this example,  $\Delta G = -1.7 \text{ kcal/mol}$ , or  $-7.1 \text{ kJ/mol}$ ).

A large, positive  $\Delta G$  for a reaction means that it proceeds hardly at all to the right ( $A \rightarrow B$ ). If the concentration of B is initially high relative to that of A, such a reaction runs "to the left" ( $A \leftarrow B$ ), and nearly all B is converted into A. A  $\Delta G$  value near zero is characteristic of a readily reversible reaction: reactants and products have almost the same free energies.

In Chapters 9 and 10 we examine the metabolic reactions that harvest energy from food and light. In turn, this energy is used to synthesize carbohydrates, lipids and proteins. All of the chemical reactions carried out by living organisms are governed by the principles of thermodynamics and equilibrium.

### 8.1 RECAP

Two laws of thermodynamics govern energy transformations in biological systems. A biochemical reaction can release or consume energy, and it may not run to completion, but instead end up at a point of equilibrium.

- What is the difference between potential energy and kinetic energy? Between anabolism and catabolism?  
**See pp. 149–150**
- What are the laws of thermodynamics? How do they relate to biology? **See pp. 150–152 and Figure 8.2**
- What is the difference between endergonic and exergonic reactions and what is the importance of  $\Delta G$ ?  
**See p. 152 and Figure 8.3**

The principles of thermodynamics that we have been discussing apply to all energy transformations in the universe, so they are very powerful and useful. Next, we'll apply them to reactions in cells that involve the currency of biological energy, ATP.

### 8.2 What Is the Role of ATP in Biochemical Energetics?

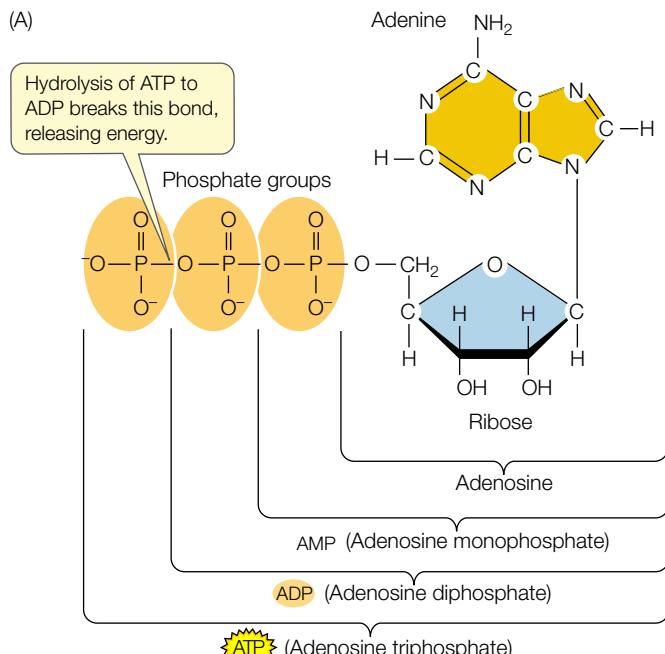
Cells rely on adenosine triphosphate (ATP) for the capture and transfer of the free energy they need to do chemical work. ATP operates as a kind of "energy currency." Just as it is more effective, efficient, and convenient for you to trade money for a lunch than to trade your actual labor, it is useful for cells to have a single currency for transferring energy between different reactions and cell processes. So some of the free energy that is released by exergonic reactions is captured in the formation of ATP from adenosine diphosphate (ADP) and inorganic phosphate ( $\text{HPO}_4^{2-}$ , which is commonly abbreviated to  $\text{P}_i$ ). The ATP can then be hydrolyzed at other sites in the cell to release free energy to drive endergonic reactions. (In some reactions, guanosine triphosphate [GTP] is used as the energy transfer molecule instead of ATP, but we will focus on ATP here.)

ATP has another important role in the cell beyond its use as an energy currency: it is a nucleotide that can be converted into a building block for nucleic acids (see Chapter 4). The structure of ATP is similar to those of other nucleotides, but two things

about ATP make it especially useful to cells. First, ATP releases a relatively large amount of energy when hydrolyzed to ADP and P<sub>i</sub>. Second, ATP can phosphorylate (donate a phosphate group to) many different molecules, which gain some of the energy that was stored in the ATP. We will examine these two properties in the discussion that follows.

### ATP hydrolysis releases energy

An ATP molecule consists of the nitrogenous base adenine bonded to ribose (a sugar), which is attached to a sequence of three phosphate groups (Figure 8.5A). The hydrolysis of a molecule of ATP yields free energy, as well as ADP and the inorganic phosphate ion (P<sub>i</sub>). Thus:



(B) *Luciola cruciata*

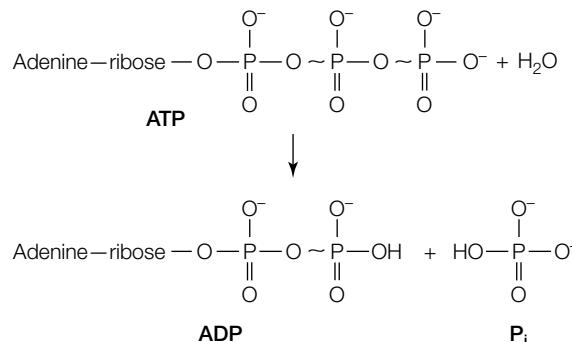


**8.5 ATP** (A) ATP is richer in energy than its relatives ADP and AMP. (B) Fireflies use ATP to initiate the oxidation of luciferin. This process converts chemical energy into light energy, emitting rhythmic flashes that signal the insect's readiness to mate.

The important property of this reaction is that it is exergonic, releasing free energy. Under standard laboratory conditions, the change in free energy for this reaction ( $\Delta G$ ) is about  $-7.3$  kcal/mol ( $-30$  kJ/mol). However, under cellular conditions, the value can be as much as  $-14$  kcal/mol. We give both values here because you will encounter both values, and you should be aware of their origins. Both are correct, but in different conditions.

Two characteristics of ATP account for the free energy released by the loss of one or two of its phosphate groups:

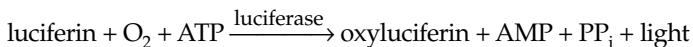
- The free energy of the P—O bond between phosphate groups (called a phosphoric acid anhydride bond) is much higher than the energy of the O—H bond that forms after hydrolysis. So some usable energy is released by hydrolysis.



- Because phosphate groups are negatively charged and so repel each other, it takes energy to get phosphates near enough to each other to make the covalent bond that links them together (e.g., to add a phosphate to ADP to make ATP). Some of this energy is conserved when the third phosphate is attached.

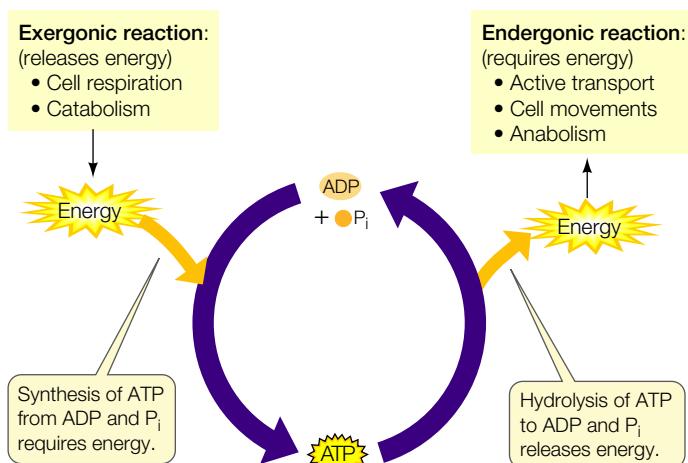
A molecule of ATP can be hydrolyzed either to ADP and P<sub>i</sub>, or to adenosine monophosphate (AMP) and a pyrophosphate ion (P<sub>2</sub>O<sub>7</sub><sup>4-</sup>; commonly abbreviated to PP<sub>i</sub>). Cells use the energy released by ATP hydrolysis to fuel endergonic reactions (such as the biosynthesis of complex molecules), for active transport, and for movement. Another interesting example of the use of ATP involves converting its chemical energy into light energy.

**BIOLUMINESCENCE** The production of light by living organisms is referred to as **bioluminescence** (Figure 8.5B). It is an example of an endergonic reaction driven by ATP hydrolysis that involves an interconversion of energy forms (chemical to light). The chemical that becomes luminescent is called luciferin (after the light-bearing fallen angel, Lucifer):



This reaction and the enzyme that catalyzes it (luciferase) occur in a wide variety of organisms in addition to the familiar firefly. These include a variety of marine organisms, microorganisms, worms, and mushrooms. The light is generally used to avoid predators or for signaling to mates.

Soft-drink companies use the firefly proteins luciferin and luciferase to detect bacterial contamination. Where there are

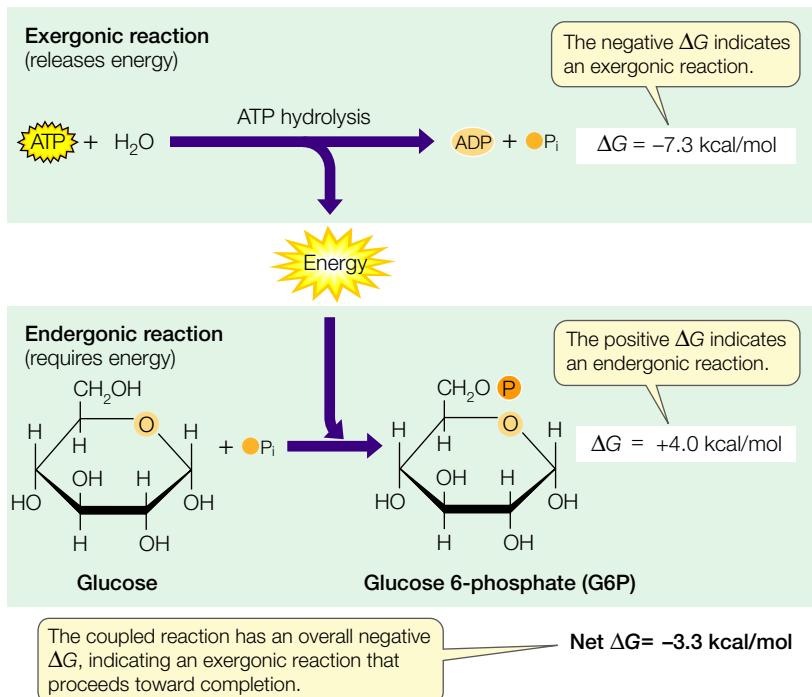


**8.6 Coupling of Reactions** Exergonic cellular reactions release the energy needed to make ATP from ADP. The energy released from the conversion of ATP back to ADP can be used to fuel endergonic reactions.

[yourBioPortal.com](http://yourBioPortal.com)

GO TO Web Activity 8.1 • ATP and Coupled Reactions

living cells there is ATP, and when the firefly proteins encounter ATP and oxygen, they give off light. Thus, a sample of soda that lights up in the test is contaminated with bacteria and is discarded.



**8.7 Coupling of ATP Hydrolysis to an Endergonic Reaction** The addition of phosphate derived from the hydrolysis of ATP to glucose forms the molecule glucose 6-phosphate (in a reaction catalyzed by hexokinase). ATP hydrolysis is exergonic and the energy released drives the second reaction, which is endergonic.

### ATP couples exergonic and endergonic reactions

As we have just seen, the hydrolysis of ATP is exergonic and yields ADP,  $P_i$ , and free energy. The reverse reaction, the formation of ATP from ADP and  $P_i$ , is endergonic and consumes as much free energy as is released by the hydrolysis of ATP:



Many different exergonic reactions in the cell can provide the energy to convert ADP into ATP. For eukaryotes and many prokaryotes, the most important of these reactions is cellular respiration, in which some of the energy released from fuel molecules is captured in ATP. The formation and hydrolysis of ATP constitute what might be called an “energy-coupling cycle,” in which ADP picks up energy from exergonic reactions to become ATP, which then donates energy to endergonic reactions. ATP is the common component of these reactions and is the agent of coupling, as illustrated in **Figure 8.6**.

Coupling of exergonic and endergonic reactions is very common in metabolism. Free energy is captured and retained in the P—O bonds of ATP. ATP then diffuses to another site in the cell, where its hydrolysis releases the free energy to drive an endergonic reaction. For example, the formation of glucose 6-phosphate from glucose (**Figure 8.7**), which has a positive  $\Delta G$  (is endergonic), will not proceed without the input of free energy from ATP hydrolysis, which has a negative  $\Delta G$  (is exergonic). The overall  $\Delta G$  for the coupled reactions (when the two  $\Delta G$ s are added together) is negative. Hence the reactions proceed exergonically when they are coupled, and glucose 6-phosphate is synthesized. As you will see in Chapter 9, this is the initial reaction in the catabolism of glucose.

An active cell requires the production of millions of molecules of ATP per second to drive its biochemical machinery. An ATP molecule is typically consumed within a second of its formation. At rest, an average person produces and hydrolyzes about 40 kg of ATP per day—as much as some people weigh. This means that each ATP molecule undergoes about 10,000 cycles of synthesis and hydrolysis every day!

### 8.2 RECAP

ATP is the “energy currency” of cells. Some of the free energy released by exergonic reactions can be captured in the form of ATP. This energy can then be released by ATP hydrolysis and used to drive endergonic reactions.

- How does ATP store energy? See p. 153
- What are coupled reactions? See p. 155 and Figure 8.7

ATP is synthesized and used up very rapidly. But these biochemical reactions could not proceed so rapidly without the help of enzymes.

## 8.3 What Are Enzymes?

When we know the change in free energy ( $\Delta G$ ) of a reaction, we know where the equilibrium point of the reaction lies: the more negative  $\Delta G$  is, the further the reaction proceeds toward completion. However,  $\Delta G$  tells us nothing about the *rate* of a reaction—the speed at which it moves toward equilibrium. The reactions that cells depend on have spontaneous rates that are so slow that the cells would not survive without a way to speed up the reactions. That is the role of catalysts: substances that speed up reactions without themselves being permanently altered. A catalyst does not cause a reaction to occur that would not proceed without it, *but merely increases the rate of the reaction*, allowing equilibrium to be approached more rapidly. This is an important point: *no catalyst makes a reaction occur that cannot otherwise occur*.

Most biological catalysts are proteins called *enzymes*. Although we will focus here on proteins, some catalysts—perhaps the earliest ones in the origin of life—are RNA molecules called ribozymes (see Section 4.3). A biological catalyst, whether protein or RNA, is a framework or scaffold within which chemical catalysis takes place. This molecular framework binds the reactants and can participate in the reaction itself; however, such participation does not permanently change the enzyme. The catalyst ends up in exactly the same chemical condition after a reaction as before it. Over time, cells have evolved to utilize proteins rather than RNA as catalysts in most biochemical reactions, probably because of the great diversity in the three-dimensional structures of proteins, and because of the variety of chemical functions provided by their functional groups (see Figure 3.1).

In this section we will discuss the energy barrier that controls the rate of a chemical reaction. Then we will focus on the roles of enzymes: how they interact with specific reactants, how they lower the energy barrier, and how they permit reactions to proceed more quickly.

### To speed up a reaction, an energy barrier must be overcome

An exergonic reaction may release a great deal of free energy, but take place very slowly. Such reactions are slow because there is an energy barrier between reactants and products. Think about the propane stove we describe in Section 2.3.

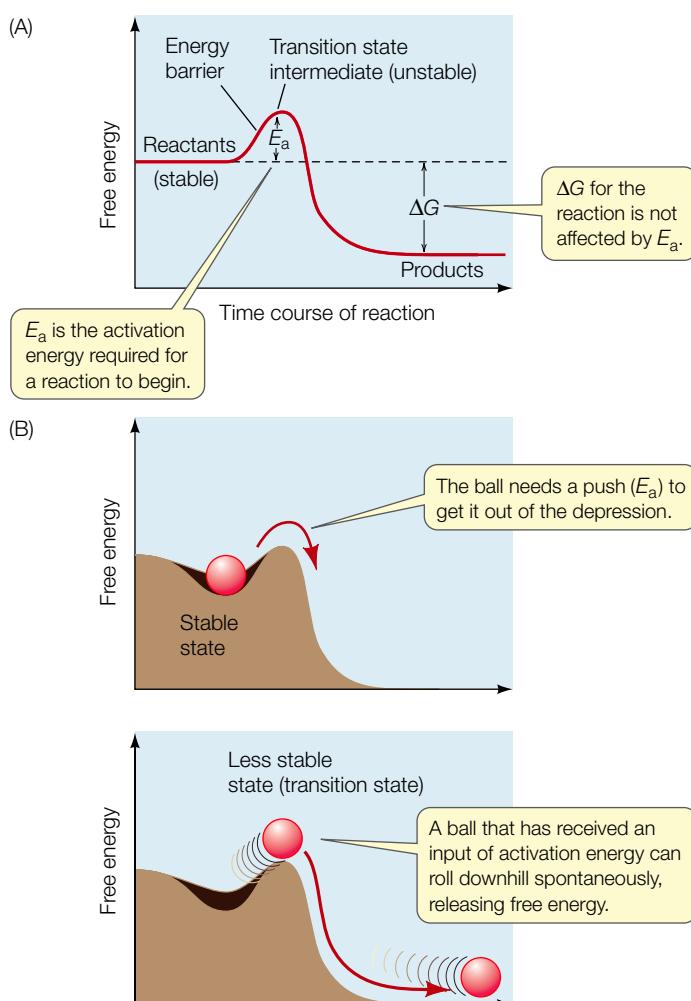
The burning of propane ( $C_3H_8 + 5 O_2 \rightarrow 3 CO_2 + 4 H_2O + \text{energy}$ ) is an exergonic reaction—energy is released in the form of heat and light. Once started, the reaction goes to completion: all of the propane reacts with oxygen to form carbon dioxide and water vapor.

Because burning propane liberates so much energy, you might expect this reaction to proceed rapidly whenever propane is exposed to oxygen. But this does not happen; propane will start burning only if a spark, an input of energy such as a burning match, is provided. A spark is needed because there is an energy barrier between the reactants and the products.

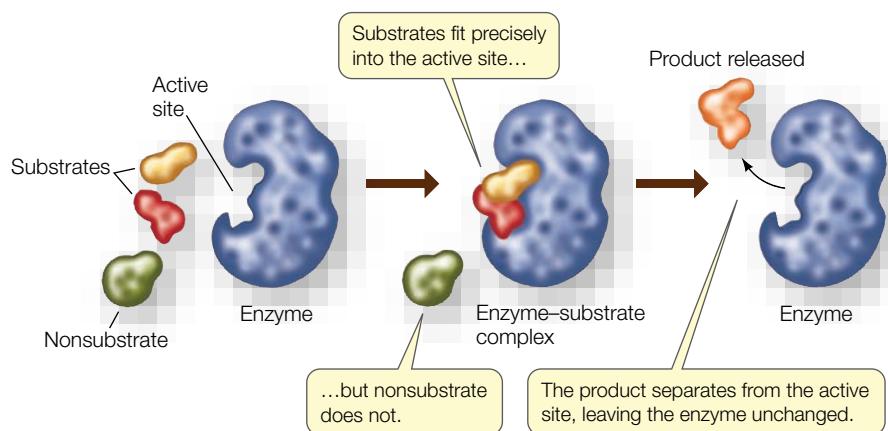
In general, exergonic reactions proceed only after the reactants are pushed over the energy barrier by some added energy.

The energy barrier thus represents the amount of energy needed to start the reaction, known as the **activation energy** ( $E_a$ ) (Figure 8.8A). Recall the ball rolling down the hill in Figure 8.3. The ball has a lot of potential energy at the top of the hill. However, if it is stuck in a small depression, it will not roll down the hill, even though that action is exergonic. To start the ball rolling, a small amount of energy (activation energy) is needed to push it out of the depression (Figure 8.8B). In a chemical reaction, the activation energy is the energy needed to change the reactants into unstable molecular forms called transition-state intermediates.

**Transition-state intermediates** have higher free energies than either the reactants or the products. Their bonds may be stretched and therefore unstable. Although the amount of activation energy needed for different reactions varies, it is often small compared with the change in free energy of the reaction. The activation energy put in to start a reaction is recovered during the ensuing “downhill” phase of the reaction, so it is not a part of the net free energy change,  $\Delta G$  (see Figure 8.8A).



**8.8 Activation Energy Initiates Reactions** (A) In any chemical reaction, an initial stable state must become less stable before change is possible. (B) A ball on a hillside provides a physical analogy to the biochemical principle graphed in (A).



Where does the activation energy come from? In any collection of reactants at room or body temperatures, the molecules are moving around. A few are moving fast enough that their kinetic energy can overcome the energy barrier, enter the transition state, and react. However, the reaction takes place very slowly at room or body temperatures. If the system were heated, all the reactant molecules would move faster and have more kinetic energy, and the reaction would speed up. You have probably used this technique in the chemistry laboratory.

However, adding enough heat to increase the average kinetic energy of the molecules would not work in living systems. Such a nonspecific approach would accelerate all reactions, including destructive ones such as the denaturation of proteins (see Figure 3.9). A more effective way to speed up a reaction in a living system is to lower the energy barrier by bringing the reactants close together. In living cells, enzymes and ribozymes accomplish this task.

### Enzymes bind specific reactants at their active sites

Catalysts increase the rates of chemical reactions. Most nonbiological catalysts are nonspecific. For example, powdered platinum catalyzes virtually any reaction in which molecular hydrogen ( $H_2$ ) is a reactant. In contrast, most biological catalysts are highly specific. An enzyme or ribozyme usually recognizes and binds to only one or a few closely related reactants, and it catalyzes only a single chemical reaction. In the discussion that follows, we focus on enzymes, but remember that similar rules of chemical behavior apply to ribozymes as well.

In an enzyme-catalyzed reaction, the reactants are called **substrates**. Substrate molecules bind to a particular site on the enzyme, called the active site, where catalysis takes place (Figure 8.9). The specificity of an enzyme results from the exact three-dimensional shape and structure of its active site, into which only a narrow range of substrates can fit. Other molecules—with different shapes, different functional groups, and different properties—cannot fit properly and bind to the active site. This specificity is comparable to the specific binding of a membrane transport protein or receptor protein to its specific ligand, as described in Chapters 6 and 7.

The names of enzymes reflect their functions and often end with the suffix "ase." For example the enzyme lactase, which you encountered in the opening story for this chapter, catalyzes the hy-

**8.9 Enzyme and Substrate** An enzyme is a protein catalyst with an active site capable of binding one or more substrate molecules.

drolysis of lactose but not another disaccharide, sucrose. The enzyme hexokinase accelerates the phosphorylation of glucose, but not ribose, to make glucose 6-phosphate (see Figure 8.7).

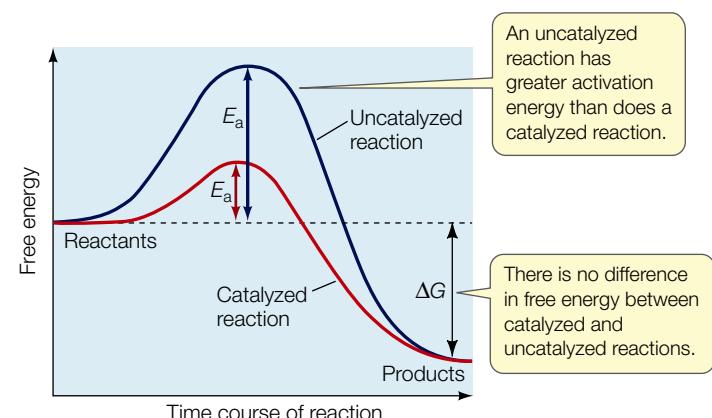
The binding of a substrate to the active site of an enzyme produces an **enzyme–substrate complex (ES)** that is held together by one or more means, such as hydrogen bonding, electrical attraction, or temporary covalent bonding. The enzyme–substrate complex gives rise to product and free enzyme:



where E is the enzyme, S is the substrate, P is the product, and ES is the enzyme–substrate complex. The free enzyme (E) is in the same chemical form at the end of the reaction as at the beginning. While bound to the substrate, it may change chemically, but by the end of the reaction it has been restored to its initial form and is ready to bind more substrate.

### Enzymes lower the energy barrier but do not affect equilibrium

When reactants are bound to the enzyme, forming an enzyme–substrate complex, they require less activation energy than the transition-state species of the corresponding uncatalyzed reaction (Figure 8.10). Thus the enzyme lowers the energy barrier for the reaction—it offers the reaction an easier path, speeding it up. When an enzyme lowers the energy bar-



**8.10 Enzymes Lower the Energy Barrier** Although the activation energy is lower in an enzyme-catalyzed reaction than in an uncatalyzed reaction, the energy released is the same with or without catalysis. In other words,  $E_a$  is lower, but  $\Delta G$  is unchanged. A lower activation energy means the reaction will take place at a faster rate.

rier, both the forward and the reverse reactions speed up, so the enzyme-catalyzed overall reaction proceeds toward equilibrium more rapidly than the uncatalyzed reaction. *The final equilibrium is the same with or without the enzyme.* Similarly, adding an enzyme to a reaction does not change the difference in free energy ( $\Delta G$ ) between the reactants and the products (see Figure 8.10).

Enzymes can change the rate of a reaction substantially. For example, if 600 molecules of a protein with arginine as its terminal amino acid just sit in solution, the protein molecules tend toward disorder and the terminal peptide bonds break, releasing the arginines ( $\Delta S$  increases). Without an enzyme this is a very slow reaction—it takes about 7 years for half (300) of the proteins to undergo this reaction. However, with the enzyme carboxypeptidase A catalyzing the reaction, the 300 arginines are released in half a second! The important consequence of this for living cells is not difficult to imagine. Such speeds make new realities possible.

### 8.3 RECAP

A chemical reaction requires a “push” over the energy barrier to get started. Enzymes provide this activation energy by binding specific reactants (substrates).

- Explain how the structure of an enzyme makes that enzyme specific. **See p. 157 and Figure 8.9**
- What is the relationship between an enzyme and the equilibrium point of a reaction? **See pp. 157–158**

Now that you have a general understanding of the structures, functions, and specificities of enzymes, let’s see how they work to speed up chemical reactions between the substrate molecules.

## 8.4 How Do Enzymes Work?

During and after the formation of the enzyme–substrate complex, chemical interactions occur. These interactions contribute directly to the breaking of old bonds and the formation of new ones. In catalyzing a reaction, an enzyme may use one or more mechanisms.

### Enzymes can orient substrates

When free in solution, substrates are moving from place to place randomly while at the same time vibrating, rotating, and tumbling around. They may not have the proper orientation to interact when they collide. Part of the activation energy needed to start a reaction is used to bring together specific atoms so that bonds can form (Figure 8.11A). For example, if acetyl coenzyme A (acetyl CoA) and oxaloacetate are to form citrate (a step in the metabolism of glucose; see Section 9.2), the two substrates must be oriented so that the carbon atom of the methyl group of acetyl CoA can form a covalent bond with the carbon atom of the carbonyl group of oxaloacetate. The active site of the enzyme

citrate synthase has just the right shape to bind these two molecules so that these atoms are adjacent.

### Enzymes can induce strain in the substrate

Once a substrate has bound to its active site, an enzyme can cause bonds in the substrate to stretch, putting it in an unstable transition state (Figure 8.11B). For example, lysozyme is a protective enzyme abundant in tears and saliva that destroys invading bacteria by cleaving polysaccharide chains in their cell walls. Lysozyme’s active site “stretches” the bonds of the bacterial polysaccharide, rendering the bonds unstable and more reactive to lysozyme’s other substrate, water.

### Enzymes can temporarily add chemical groups to substrates

The side chains (R groups) of an enzyme’s amino acids may be direct participants in making its substrates more chemically reactive (Figure 8.11C).

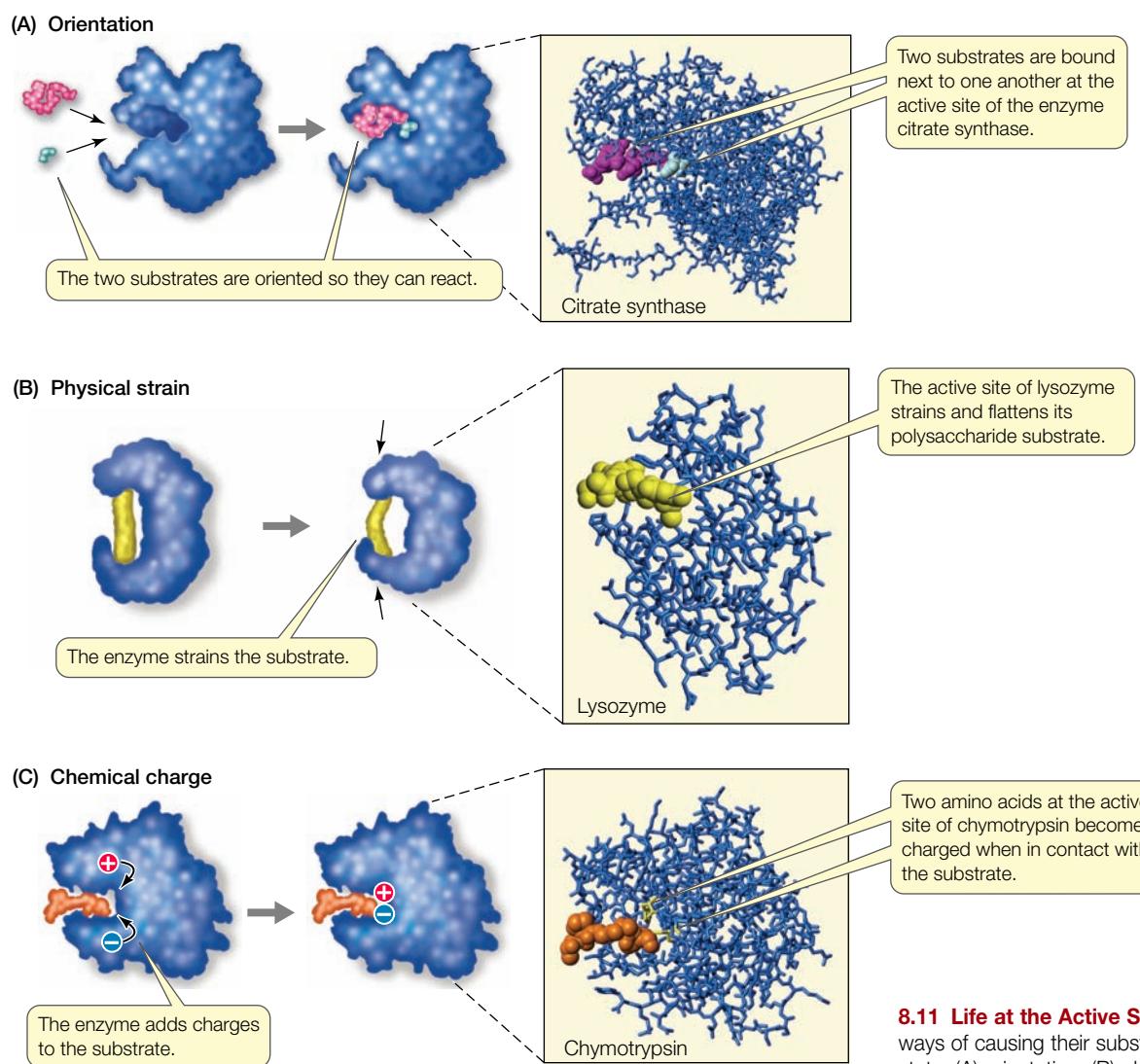
- In *acid–base catalysis*, the acidic or basic side chains of the amino acids in the active site transfer H<sup>+</sup> to or from the substrate, destabilizing a covalent bond in the substrate, and permitting it to break.
- In *covalent catalysis*, a functional group in a side chain forms a temporary covalent bond with a portion of the substrate.
- In *metal ion catalysis*, metal ions such as copper, iron, and manganese, which are often firmly bound to side chains of enzymes, can lose or gain electrons without detaching from the enzymes. This ability makes them important participants in oxidation–reduction reactions, which involve the loss or gain of electrons.

### Molecular structure determines enzyme function

Most enzymes are much larger than their substrates. An enzyme is typically a protein containing hundreds of amino acids and may consist of a single folded polypeptide chain or of several subunits (see Section 3.2). Its substrate is generally a small molecule or a small part of a large molecule. The active site of the enzyme is usually quite small, not more than 6–12 amino acids. Two questions arise from these observations:

- What features of the active site allow it to recognize and bind the substrate?
- What is the role of the rest of the huge protein?

**THE ACTIVE SITE IS SPECIFIC TO THE SUBSTRATE** The remarkable ability of an enzyme to select exactly the right substrate depends on a precise interlocking of molecular shapes and interactions of chemical groups at the active site. The binding of the substrate to the active site depends on the same kinds of forces that maintain the tertiary structure of the enzyme: hydrogen bonds, the attraction and repulsion of electrically charged groups, and hydrophobic interactions.



**8.11 Life at the Active Site** Enzymes have several ways of causing their substrates to enter the transition state: (A) orientation, (B) physical strain, and (C) chemical charge.

In 1894, the German chemist Emil Fischer compared the fit between an enzyme and its substrate to that of a lock and key. Fischer's model persisted for more than half a century with only indirect evidence to support it. The first direct evidence came in 1965, when David Phillips and his colleagues at the Royal Institution in London crystallized the enzyme lysozyme and determined its tertiary structure using the technique of X-ray crystallography (described in Section 13.2). They observed a pocket in lysozyme that neatly fits its substrate (see Figure 8.11B).

**AN ENZYME CHANGES SHAPE WHEN IT BINDS A SUBSTRATE** Just as a membrane receptor protein may undergo precise changes in conformation upon binding to its ligand (see Chapter 7), some enzymes change their shapes when they bind their substrate(s). These shape changes, which are called **induced fit**, expose the active site (or sites) of the enzyme.

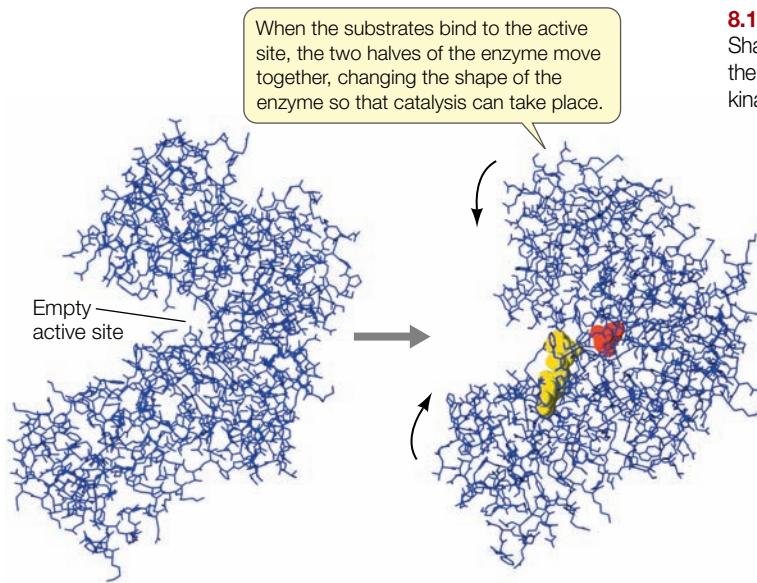
An example of induced fit can be seen in the enzyme hexokinase (see Figure 8.7), which catalyzes the reaction



Induced fit brings reactive side chains from the hexokinase active site into alignment with the substrates (Figure 8.12), facilitating its catalytic mechanisms. Equally important, the folding of hexokinase to fit around the substrates (glucose and ATP) excludes water from the active site. This is essential, because if water were present, the ATP could be hydrolyzed to ADP and P<sub>i</sub>. But since water is absent, the transfer of a phosphate from ATP to glucose is favored.

Induced fit at least partly explains why enzymes are so large. The rest of the macromolecule may have three roles:

- It provides a framework so that the amino acids of the active site are properly positioned in relation to the substrate(s).
- It participates in significant changes in protein shape and structure that result in induced fit.
- It provides binding sites for regulatory molecules (see Section 8.5).



### Some enzymes require other molecules in order to function

As large and complex as enzymes are, many of them require the presence of nonprotein chemical “partners” in order to function (**Table 8.1**):

- **Prosthetic groups** are distinctive, non-amino acid atoms or molecular groupings that are permanently bound to their enzymes. An example is a flavin nucleotide, which binds to succinate dehydrogenase, an important enzyme in cellular respiration (see Section 9.2).
- **Cofactors** are inorganic ions such as copper, zinc, and iron that bind to certain enzymes. For example, the cofactor zinc binds to the enzyme alcohol dehydrogenase.

**TABLE 8.1**  
**Some Examples of Nonprotein “Partners” of Enzymes**

TYPE OF MOLECULE	ROLE IN CATALYZED REACTIONS
<b>COFACTORS</b>	
Iron ( $\text{Fe}^{2+}$ or $\text{Fe}^{3+}$ )	Oxidation/reduction
Copper ( $\text{Cu}^+$ or $\text{Cu}^{2+}$ )	Oxidation/reduction
Zinc ( $\text{Zn}^{2+}$ )	Helps bind NAD
<b>COENZYMES</b>	
Biotin	Carries $-\text{COO}^-$
Coenzyme A	Carries $-\text{CO}-\text{CH}_3$
NAD	Carries electrons
FAD	Carries electrons
ATP	Provides/extracts energy
<b>PROSTHETIC GROUPS</b>	
Heme	Binds ions, $\text{O}_2$ , and electrons; contains iron cofactor
Flavin	Binds electrons
Retinal	Converts light energy

### 8.12 Some Enzymes Change Shape When Substrate Binds to Them

Shape changes result in an induced fit between enzyme and substrate, improving the catalytic ability of the enzyme. Induced fit can be observed in the enzyme hexokinase, seen here with and without its substrates, glucose (red) and ATP (yellow).

- A **coenzyme** is a carbon-containing molecule that is required for the action of one or more enzymes. It is usually relatively small compared with the enzyme to which it temporarily binds.

A coenzyme moves from enzyme to enzyme, adding or removing chemical groups from the substrate. A coenzyme is like a substrate in that it does not permanently bind to the enzyme; it binds to the active site, changes chemically during the reaction, and then separates from the enzyme to participate in other reactions. ATP and ADP, as energy carriers, can be considered coenzymes, even though they are really substrates. The term coenzyme was coined before the functions of these molecules were fully understood. Biochemists continue to use the term, and to be consistent with the field, we will use the term in this book.

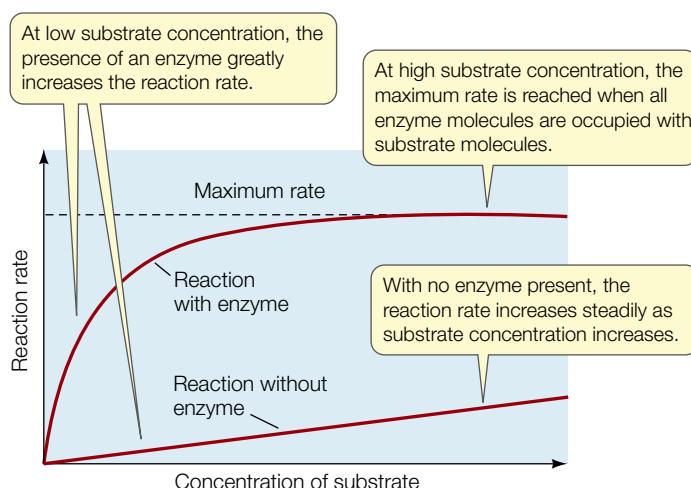
In the next chapter we will encounter other coenzymes that function in energy-harvesting reactions by accepting or donating electrons or hydrogen atoms. In animals, some coenzymes are produced from vitamins—substances that must be obtained from food because they cannot be synthesized by the body. For example, the B vitamin niacin is used to make the coenzyme nicotinamide adenine dinucleotide (NAD).

### The substrate concentration affects the reaction rate

For a reaction of the type  $\text{A} \rightarrow \text{B}$ , the rate of the uncatalyzed reaction is directly proportional to the concentration of A. The higher the concentration of substrate, the more reactions per unit of time. Addition of the appropriate enzyme speeds up the reaction, of course, but it also changes the shape of a plot of rate versus substrate concentration (**Figure 8.13**). For a given concentration of enzyme, the rate of the enzyme-catalyzed reaction initially increases as the substrate concentration increases from zero, but then it levels off. At some point, further increases in the substrate concentration do not significantly increase the reaction rate—the maximum rate has been reached.

Since the concentration of an enzyme is usually much lower than that of its substrate and does not change as substrate concentration changes, what we see is a saturation phenomenon like the one that occurs in facilitated diffusion (see Figure 6.14). When all the enzyme molecules are bound to substrate molecules, the enzyme is working as fast as it can—at its maximum rate. Nothing is gained by adding more substrate, because no free enzyme molecules are left to act as catalysts. Under these conditions the active sites are said to be saturated.

The maximum rate of a catalyzed reaction can be used to measure how efficient the enzyme is—that is, how many molecules of substrate are converted into product per unit of time when there is an excess of substrate present. This *turnover number* ranges from one molecule every two seconds for lysozyme to an amazing 40 million molecules per second for the liver enzyme catalase.



**8.13 Catalyzed Reactions Reach a Maximum Rate** Because there is usually less enzyme than substrate present, the reaction rate levels off when the enzyme becomes saturated.

## 8.4 RECAP

Enzymes orient their substrates to bring together specific atoms so that bonds can form. An enzyme can participate in the reaction it catalyzes by temporarily changing shape or destabilizing the enzyme-substrate complex. Some enzymes require cofactors, coenzymes, or prosthetic groups in order to function.

- What are three mechanisms of enzyme catalysis? See p. 158 and Figure 8.11
- What are the chemical roles of coenzymes in enzymatic reactions? See p. 160

Now that you understand more about how enzymes function, let's see how different enzymes work together in a complex organism.

## 8.5 How Are Enzyme Activities Regulated?

A major characteristic of life is homeostasis—the maintenance of stable internal conditions (see Chapter 40). How does a cell maintain a relatively constant internal environment while thousands of chemical reactions are going on? These chemical reactions operate within *metabolic pathways* in which the product of one reaction is a reactant for the next. The pathway for the metabolism of lactose begins with lactase (as we described in the chapter's opening story), and is just one of many pathways that regulate the internal environment of the cell. These pathways have such diverse functions as the catabolism of glucose to yield energy,  $\text{CO}_2$ , and  $\text{H}_2\text{O}$ , and the anabolism of amino acids to yield proteins. Metabolic pathways do not exist in isolation, but interact extensively, and each reaction in each pathway is catalyzed by a specific enzyme.

Within a cell or organism, the presence and activity of enzymes determine the “flow” of chemicals through different metabolic pathways. The amount of enzyme activity, in turn, is controlled in part via the regulation of gene expression. Many signal transduction pathways (described in Chapter 7) end with changes in gene expression, and often the genes that are switched on or off encode enzymes. But the simple presence of an enzyme does not ensure that it is functioning. Another means by which cells can control which pathways are active at a particular time is by the activation or inactivation of enzymes. If one enzyme in the pathway is inactive, that step and all subsequent steps shut down. Thus, enzymes are target points for the regulation of entire sequences of chemical reactions.

Regulation of the rates at which thousands of different enzymes operate contributes to homeostasis within an organism. Such control permits cells to make orderly changes in their functions in response to changes in the external environment. In Chapter 7 we describe a number of enzymes that become activated in signal transduction pathways, illustrating how enzyme activation can dramatically alter cell functions. (For example, see the activation of glycogen phosphorylase in Figure 7.20.)

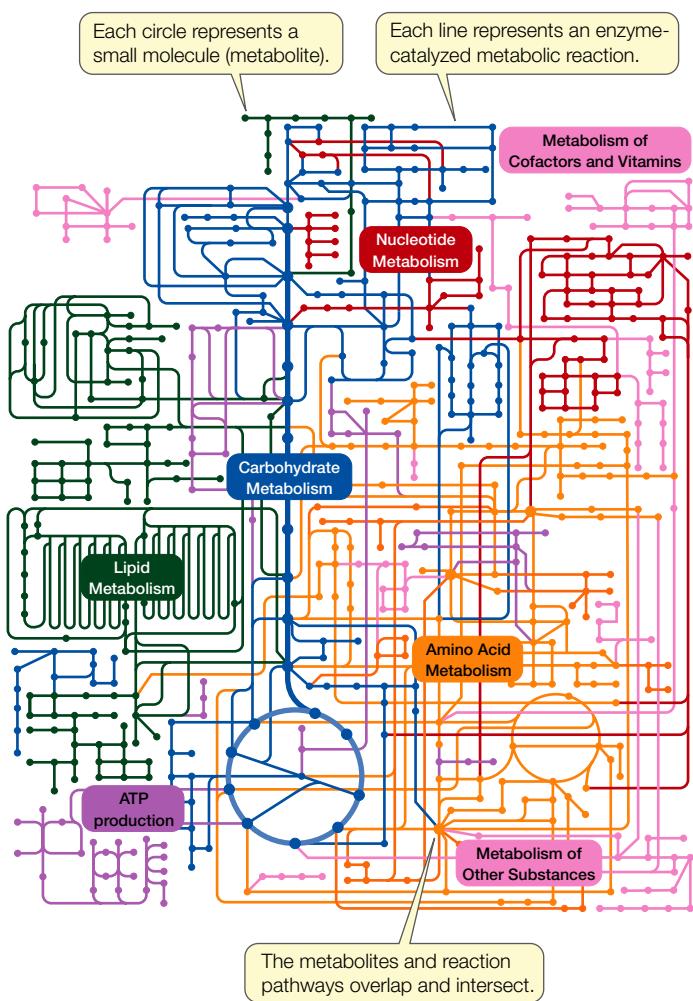
The flow of chemicals such as carbon atoms through interacting metabolic pathways can be studied, but this process becomes complicated quickly, because each pathway influences the others. Computer algorithms are used to model these pathways and show how they mesh in an interdependent system (Figure 8.14). Such models can help predict what will happen if the concentration of one molecule or another is altered. This new field of biology is called **systems biology**, and it has numerous applications.

In this section we will investigate the roles of enzymes in organizing and regulating metabolic pathways. In living cells, enzymes can be activated or inhibited in various ways, and there are also mechanisms for controlling the rates at which some enzymes catalyze reactions. We will also examine how the environment—particularly temperature and pH—affects enzyme activity.

### Enzymes can be regulated by inhibitors

Various chemical inhibitors can bind to enzymes, slowing down the rates of the reactions they catalyze. Some inhibitors occur naturally in cells; others are artificial. Naturally occurring inhibitors regulate metabolism; artificial ones can be used to treat disease, to kill pests, or to study how enzymes work. In some cases the inhibitor binds the enzyme irreversibly, and the enzyme becomes permanently inactivated. In other cases the inhibitor has reversible effects; it can separate from the enzyme, allowing the enzyme to function fully as before. The removal of a natural reversible inhibitor increases an enzyme's rate of catalysis.

**IRREVERSIBLE INHIBITION** If an inhibitor covalently binds to certain side chains at the active site of an enzyme, it will permanently inactivate the enzyme by destroying its capacity to interact with its normal substrate. An example of an irreversible inhibitor is DIPF (diisopropyl phosphorofluoridate), which



**8.14 Metabolic Pathways** The complex interactions of metabolic pathways can be modeled by the tools of systems biology. In cells, the main elements controlling these pathways are enzymes.

reacts with serine (Figure 8.15). DIPF is an irreversible inhibitor of acetylcholinesterase, whose operation is essential for the normal functioning of the nervous system. Because of their effect on acetylcholinesterase, DIPF and other similar compounds are classified as nerve gases, and were developed for biological warfare. One of these compounds, Sarin, was used in an attack on the Tokyo subway in 1995, resulting in a dozen deaths and the hospitalization of hundreds more. The widely used insecticide malathion is a derivative of DIPF that inhibits only insect acetylcholinesterase, not the mammalian enzyme. The irreversible inhibition of enzymes is of practical use to humans, but this form of regulation is not common in the cell, because the enzyme is permanently inactivated and cannot be recycled. Instead, cells use reversible inhibition.

**REVERSIBLE INHIBITION** In some cases an inhibitor is similar enough to a particular enzyme's natural substrate to bind non-covalently to its active site, yet different enough that the enzyme catalyzes no chemical reaction. While such a molecule is bound to the enzyme, the natural substrate cannot enter the active site

and the enzyme is unable to function. Such a molecule is called a **competitive inhibitor** because it competes with the natural substrate for the active site (Figure 8.16A). In this case, the inhibition is reversible. When the concentration of the competitive inhibitor is reduced, it detaches from the active site, and the enzyme is active again.

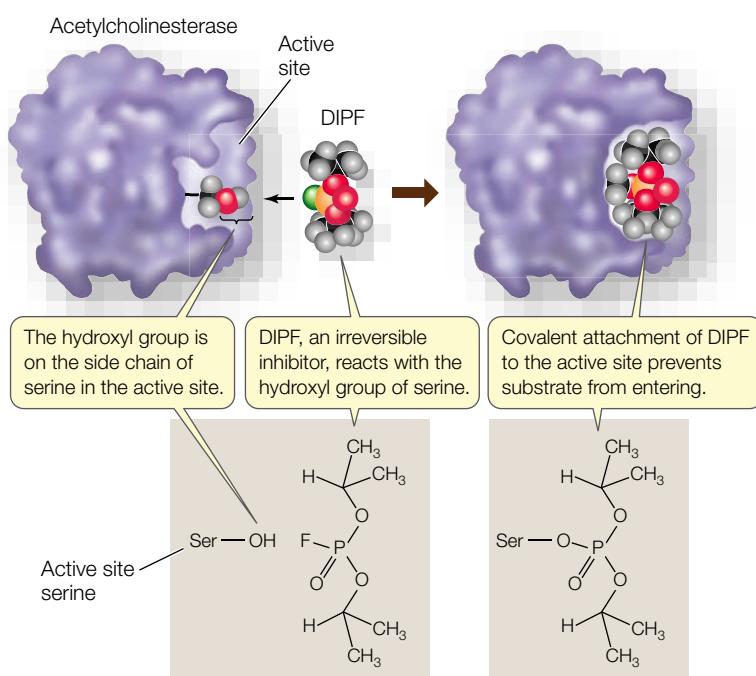
A **noncompetitive inhibitor** binds to an enzyme at a site distinct from the active site. This binding causes a change in the shape of the enzyme that alters its activity (Figure 8.16B). The active site may no longer bind the substrate, or if it does, the rate of product formation may be reduced. Like competitive inhibitors, noncompetitive inhibitors can become unbound, so their effects are reversible.

### Allosteric enzymes control their activity by changing shape

The change in enzyme shape due to noncompetitive inhibitor binding is an example of allostery (*allo*, “different”; *stereos*, “shape”). **Allosteric regulation** occurs when an effector molecule binds to a site other than the active site of an enzyme, *inducing the enzyme to change its shape*. The change in shape alters the affinity of the active site for the substrate, and so the rate of the reaction is changed.

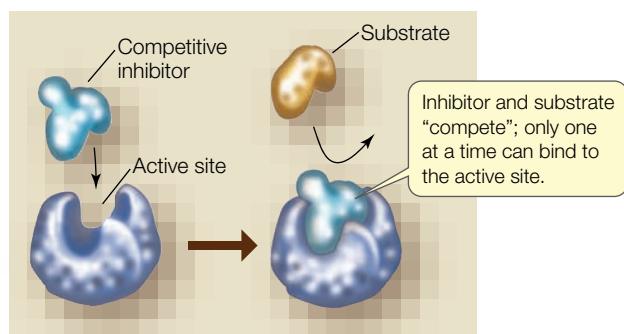
Often, an enzyme will exist in the cell in more than one possible shape (Figure 8.17):

- The *active form* of the enzyme has the proper shape for substrate binding.
- The *inactive form* of the enzyme has a shape that cannot bind the substrate.

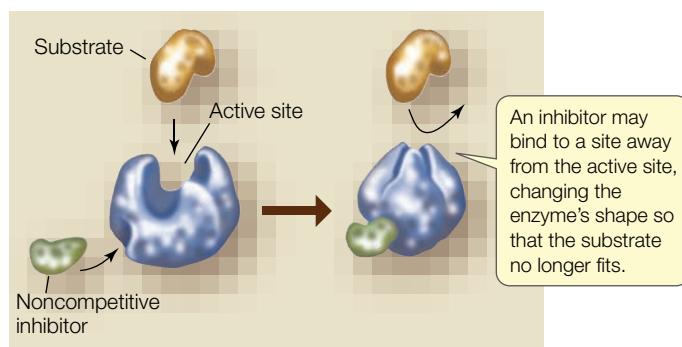


**8.15 Irreversible Inhibition** DIPF forms a stable covalent bond with the side chain of the amino acid serine at the active site of the enzyme acetylcholinesterase, thus irreversibly disabling the enzyme.

## (A) Competitive inhibition



## (B) Noncompetitive inhibition



**8.16 Reversible Inhibition** (A) A competitive inhibitor binds temporarily to the active site of an enzyme. (B) A noncompetitive inhibitor binds temporarily to the enzyme at a site away from the active site. In both cases, the enzyme's function is disabled for only as long as the inhibitor remains bound.

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Other molecules, collectively referred to as effectors, can influence which form the enzyme takes:

- Binding of an inhibitor to a site separate from the active site can stabilize the inactive form of the enzyme, making it less likely to convert to the active form.
- The active form can be stabilized by the binding of an activator to another site on the enzyme.

Like substrate binding, the binding of inhibitors and activators to their regulatory sites (also called allosteric sites) is highly specific. Most (but not all) enzymes that are allosterically regulated are proteins with quaternary structure; that is, they are made up of multiple polypeptide subunits. The polypeptide that has the active site is called the catalytic subunit. The allosteric sites are often on different polypeptides, called the regulatory subunits.

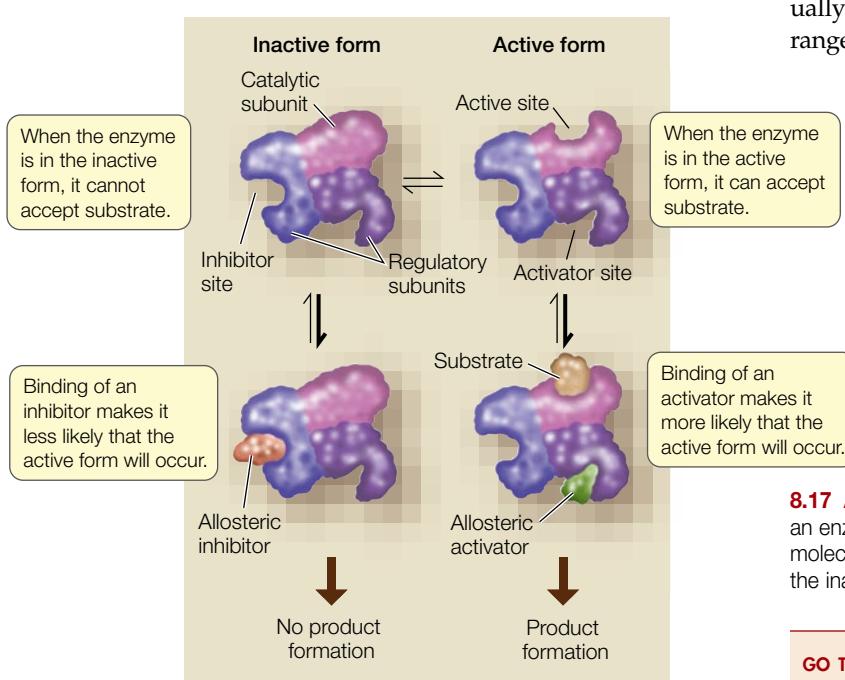
Some enzymes have multiple subunits containing active sites, and the binding of substrate to one of the active sites causes allosteric effects. When substrate binds to one subunit, there is a slight change in protein structure that influences the adjacent subunit. The slight change to the second subunit makes its active site more likely to bind to the substrate. So the reaction speeds up as the sites become sequentially activated.

As a result, an allosteric enzyme with multiple active sites and a nonallosteric enzyme with a single active site differ greatly in their reaction rates when the substrate concentration is low. Graphs of reaction rates plotted against substrate concentrations show this relationship. For a nonallosteric enzyme, the plot looks like that in **Figure 8.18A**. The reaction rate first increases sharply with increasing substrate concentration, then tapers off to a constant maximum rate as the supply of enzyme becomes saturated.

The plot for a multisubunit allosteric enzyme is radically different, having a sigmoid (S-shaped) appearance (**Figure 8.18B**). At low substrate concentrations, the reaction rate increases gradually as substrate concentration increases. But within a certain range, the reaction rate is extremely sensitive to relatively small changes in substrate concentration. In addition, allosteric enzymes are very sensitive to low concentrations of inhibitors. Because of this sensitivity, allosteric enzymes are important in regulating entire metabolic pathways.

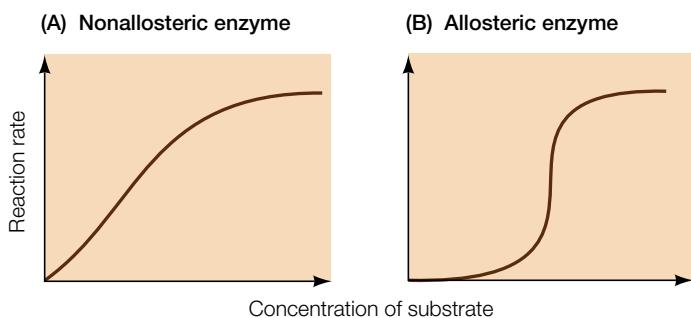
**Allosteric effects regulate metabolism**

Metabolic pathways typically involve a starting material, various intermediate products, and an end product that is used for some purpose by the cell. In each pathway there are a number of reactions, each



**8.17 Allosteric Regulation of Enzymes** Active and inactive forms of an enzyme can be interconverted, depending on the binding of effector molecules at sites other than the active site. Binding an inhibitor stabilizes the inactive form and binding an activator stabilizes the active form.

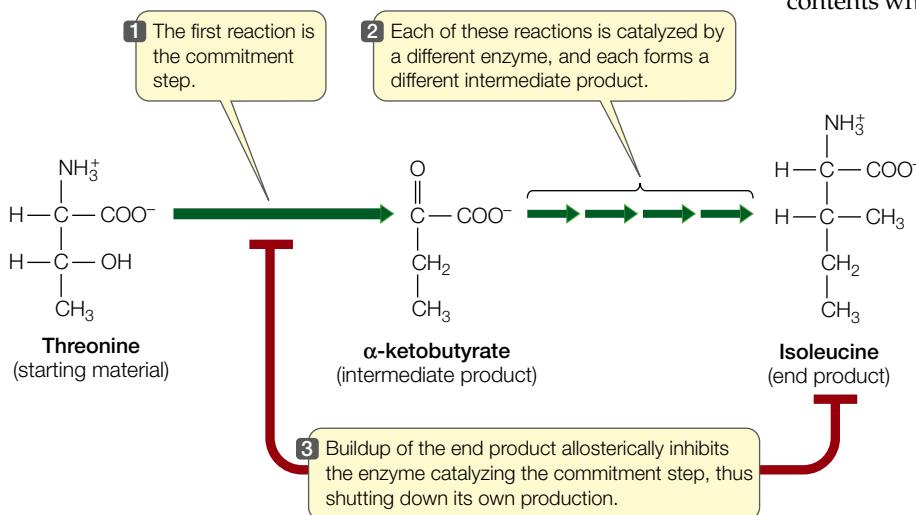
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**8.18 Allostery and Reaction Rate** The number of active sites on an enzyme determines how the rate of the enzyme-catalyzed reaction changes as substrate concentration increases. A sigmoid curve (B) is typical for an enzyme with multiple subunits, each with an active site. After one subunit binds the substrate, changes in structure make it more likely that the next subunit will also bind substrate. So the reaction speeds up more rapidly than in the case of an enzyme with a single active site (A).

forming an intermediate product and each catalyzed by a different enzyme. The first step in a pathway is called the commitment step, meaning that once this enzyme-catalyzed reaction occurs, the “ball is rolling,” and the other reactions happen in sequence, leading to the end product. But what if the cell has no need for that product—for example, if that product is available from its environment in adequate amounts? It would be energetically wasteful for the cell to continue making something it does not need.

One way to avoid this problem is to shut down the metabolic pathway by having the final product inhibit the enzyme that catalyzes the commitment step (**Figure 8.19**). Often this inhibition occurs allosterically. When the end product is present at a high concentration, some of it binds to an allosteric site on the commitment step enzyme, thereby causing it to become inactive. Thus, the final product acts as a *noncompetitive inhibitor* (described earlier in this section) of the first enzyme in the pathway. This mechanism is known as feedback inhibition or end-product inhibition. We will describe many other examples of such inhibition in later chapters.



### Enzymes are affected by their environment

Enzymes enable cells to perform chemical reactions and carry out complex processes rapidly without using the extremes of temperature and pH employed by chemists in the laboratory. However, because of their three-dimensional structures and the chemistry of the side chains in their active sites, enzymes (and their substrates) are highly sensitive to changes in temperature and pH. In Section 3.2 we describe the general effects of these environmental factors on proteins. Here we will examine their effects on enzyme function (which, of course, depends on enzyme structure and chemistry).

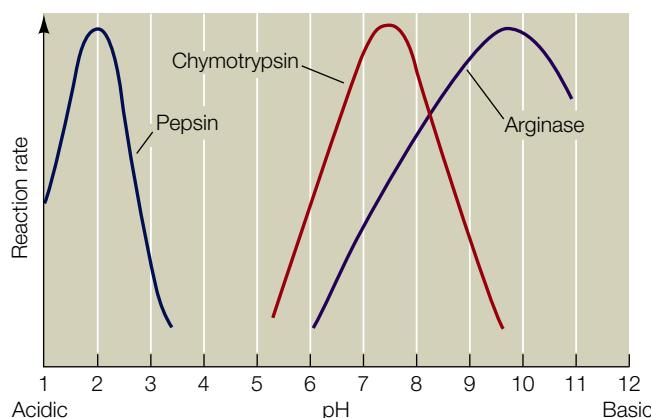
**pH AFFECTS ENZYME ACTIVITY** The rates of most enzyme-catalyzed reactions depend on the pH of the solution in which they occur. While the water inside cells is generally at a neutral pH of 7, the presence of acids, bases, and buffers can alter this. Each enzyme is most active at a particular pH; its activity decreases as the solution is made more acidic or more basic than the ideal (optimal) pH (**Figure 8.20**). As an example, consider the human digestive system (see Section 51.3). The pH inside the human stomach is highly acidic, around pH 1.5. Many enzymes that hydrolyze macromolecules, such as proteases, have pH optima in the neutral range. So when food enters the small intestine, a buffer (bicarbonate) is secreted into the intestine to raise the pH to 6.5. This allows the hydrolytic enzymes to be active and digest the food.

Several factors contribute to this effect. One factor is ionization of the carboxyl, amino, and other groups on either the substrate or the enzyme. In neutral or basic solutions, carboxyl groups ( $-\text{COOH}$ ) release  $\text{H}^+$  to become negatively charged carboxylate groups ( $-\text{COO}^-$ ). On the other hand, in neutral or acidic solutions, amino groups ( $-\text{NH}_2$ ) accept  $\text{H}^+$  to become positively charged  $-\text{NH}_3^+$  groups (see the discussion of acids and bases in Section 2.4). Thus, in a neutral solution, an amino group is electrically attracted to a carboxyl group on another molecule or another part of the same molecule, because both groups are ionized and have opposite charges. If the pH changes, however, the ionization of these groups may change. For example, at a low pH (high  $\text{H}^+$  concentration, such as the stomach contents where the enzyme pepsin is active), the excess  $\text{H}^+$  may

react with  $-\text{COO}^-$  to form  $-\text{COOH}$ . If this happens, the group is no longer charged and cannot interact with other charged groups in the protein, so the folding of the protein may be altered. If such a change occurs at the active site of an enzyme, the enzyme may no longer be able to bind to its substrate.

### 8.19 Feedback Inhibition of Metabolic Pathways

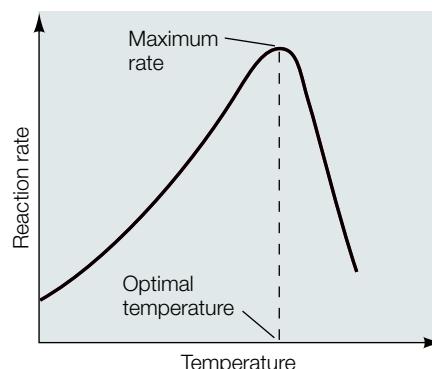
The first reaction in a metabolic pathway is referred to as the commitment step. It is often catalyzed by an enzyme that can be allosterically inhibited by the end product of the pathway. The specific pathway shown here is the synthesis of isoleucine from threonine in bacteria. It is typical of many enzyme-catalyzed biosynthetic pathways.



**8.20 pH Affects Enzyme Activity** An enzyme catalyzes its reaction at a maximum rate. The activity curve for each enzyme peaks at its optimal pH. For example, pepsin is active in the acidic environment of the stomach, while chymotrypsin is active in the small intestine.

**TEMPERATURE AFFECTS ENZYME ACTIVITY** In general, warming increases the rate of a chemical reaction because a greater proportion of the reactant molecules have enough kinetic energy to provide the activation energy for the reaction. Enzyme-catalyzed reactions are no different (Figure 8.21). However, temperatures that are too high inactivate enzymes, because at high temperatures enzyme molecules vibrate and twist so rapidly that some of their noncovalent bonds break. When an enzyme's tertiary structure is changed by heat it loses its function. Some enzymes denature at temperatures only slightly above that of the human body, but a few are stable even at the boiling point (or freezing point) of water. All enzymes, however, have an optimal temperature for activity.

Individual organisms adapt to changes in the environment in many ways, one of which is based on groups of enzymes, called *isozymes*, that catalyze the same reaction but have different chemical compositions and physical properties. Different isozymes within a given group may have different optimal temperatures. The rainbow trout, for example, has several isozymes of the enzyme acetylcholinesterase. If a rainbow trout is transferred from warm water to near-freezing water (2°C), the fish produces an isozyme of acetylcholinesterase that is different from the one it produces at the higher temperature. The new isozyme has a lower optimal temperature, allowing the fish's nervous system to perform normally in the colder water.



**8.21 Temperature Affects Enzyme Activity** Each enzyme is most active at a particular optimal temperature. At higher temperatures the enzyme becomes denatured and inactive; this explains why the activity curve falls off abruptly at temperatures above the optimal.

In general, enzymes adapted to warm temperatures do not denature at those temperatures because their tertiary structures are held together largely by covalent bonds, such as charge interactions or disulfide bridges, instead of the more heat-sensitive weak chemical interactions. Most enzymes in humans are more stable at high temperatures than those of the bacteria that infect us, so that a moderate fever tends to denature bacterial enzymes, but not our own.

## 8.5 RECAP

The rates of most enzyme-catalyzed reactions are affected by interacting molecules (such as inhibitors and activators) and by environmental factors (such as temperature and pH).

- What is the difference between reversible and irreversible enzyme inhibition? See pp. 161–162
- How are allosteric enzymes regulated? See pp. 162–163 and Figure 8.17
- Explain the concept of feedback inhibition. How might the reactions shown in Figure 8.19 fit into a systems diagram such as the one shown in Figure 8.14?

## CHAPTER SUMMARY

### 8.1 What Physical Principles Underlie Biological Energy Transformations?

- Energy is the capacity to do work. In a biological system, the usable energy is called **free energy (G)**. The unusable energy is **entropy**, a measure of the disorder in the system.
- **Potential energy** is the energy of state or position; it includes the energy stored in chemical bonds. **Kinetic energy** is the energy of motion; it is the type of energy that can do work.

- The **laws of thermodynamics** apply to living organisms. The first law states that energy cannot be created or destroyed. The second law states that energy transformations decrease the amount of energy available to do work (free energy) and increase disorder. Review Figure 8.2
- The **change in free energy ( $\Delta G$ )** of a reaction determines its point of **chemical equilibrium**, at which the forward and reverse reactions proceed at the same rate.

- An **exergonic reaction** releases free energy and has a negative  $\Delta G$ . An **endergonic reaction** consumes or requires free energy and has a positive  $\Delta G$ . Endergonic reactions proceed only if free energy is provided. [Review Figure 8.3](#)
- Metabolism** is the sum of all the biochemical (metabolic) reactions in an organism. **Catabolic reactions** are associated with the breakdown of complex molecules and release energy (are exergonic). **Anabolic reactions** build complexity in the cell and are endergonic.

## 8.2 What Is the Role of ATP in Biochemical Energetics?

- Adenosine triphosphate (ATP)** serves as an energy currency in cells. Hydrolysis of ATP releases a relatively large amount of free energy.
- The **ATP cycle** couples exergonic and endergonic reactions, harvesting free energy from exergonic reactions, and providing free energy for endergonic reactions. [Review Figure 8.6](#), [WEB ACTIVITY 8.1](#)

## 8.3 What Are Enzymes?

- The rate of a chemical reaction is independent of  $\Delta G$ , but is determined by the **energy barrier**. **Enzymes** are protein catalysts that affect the rates of biological reactions by lowering the energy barrier, supplying the **activation energy ( $E_a$ )** needed to initiate reactions. [Review Figure 8.10](#), [WEB ACTIVITY 8.2](#)
- A **substrate** binds to the enzyme's **active site**—the site of catalysis—forming an **enzyme–substrate complex**. Enzymes are highly specific for their substrates.

## 8.4 How Do Enzymes Work?

- At the active site, a substrate can be oriented correctly, chemically modified, or strained. As a result, the substrate readily forms its **transition state**, and the reaction proceeds. [Review Figure 8.11](#)
- Binding substrate causes many enzymes to change shape, exposing their active site(s) and allowing catalysis. The change in enzyme shape caused by substrate binding is known as **induced fit**. [Review Figure 8.12](#)
- Some enzymes require other substances, known as **cofactors**, to carry out catalysis. **Prosthetic groups** are permanently bound to enzymes; **coenzymes** are not. A coenzyme can be considered a substrate, as it is changed by the reaction and then released from the enzyme.
- Substrate concentration affects the rate of an enzyme-catalyzed reaction.

## 8.5 How Are Enzyme Activities Regulated?

- Metabolism is organized into pathways in which the product of one reaction is a reactant for the next reaction. Each reaction in the pathway is catalyzed by an enzyme.
- Enzyme activity is subject to regulation. Some inhibitors bind irreversibly to enzymes. Others bind reversibly. [Review Figures 8.15 and 8.16](#), [ANIMATED TUTORIAL 8.1](#)
- An **allosteric effector** binds to a site other than the active site and stabilizes the active or inactive form of an enzyme. [Review Figure 8.17](#), [ANIMATED TUTORIAL 8.2](#)
- The end product of a metabolic pathway may inhibit an enzyme that catalyzes the **commitment step** of that pathway. [Review Figure 8.19](#)
- Enzymes are sensitive to their environments. Both pH and temperature affect enzyme activity. [Review Figures 8.20 and 8.21](#)

## SELF-QUIZ

- Coenzymes differ from enzymes in that coenzymes are
  - only active outside the cell.
  - polymers of amino acids.
  - smaller molecules, such as vitamins.
  - specific for one reaction.
  - always carriers of high-energy phosphate.
- Which statement about thermodynamics is true?
  - Free energy is used up in an exergonic reaction.
  - Free energy cannot be used to do work.
  - The total amount of energy can change after a chemical transformation.
  - Free energy can be kinetic but not potential energy.
  - Entropy has a tendency to increase.
- In a chemical reaction,
  - the rate depends on the value of  $\Delta G$ .
  - the rate depends on the activation energy.
  - the entropy change depends on the activation energy.
  - the activation energy depends on the value of  $\Delta G$ .
  - the change in free energy depends on the activation energy.
- Which statement about enzymes is *not* true?
  - They usually consist of proteins.
  - They change the rate of the catalyzed reaction.
  - They change the  $\Delta G$  of the reaction.
  - They are sensitive to heat.
  - They are sensitive to pH.
- The active site of an enzyme
  - never changes shape.
  - forms no chemical bonds with substrates.
  - determines, by its structure, the specificity of the enzyme.
  - looks like a lump projecting from the surface of the enzyme.
  - changes the  $\Delta G$  of the reaction.
- The molecule ATP is
  - a component of most proteins.
  - high in energy because of the presence of adenine.
  - required for many energy-transforming biochemical reactions.
  - a catalyst.
  - used in some exergonic reactions to provide energy.
- In an enzyme-catalyzed reaction,
  - a substrate does not change.
  - the rate decreases as substrate concentration increases.
  - the enzyme can be permanently changed.
  - strain may be added to a substrate.
  - the rate is not affected by substrate concentration.

8. Which statement about enzyme inhibitors is *not* true?
    - a. A competitive inhibitor binds the active site of the enzyme.
    - b. An allosteric inhibitor binds a site on the active form of the enzyme.
    - c. A noncompetitive inhibitor binds a site other than the active site.
    - d. Noncompetitive inhibition cannot be completely overcome by the addition of more substrate.
    - e. Competitive inhibition can be completely overcome by the addition of more substrate.
  9. Which statement about the feedback inhibition of enzymes is *not* true?
    - a. It is usually exerted through allosteric effects.
- b. It is directed at the enzyme that catalyzes the commitment step in a metabolic pathway.
  - c. It affects the rate of reaction, not the concentration of enzyme.
  - d. It acts by permanently modifying the active site.
  - e. It is an example of reversible inhibition.
10. Which statement about temperature effects is *not* true?
    - a. Raising the temperature may reduce the activity of an enzyme.
    - b. Raising the temperature may increase the activity of an enzyme.
    - c. Raising the temperature may denature an enzyme.
    - d. Some enzymes are stable at the boiling point of water.
    - e. All enzymes have the same optimal temperature.

## FOR DISCUSSION

1. What makes it possible for endergonic reactions to proceed in organisms?
2. Consider two proteins: one is an enzyme dissolved in the cytosol of a cell, the other is an ion channel in its plasma membrane. Contrast the structures of the two proteins, indicating at least two important differences.
3. Plot free energy versus the time course of an endergonic reaction, and the same for an exergonic reaction. Include

the activation energy on both plots. Label  $E_a$  and  $\Delta G$  on both graphs.

4. Consider an enzyme that is subject to allosteric regulation. If a competitive inhibitor (not an allosteric inhibitor) is added to a solution containing such an enzyme, the ratio of enzyme molecules in the active form to those in the inactive form increases. Explain this observation.

## ADDITIONAL INVESTIGATION

In humans, hydrogen peroxide ( $H_2O_2$ ) is a dangerous toxin produced as a by-product of several metabolic pathways. The accumulation of  $H_2O_2$  is prevented by its conversion to harmless  $H_2O$ , a reaction catalyzed by the appropriately named enzyme catalase. Air pollutants can inhibit this enzyme and leave indi-

viduals susceptible to tissue damage by  $H_2O_2$ . How would you investigate whether catalase has an allosteric or a nonallosteric mechanism, and whether the pollutants are acting as competitive or noncompetitive inhibitors?

## 9

# Pathways that Harvest Chemical Energy

## Of mice and marathons

Like success in your biology course, winning a prestigious marathon comes only after a lot of hard work. Distance runners have more mitochondria in the leg muscles than most of us. The chemical energy stored in the bonds of ATP in those mitochondria is converted into mechanical energy to move the muscles.

There are two types of muscle fibers. Most people have about equal proportions of each type. But in a top marathon racer, 90 percent of the body's muscle is made up of so-called *slow-twitch* fibers. Cells of these fibers have lots of mitochondria and use oxygen to break down fats and carbohydrates, forming ATP. In contrast, the muscles of sprinters are about 80 percent *fast-twitch* fibers, which have fewer mitochondria. Fast-twitch fibers generate short bursts of ATP in the absence of O<sub>2</sub>, but the ATP is soon used up. Extensive research with athletes has shown that training can improve the efficiency of blood circulation to the muscle fibers, providing more oxygen, and can even change the ratio of fast-twitch to slow-twitch fibers.

Now enter Marathon Mouse. No, this is not a cartoon character or a computer game, but a very real mouse that was genetically programmed by Ron Evans at the Salk Institute to express high levels of the protein PPARδ in its muscles. This protein is a receptor located inside cell nuclei, where it regulates the transcription of genes involved with the breakdown of fat to yield ATP. Evans's mouse was supposed to break down fats better, and thus be leaner—but there was an unexpected bonus. With high levels of PPARδ came an increase in slow-twitch fibers and a decrease in fast-twitch ones. It was as if the mouse had been in marathon training for a long time!

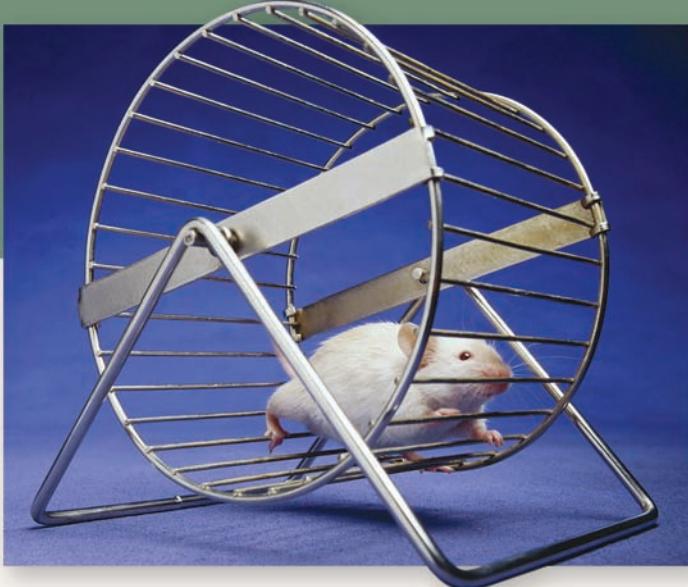
Marathon mice are leaner and meaner than ordinary mice. Leaner, because they are good at burning fat; and meaner in terms of their ability to run long distances. On an exercise wheel, a normal mouse can run for 90 minutes and about a half-mile (900 meters) before it gets tired. PPARδ-enhanced mice can run almost twice as long and twice as far—marks of true distance runners. Could we

also manipulate genes to enhance performance (and fat burning) in humans?

The genetic engineering of people, if it is feasible, is probably far in the future. But implanting genetically altered muscle tissue is actually not such a far-fetched idea, and has already raised concerns over improper athletic enhancement. More likely in the near term is the use of an experimental drug called Aicar, which activates the PPARδ



**Marathon Men** It takes a lot of training to run a marathon. One of the results of all that training is that the leg muscles become packed with slow-twitch muscle fibers, containing cells rich in energy-metabolizing mitochondria.



**Marathon Mouse** This mouse can run for much longer than a normal mouse because its energy metabolism has been genetically altered.

protein. When Evans and colleagues gave the drug to normal mice, they achieved the same results as with the genetically modified mice. A test for Aicar in blood and urine has been developed to prevent its use by human athletes to gain a competitive advantage. Of more importance is the drug's potential in the treatment of obesity and diabetes, since the drug stimulates fat breakdown. Obesity is a key part of a disorder called metabolic syndrome, which also includes high blood pressure, heart disease, and diabetes.

The free energy trapped in ATP is the energy you use all the time to fuel both conscious actions, like running a marathon or turning the pages of a book, and your body's automatic actions, such as breathing or contracting your heart muscles.

**IN THIS CHAPTER** we will describe how cells extract usable energy from food, usually in the form of ATP. We describe the general principles of energy transformations in cells, and illustrate these principles by describing the pathways for the catabolism of glucose in the presence and absence of O<sub>2</sub>. Finally, we describe the relationships between the metabolic pathways that use and produce the four biologically important classes of molecules—carbohydrates, fats, proteins, and nucleic acids.

## CHAPTER OUTLINE

- 9.1 How Does Glucose Oxidation Release Chemical Energy?
- 9.2 What Are the Aerobic Pathways of Glucose Metabolism?
- 9.3 How Does Oxidative Phosphorylation Form ATP?
- 9.4 How Is Energy Harvested from Glucose in the Absence of Oxygen?
- 9.5 How Are Metabolic Pathways Interrelated and Regulated?

### 9.1 How Does Glucose Oxidation Release Chemical Energy?

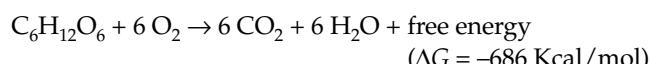
Energy is stored in the covalent bonds of fuels, and it can be released and transformed. Wood burning in a campfire releases energy as heat and light. In cells, fuel molecules release chemical energy that is used to make ATP, which in turn drives endergonic reactions. ATP is central to the energy transformations of all living organisms. Photosynthetic organisms use energy from sunlight to synthesize their own fuels, as we describe in Chapter 10. In nonphotosynthetic organisms, the most common chemical fuel is the sugar glucose (C<sub>6</sub>H<sub>12</sub>O<sub>6</sub>). Other molecules, including other carbohydrates, fats, and proteins, can also supply energy. However, to release their energy they must be converted into glucose or intermediate compounds that can enter into the various pathways of glucose metabolism.

In this section we explore how cells obtain energy from glucose by the chemical process of oxidation, which is carried out through a series of metabolic pathways. Five principles govern metabolic pathways:

- A complex chemical transformation occurs in a series of separate reactions that form a metabolic pathway.
- Each reaction is catalyzed by a specific enzyme.
- Most metabolic pathways are similar in all organisms, from bacteria to humans.
- In eukaryotes, many metabolic pathways are compartmentalized, with certain reactions occurring inside specific organelles.
- Each metabolic pathway is regulated by key enzymes that can be inhibited or activated, thereby determining how fast the reactions will go.

#### Cells trap free energy while metabolizing glucose

As we saw in Section 2.3, the familiar process of combustion (burning) is very similar to the chemical processes that release energy in cells. If glucose is burned in a flame, it reacts with oxygen gas (O<sub>2</sub>), forming carbon dioxide and water and releasing energy in the form of heat. The balanced equation for the complete combustion reaction is



This is an oxidation-reduction reaction. Glucose ( $C_6H_{12}O_6$ ) becomes completely oxidized and six molecules of  $O_2$  are reduced to six molecules of water. The energy that is released can be used to do work. The same equation applies to the overall metabolism of glucose in cells. However, in contrast to combustion, the metabolism of glucose is a multistep pathway—each step is catalyzed by an enzyme, and the process is compartmentalized. Unlike combustion, glucose metabolism is tightly regulated and occurs at temperatures compatible with life.

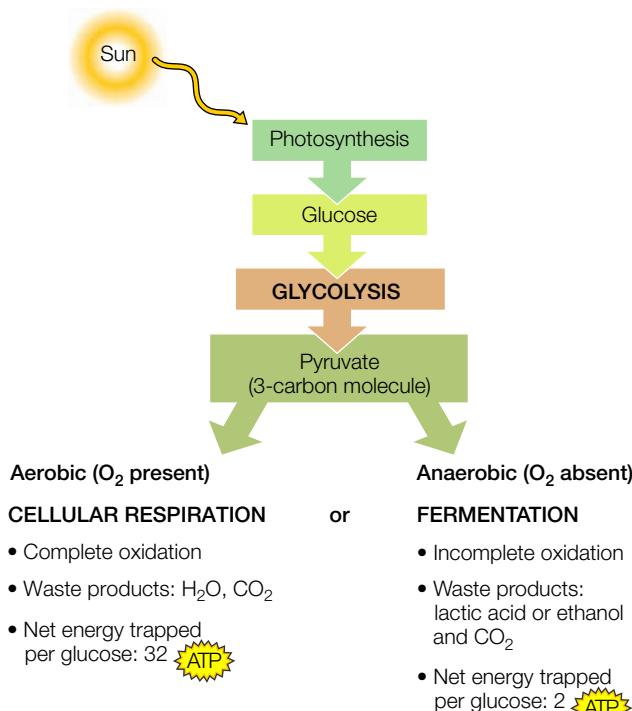
The glucose metabolism pathway “traps” the energy stored in the covalent bonds of glucose and stores it instead in ATP molecules, via the phosphorylation reaction:



As we introduce in Chapter 8, ATP is the energy currency of cells. The energy trapped in ATP can be used to do cellular work—such as movement of muscles or active transport across membranes—just as the energy captured from combustion can be used to do work.

The change in free energy ( $\Delta G$ ) resulting from the complete conversion of glucose and  $O_2$  to  $CO_2$  and water, whether by combustion or by metabolism, is  $-686\text{ kcal/mol}$  ( $-2,870\text{ kJ/mol}$ ). Thus the overall reaction is highly exergonic and can drive the endergonic formation of a great deal of ATP from ADP and phosphate. Note that in the discussion that follows, “energy” means free energy.

Three metabolic processes harvest the energy in the chemical bonds of glucose: glycolysis, cellular respiration, and fermentation (Figure 9.1). All three processes involve pathways made up of many distinct chemical reactions.



**9.1 Energy for Life** Living organisms obtain their energy from the food compounds produced by photosynthesis. They convert these compounds into glucose, which they metabolize to trap energy in ATP.

- **Glycolysis** begins glucose metabolism in all cells. Through a series of chemical rearrangements, glucose is converted to two molecules of the three-carbon product **pyruvate**, and a small amount of energy is captured in usable forms. Glycolysis is an **anaerobic** process because it does not require  $O_2$ .

- **Cellular respiration** uses  $O_2$  from the environment, and thus it is **aerobic**. Each pyruvate molecule is completely converted into three molecules of  $CO_2$  through a set of metabolic pathways including pyruvate oxidation, the citric acid cycle, and an electron transport system (the respiratory chain). In the process, a great deal of the energy stored in the covalent bonds of pyruvate is captured to form ATP.

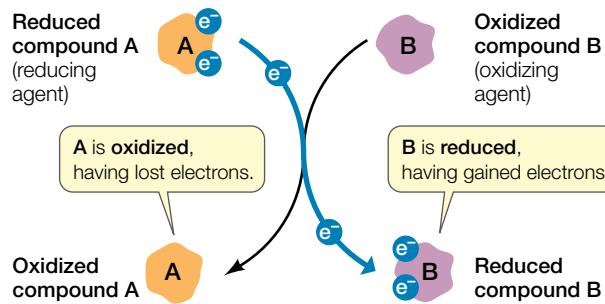
- **Fermentation** does not involve  $O_2$  (it is anaerobic). Fermentation converts pyruvate into lactic acid or ethyl alcohol (ethanol), which are still relatively energy-rich molecules. Because the breakdown of glucose is incomplete, much less energy is released by fermentation than by cellular respiration.

### Redox reactions transfer electrons and energy

As is illustrated in Figure 8.6, the addition of a phosphate group to ADP to make ATP is an endergonic reaction that can extract and transfer energy from exergonic to endergonic reactions. Another way of transferring energy is to transfer electrons. A reaction in which one substance transfers one or more electrons to another substance is called an oxidation–reduction reaction, or **redox** reaction.

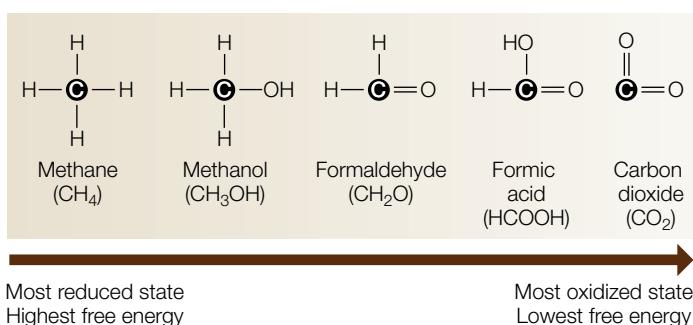
- **Reduction** is the gain of one or more electrons by an atom, ion, or molecule.
- **Oxidation** is the loss of one or more electrons.

Oxidation and reduction *always occur together*: as one chemical is oxidized, the electrons it loses are transferred to another chemical, reducing it. In a redox reaction, we call the reactant that becomes reduced an **oxidizing agent** and the one that becomes oxidized a **reducing agent**:



In both the combustion and the metabolism of glucose, glucose is the reducing agent (electron donor) and  $O_2$  is the oxidizing agent (electron acceptor).

Although oxidation and reduction are always defined in terms of traffic in electrons, it is often helpful to think in terms of the gain or loss of hydrogen atoms. Transfers of hydrogen atoms involve transfers of electrons ( $H = H^+ + e^-$ ). So when a molecule loses hydrogen atoms, it becomes oxidized.

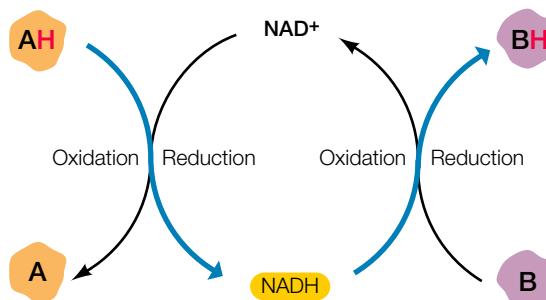


**9.2 Oxidation, Reduction, and Energy** The more oxidized a carbon atom in a molecule is, the less its free energy.

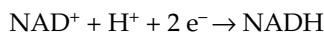
In general, the more reduced a molecule is, the more energy is stored in its covalent bonds (Figure 9.2). In a redox reaction, some energy is transferred from the reducing agent to the reduced product. The rest remains in the reducing agent or is lost to entropy. As we will see, some of the key reactions of glycolysis and cellular respiration are highly exergonic redox reactions.

### The coenzyme $\text{NAD}^+$ is a key electron carrier in redox reactions

Section 8.4 describes the role of coenzymes, small molecules that assist in enzyme-catalyzed reactions. ADP acts as a coenzyme when it picks up energy released in an exergonic reaction and packages it to form ATP. On the other hand, the coenzyme nicotinamide adenine dinucleotide ( $\text{NAD}^+$ ) acts as an electron carrier in redox reactions:

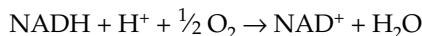


As you can see,  $\text{NAD}^+$  exists in two chemically distinct forms, one oxidized ( $\text{NAD}^+$ ) and the other reduced ( $\text{NADH}$ ) (Figure 9.3). Both forms participate in redox reactions. The reduction reaction



is actually the transfer of a proton (the hydrogen ion,  $\text{H}^+$ ) and two electrons, which are released by the accompanying oxidization reaction.

The electrons do not remain with the coenzyme. Oxygen is highly electronegative and readily accepts electrons from  $\text{NADH}$ . The oxidation of  $\text{NADH}$  by  $\text{O}_2$  (which occurs in several steps)



is highly exergonic, with a  $\Delta G$  of  $-52.4 \text{ kcal/mol}$  ( $-219 \text{ kJ/mol}$ ). Note that the oxidizing agent appears here as “ $\frac{1}{2} \text{O}_2$ ” instead of “ $\text{O}_2$ .” This notation emphasizes that it is molecular oxygen,  $\text{O}_2$ , that acts as the oxidizing agent.

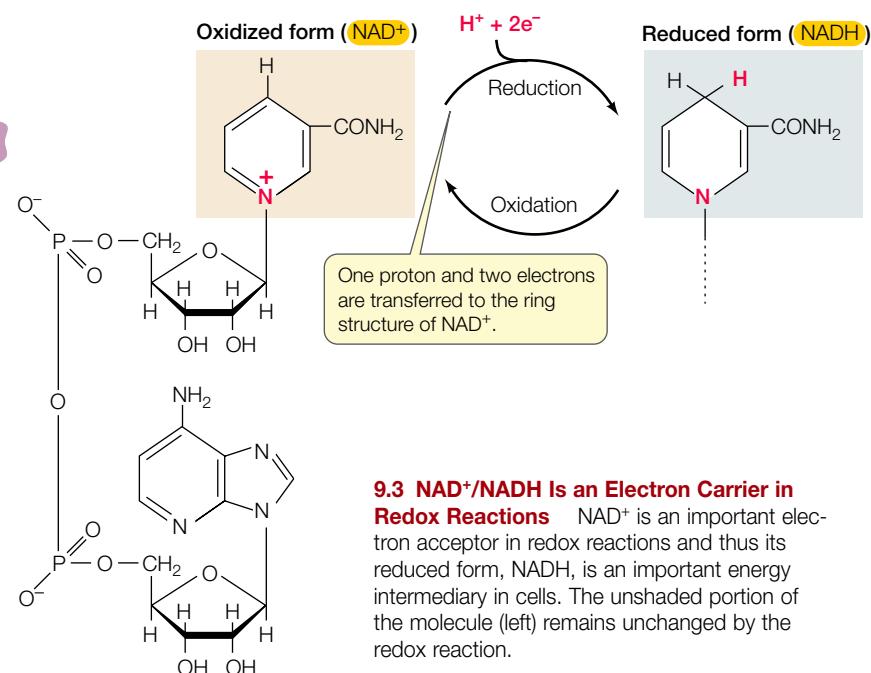
Just as a molecule of ATP can be thought of as a package of about  $12 \text{ kcal/mol}$  ( $50 \text{ kJ/mol}$ ) of free energy,  $\text{NADH}$  can be thought of as a larger package of free energy (approximately  $50 \text{ kcal/mol}$ , or  $200 \text{ kJ/mol}$ ).  $\text{NAD}^+$  is a common electron carrier in cells, but not the only one. Another carrier, flavin adenine dinucleotide (FAD), also transfers electrons during glucose metabolism.

### An overview: Harvesting energy from glucose

The energy-harvesting processes in cells use different combinations of metabolic pathways depending on the presence or absence of  $\text{O}_2$ :

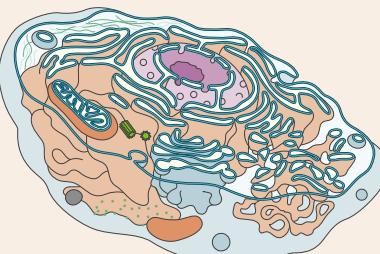
- Under aerobic conditions, when  $\text{O}_2$  is available as the final electron acceptor, four pathways operate (Figure 9.4A). Glycolysis is followed by the three pathways of cellular respiration: pyruvate oxidation, the citric acid cycle (also called the Krebs cycle or the tricarboxylic acid cycle), and electron transport/ATP synthesis (also called the respiratory chain).
- Under anaerobic conditions when  $\text{O}_2$  is unavailable, pyruvate oxidation, the citric acid cycle, and the respiratory chain do not function, and the pyruvate produced by glycolysis is further metabolized by fermentation (Figure 9.4B).

These five metabolic pathways occur in different locations in the cell (Table 9.1).



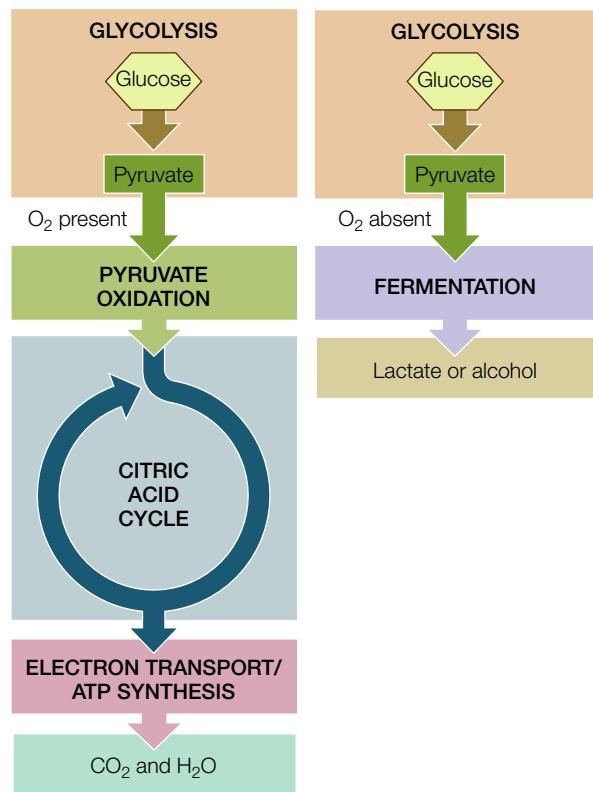
**9.3  $\text{NAD}^+/\text{NADH}$  Is an Electron Carrier in Redox Reactions**  $\text{NAD}^+$  is an important electron acceptor in redox reactions and thus its reduced form,  $\text{NADH}$ , is an important energy intermediary in cells. The unshaded portion of the molecule (left) remains unchanged by the redox reaction.

**TABLE 9.1**  
**Cellular Locations for Energy Pathways in Eukaryotes and Prokaryotes**

EUKARYOTES	PROKARYOTES
	<b>External to mitochondrion</b> Glycolysis Fermentation
<b>Inside mitochondrion</b> Inner membrane Respiratory chain Matrix Citric acid cycle Pyruvate oxidation	<b>In cytoplasm</b> Glycolysis Fermentation Citric acid cycle <b>On plasma membrane</b> Pyruvate oxidation Respiratory chain

[yourBioPortal.com](http://yourBioPortal.com)  
GO TO Web Activity 9.1 • Energy Pathways in Cells

(A) Glycolysis and cellular respiration      (B) Glycolysis and fermentation



**9.4 Energy-Producing Metabolic Pathways** Energy-producing reactions can be grouped into five metabolic pathways: glycolysis, pyruvate oxidation, the citric acid cycle, the respiratory chain/ATP synthesis, and fermentation. (A) The three lower pathways occur only in the presence of  $O_2$  and are collectively referred to as cellular respiration. (B) When  $O_2$  is unavailable, glycolysis is followed by fermentation.

[yourBioPortal.com](http://yourBioPortal.com)  
GO TO Web Activity 9.2 • Glycolysis and Fermentation

## 9.1 RECAP

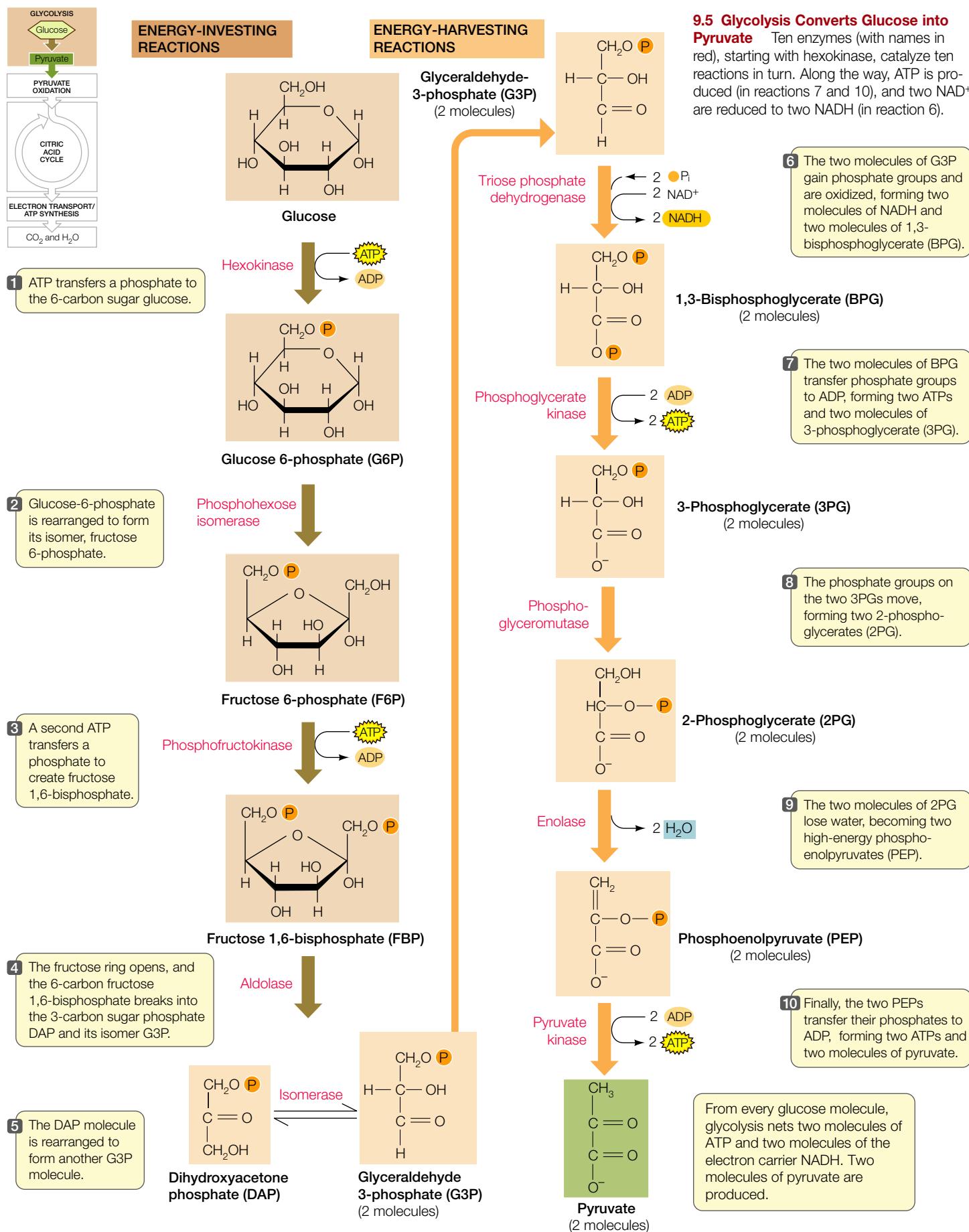
The free energy released from the oxidation of glucose is trapped in the form of ATP. Five metabolic pathways combine in different ways to produce ATP, which supplies the energy for myriad other reactions in living cells.

- What principles govern metabolic pathways in cells? [See p. 169](#)
- Describe how the coupling of oxidation and reduction transfers energy from one molecule to another. [See pp. 170–171](#)
- Explain the roles of  $NAD^+$  and  $O_2$  with respect to electrons in a redox reaction. [See p. 171 and Figure 9.3](#)

Now that you have an overview of the metabolic pathways that harvest energy from glucose, let's take a closer look at the three pathways involved in aerobic catabolism: glycolysis, pyruvate oxidation, and the citric acid cycle.

## 9.2 What Are the Aerobic Pathways of Glucose Metabolism?

The aerobic pathways of glucose metabolism oxidize glucose completely to  $CO_2$  and  $H_2O$ . Initially, the glycolysis reactions convert the six-carbon glucose molecule to two 3-carbon pyruvate molecules (**Figure 9.5**). Pyruvate is then converted to  $CO_2$  in a second series of reactions beginning with pyruvate oxidation and followed by the citric acid cycle. In addition to generating  $CO_2$ , the oxidation events are coupled with the reduction of electron carriers, mostly  $NAD^+$ . So much of the chemical energy in the C—C and C—H bonds of glucose is transferred to NADH. Ultimately, this energy will be transferred to ATP, but this comes in a separate series of reactions involving electron transport, called the respiratory chain. In the respiratory chain, redox reactions result in the oxidative phosphorylation of ADP by ATP synthase. We will begin our consideration of the metabolism of glucose with a closer look at glycolysis.



Glycolysis takes place in the cytosol. It converts glucose into pyruvate, produces a small amount of energy, and generates no  $\text{CO}_2$ . During glycolysis, some of the covalent bonds between carbon and hydrogen in the glucose molecule are oxidized, releasing some of the stored energy. The ten enzyme-catalyzed reactions of glycolysis result in the net production of two molecules of pyruvate (pyruvic acid), two molecules of ATP, and two molecules of NADH. Glycolysis can be divided into two stages: energy-investing reactions that consume ATP, and energy-harvesting reactions that produce ATP (see Figure 9.5). We'll begin with the energy-investing reactions.

### The energy-investing reactions 1–5 of glycolysis require ATP

Using Figure 9.5 as a guide, let's work our way through the glycolytic pathway.

Two of the reactions (1 and 3 in Figure 9.5), involve the transfer of phosphate groups from ATP to form phosphorylated intermediates. The second of these intermediates, fructose 1,6-bisphosphate, has a free energy substantially higher than that of glucose. Later in the pathway, these phosphate groups are transferred to ADP to make new molecules of ATP. Although both of these steps use ATP as a substrate, each is catalyzed by a different, specific enzyme.

*In reaction 1*, the enzyme hexokinase catalyzes the transfer of a phosphate group from ATP to glucose, forming the sugar phosphate glucose 6-phosphate.

*In reaction 2*, the six-membered glucose ring is rearranged into a five-membered fructose ring.

*In reaction 3*, the enzyme phosphofructokinase adds a second phosphate to the fructose ring, forming fructose 1,6-bisphosphate.

*Reaction 4* opens up the ring and cleaves it to produce two different three-carbon sugar (triose) phosphates: dihydroxyacetone phosphate and glyceraldehyde 3-phosphate.

*In reaction 5*, one of those products, dihydroxyacetone phosphate, is converted into a second molecule of the other, glyceraldehyde 3-phosphate (G3P).

In summary, by the halfway point of the glycolytic pathway, two things have happened:

- Two molecules of ATP have been invested.
- The six-carbon glucose molecule has been converted into two molecules of a three-carbon sugar phosphate, glyceraldehyde 3-phosphate (G3P).

### The energy-harvesting reactions 6–10 of glycolysis yield NADH and ATP

In the discussion that follows, remember that each reaction occurs twice for each glucose molecule because each glucose molecule has been split into two molecules of G3P. The transformation of G3P generates both NADH and ATP. Again, follow the sequence by referring to Figure 9.5.

**PRODUCING NADH** *Reaction 6* is catalyzed by the enzyme triose phosphate dehydrogenase, and its end product is a phosphate

ester, 1,3-bisphosphoglycerate (BPG). This is an exergonic oxidation reaction, and it is accompanied by a large drop in free energy—more than 100 kcal of energy is released per mole of glucose (**Figure 9.6, left**). The free energy released in this reaction is not lost to heat, but is captured by the accompanying reduction reaction. For each molecule of G3P that is oxidized, one molecule of  $\text{NAD}^+$  is reduced to make a molecule of NADH.

$\text{NAD}^+$  is present in only small amounts in the cell, and it must be recycled to allow glycolysis to continue. As we will see, NADH is oxidized back to  $\text{NAD}^+$  in the metabolic pathways that follow glycolysis.

**PRODUCING ATP** *In reactions 7–10* of glycolysis, the two phosphate groups of BPG are transferred one at a time to molecules of ADP, with a rearrangement in between. More than 20 kcal (83.6 kJ/mol) of free energy is stored in ATP for every mole of BPG broken down. Finally, we are left with two moles of pyruvate for every mole of glucose that entered glycolysis.

The enzyme-catalyzed transfer of phosphate groups from donor molecules to ADP to form ATP is called **substrate-level phosphorylation**. (Phosphorylation is the addition of a phosphate group to a molecule.) Substrate-level phosphorylation is distinct from oxidative phosphorylation, which is carried out by the respiratory chain and ATP synthase, and will be discussed later in this chapter. Reaction 7 is an example of substrate-level phosphorylation, in which phosphoglycerate kinase catalyzes the transfer of a phosphate group from BPG to ADP, forming ATP. It is exergonic, even though a substantial amount of energy is consumed in the formation of ATP.

To summarize:

- The energy-investing steps of glycolysis use the energy of hydrolysis of two ATP molecules per glucose molecule.
- The energy-releasing steps of glycolysis produce four ATP molecules per glucose molecule, so the net production of ATP is two molecules.
- The energy-releasing steps of glycolysis produce two molecules of NADH.

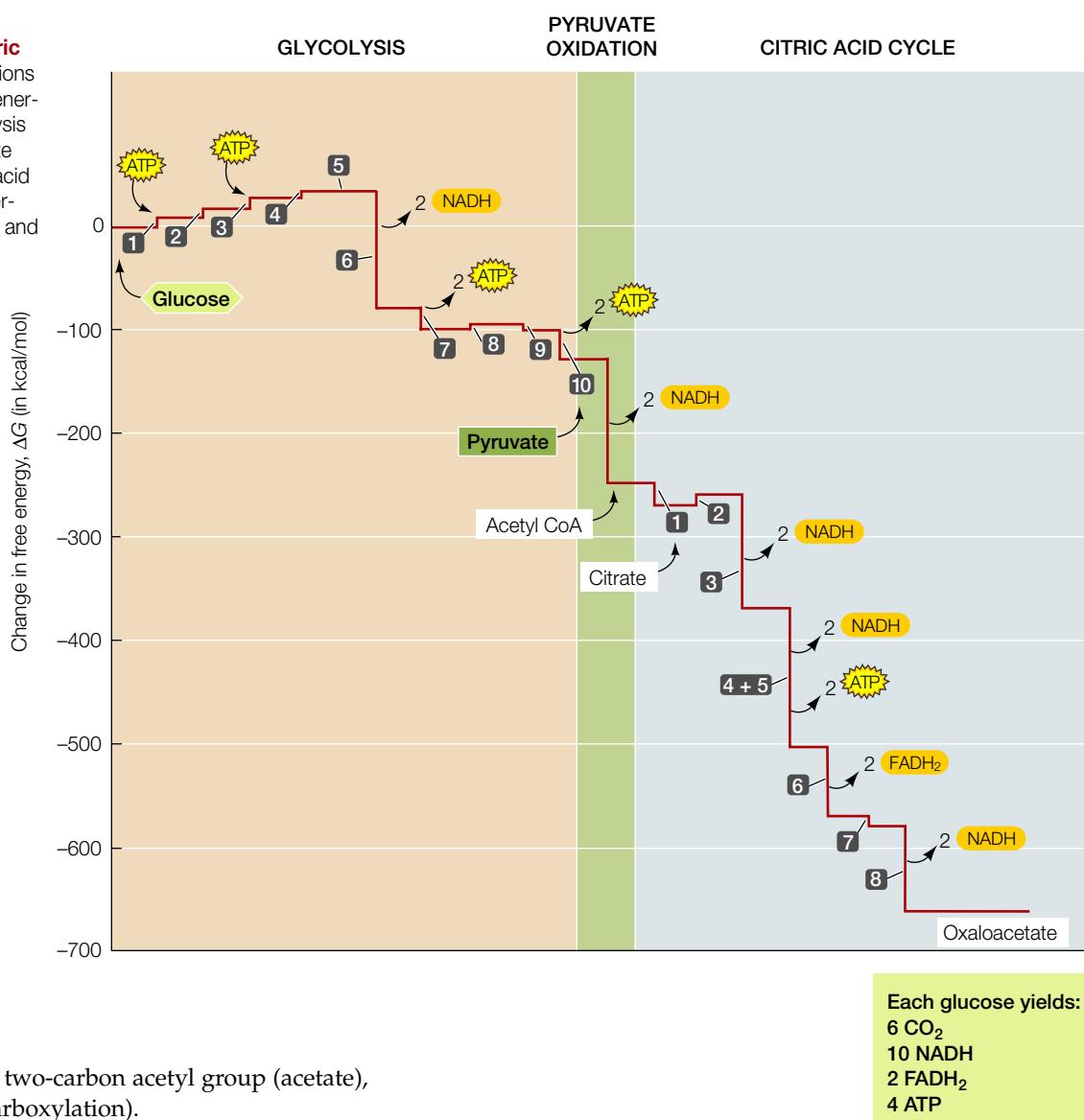
If  $\text{O}_2$  is present, glycolysis is followed by the three stages of cellular respiration: pyruvate oxidation, the citric acid cycle, and the respiratory chain/ATP synthesis.

### Pyruvate oxidation links glycolysis and the citric acid cycle

In the process of **pyruvate oxidation**, pyruvate is oxidized to the two-carbon acetate molecule, which is then converted to acetyl CoA. This is the link between glycolysis and all the other reactions of cellular respiration. **Coenzyme A (CoA)** is a complex molecule responsible for binding the two-carbon acetate molecule. Acetyl CoA formation is a multi-step reaction catalyzed by the pyruvate dehydrogenase complex, an enormous complex containing 60 individual proteins and 5 different coenzymes. In eukaryotic cells, pyruvate dehydrogenase is located in the mitochondrial matrix (see Figure 5.12). Pyruvate enters the mitochondrion by active transport, and then a series of coupled reactions takes place:

### 9.6 Changes in Free Energy During Glycolysis and the Citric Acid Cycle

The first five reactions of glycolysis (left) consume free energy, and the remaining five glycolysis reactions release energy. Pyruvate oxidation (middle) and the citric acid cycle (right) both release considerable energy. Refer to Figures 9.5 and 9.7 for the reaction numbers.



- Pyruvate is oxidized to a two-carbon acetyl group (acetate), and CO<sub>2</sub> is released (decarboxylation).
- Part of the energy from this oxidation is captured by the reduction of NAD<sup>+</sup> to NADH.
- Some of the remaining energy is stored temporarily by combining the acetyl group with CoA, forming acetyl CoA:  
 $\text{pyruvate} + \text{NAD}^+ + \text{CoA} + \text{H}^+ \rightarrow \text{acetyl CoA} + \text{NADH} + \text{CO}_2$

(In this reaction, the proton and electrons used to reduce NAD<sup>+</sup> are derived from the oxidation of both pyruvate and CoA.) Acetyl CoA has 7.5 kcal/mol (31.4 kJ/mol) more energy than simple acetate. Acetyl CoA can donate its acetyl group to various acceptor molecules, much as ATP can donate phosphate groups to various acceptors. But the main role of acetyl CoA is to donate its acetyl group to the four-carbon compound oxaloacetate, forming the six-carbon molecule citrate. This initiates the citric acid cycle, one of life's most important energy-harvesting pathways.

Arsenic, the classic poison of rodent exterminators and murder mysteries, acts by inhibiting pyruvate dehydrogenase, thus decreasing acetyl CoA production. The lack of acetyl CoA stops the citric acid cycle and all the subsequent reactions that de-

pend on it. Consequently, cells eventually run out of ATP and cannot perform essential processes that are powered by ATP hydrolysis.

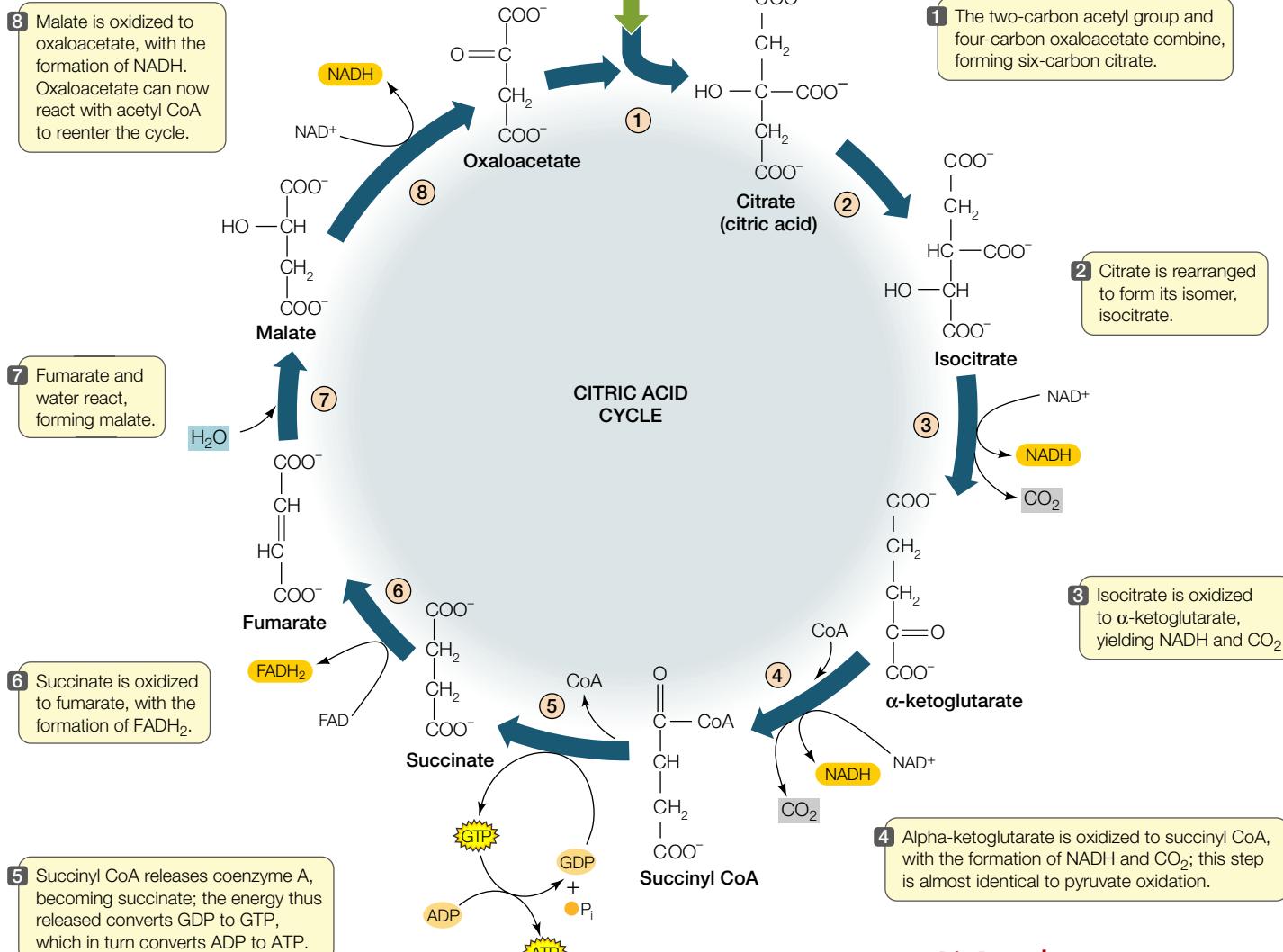
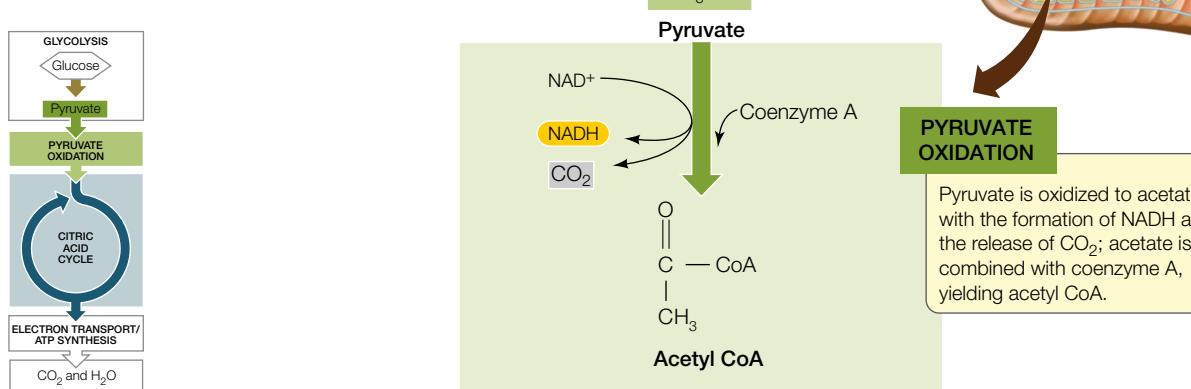
#### The citric acid cycle completes the oxidation of glucose to CO<sub>2</sub>

Acetyl CoA is the starting point for the **citric acid cycle**. This pathway of eight reactions completely oxidizes the two-carbon acetyl group to two molecules of carbon dioxide. The free energy released from these reactions is captured by ADP and the electron carriers NAD<sup>+</sup> and FAD. **Figure 9.6 right** shows the free energy changes during each step of the pathway.

The citric acid cycle is maintained in a steady state—that is, although the intermediate compounds in the cycle enter and leave it, the concentrations of those intermediates do not change much. Refer to the numbered reactions in **Figure 9.7** as you read the description of each reaction.

### 9.7 Pyruvate Oxidation and the Citric Acid Cycle

Pyruvate enters the mitochondrion and is oxidized to acetyl CoA, which enters the citric acid cycle. Reactions 3, 4, 5, 6, and 8 accomplish the major overall effects of the cycle—the trapping of energy. This is accomplished by reducing NAD<sup>+</sup> or FAD, or by producing GTP (reaction 5), whose energy is then transferred to ATP. Each reaction is catalyzed by a specific enzyme, although the enzymes are not shown in this figure.



In reaction 1, the energy temporarily stored in acetyl CoA drives the formation of citrate from oxaloacetate. During this reaction, the CoA molecule is removed and can be reused by pyruvate dehydrogenase.

In reaction 2, the citrate molecule is rearranged to form isocitrate.

In reaction 3, a CO<sub>2</sub> molecule, a proton, and two electrons are removed, converting isocitrate into α-ketoglutarate. This reaction releases a large amount of free energy, some of which is stored in NADH.

In reaction 4, α-ketoglutarate is oxidized to succinyl CoA. This reaction is similar to the oxidation of pyruvate to form acetyl CoA. Like that reaction, it is catalyzed by a multi-enzyme complex and produces CO<sub>2</sub> and NADH.

In reaction 5, some of the energy in succinyl CoA is harvested to make GTP (guanosine triphosphate) from GDP and P<sub>i</sub>. This is another example of substrate-level phosphorylation. GTP is then used to make ATP from ADP and P<sub>i</sub>.

In reaction 6, the succinate released from succinyl CoA in reaction 5 is oxidized to fumarate. In the process, free energy is released and two hydrogens are transferred to the electron carrier FAD, forming FADH<sub>2</sub>.

Reaction 7 is a molecular rearrangement in which water is added to fumarate, forming malate.

In reaction 8, one more NAD<sup>+</sup> reduction occurs, producing oxaloacetate from malate. Reactions 7 and 8 illustrate a common biochemical mechanism: in reaction 7, water (H<sub>2</sub>O) is added to form a hydroxyl (—OH) group, and then in reaction 8 the H from the hydroxyl group is removed, generating a carbonyl group and reducing NAD<sup>+</sup> to NADH.

The final product, oxaloacetate, is ready to combine with another acetyl group from acetyl CoA and go around the cycle again. The citric acid cycle operates twice for each glucose molecule that enters glycolysis (once for each pyruvate that enters the mitochondrion).

To summarize:

- The *inputs* to the citric acid cycle are acetate (in the form of acetyl CoA), water, and the oxidized electron carriers NAD<sup>+</sup>, FAD, and GDP.
- The *outputs* are carbon dioxide, reduced electron carriers (NADH and FADH<sub>2</sub>), and a small amount of GTP. Overall, the citric acid cycle releases two carbons as CO<sub>2</sub> and produces four reduced electron carrier molecules.

### The citric acid cycle is regulated by the concentrations of starting materials

We have seen how pyruvate, a three-carbon molecule, is completely oxidized to CO<sub>2</sub> by pyruvate dehydrogenase and the citric acid cycle. For the cycle to continue, the starting molecules—acetyl CoA and oxidized electron carriers—must all be replenished. The electron carriers are reduced during the cycle and in reaction 6 of glycolysis (see Figure 9.5), and they must be reoxidized:



The oxidation of these electron carriers take place in coupled redox reactions, in which other molecules get reduced. When it is present, O<sub>2</sub> is the molecule that eventually accepts these electrons and gets reduced to form H<sub>2</sub>O.

## 9.2 RECAP

The oxidation of glucose in the presence of O<sub>2</sub> involves glycolysis, pyruvate oxidation, and the citric acid cycle. In glycolysis, glucose is converted to pyruvate with some energy capture. Following the initial oxidation of pyruvate, the citric acid cycle completes its oxidation to CO<sub>2</sub> and more energy is captured in the form of reduced electron carriers.

- What is the net energy yield of glycolysis in terms of energy invested and energy harvested? See p. 174 and Figure 9.6
- What role does pyruvate oxidation play in the citric acid cycle? See pp. 174–175 and Figure 9.7
- Explain why reoxidation of NADH is crucial for the continuation of the citric acid cycle. See p. 177

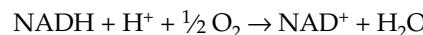
Pyruvate oxidation and the citric acid cycle cannot continue operating unless O<sub>2</sub> is available to receive electrons during the reoxidation of reduced electron carriers. However, these electrons are not passed directly to O<sub>2</sub>, as you will learn next.

## 9.3 How Does Oxidative Phosphorylation Form ATP?

The overall process of ATP synthesis resulting from the reoxidation of electron carriers in the presence of O<sub>2</sub> is called **oxidative phosphorylation**. Two components of the process can be distinguished:

1. *Electron transport*. The electrons from NADH and FADH<sub>2</sub> pass through the **respiratory chain**, a series of membrane-associated electron carriers. The flow of electrons along this pathway results in the active transport of protons out of the mitochondrial matrix and across the inner mitochondrial membrane, creating a proton concentration gradient.
2. *Chemiosmosis*. The protons diffuse back into the mitochondrial matrix through a channel protein, **ATP synthase**, which couples this diffusion to the synthesis of ATP. The inner mitochondrial membrane is otherwise impermeable to protons, so the only way for them to follow their concentration gradient is through the channel.

Before we proceed with the details of these pathways, let's consider an important question: Why should the respiratory chain be such a complex process? Why don't cells use the following single step?



The answer is that this reaction would be untamable. It is extremely exergonic—and would be rather like setting off a stick

of dynamite in the cell. There is no biochemical way to harvest that burst of energy efficiently and put it to physiological use (that is, no single metabolic reaction is so endergonic as to consume a significant fraction of that energy in a single step). To control the release of energy during the oxidation of glucose, cells have evolved a lengthy respiratory chain: a series of reactions, each of which releases a small, manageable amount of energy, one step at a time.

### The respiratory chain transfers electrons and releases energy

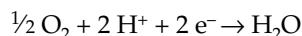
The respiratory chain is located in the inner mitochondrial membrane and contains several interactive components, including large integral proteins, smaller mobile proteins, and a small lipid molecule. **Figure 9.8** shows a plot of the free energy released as electrons are passed between the carriers.

- Four large protein complexes (I, II, III, and IV) contain electron carriers and associated enzymes. In eukaryotes they are integral proteins of the inner mitochondrial membrane (see Figure 5.12), and three are transmembrane proteins.
- Cytochrome *c* is a small peripheral protein that lies in the intermembrane space. It is loosely attached to the outer surface of the inner mitochondrial membrane.
- Ubiquinone (abbreviated Q) is a small, nonpolar, lipid molecule that moves freely within the hydrophobic interior

of the phospholipid bilayer of the inner mitochondrial membrane.

As illustrated in Figure 9.8, NADH passes electrons to protein complex I (called NADH-Q reductase), which in turn passes the electrons to Q. This electron transfer is accompanied by a large drop in free energy. Complex II (succinate dehydrogenase) passes electrons to Q from FADH<sub>2</sub>, which was generated in reaction 6 of the citric acid cycle (see Figure 9.7). These electrons enter the chain later than those from NADH and will ultimately produce less ATP.

Complex III (cytochrome *c* reductase) receives electrons from Q and passes them to cytochrome *c*. Complex IV (cytochrome *c* oxidase) receives electrons from cytochrome *c* and passes them to oxygen. Finally the reduction of oxygen to H<sub>2</sub>O occurs:



Notice that two protons (H<sup>+</sup>) are also consumed in this reaction. This contributes to the proton gradient across the inner mitochondrial membrane.

During electron transport, protons are also actively transported across the membrane—electron transport within each of the three transmembrane complexes (I, III, and IV) results in the transfer of protons from the matrix to the intermembrane space (**Figure 9.9**). So an imbalance of protons is set up, with the impermeable inner mitochondrial membrane as a barrier. The concentration of H<sup>+</sup> in the intermembrane space is higher than in the matrix, and this gradient represents a source of potential energy. The diffusion of those protons across the membrane is coupled with the formation of ATP. Thus the energy originally contained in glucose and other fuel molecules is finally captured in cellular energy currency, ATP. For each pair of electrons passed along the chain from NADH to oxygen, about 2.5 molecules of ATP are formed. FADH<sub>2</sub> oxidation produces about 1.5 ATP molecules.

Electrons from NADH are accepted by NADH-Q reductase at the start of the electron transport chain.

Electrons also come from succinate by way of FADH<sub>2</sub>; these electrons are accepted by succinate dehydrogenase.

NADH-Q reductase complex

I

FADH<sub>2</sub>

Succinate dehydrogenase

Ubiquinone (Q)

III

Cytochrome c reductase complex

Cytochrome c

IV

Cytochrome c oxidase complex

O<sub>2</sub>

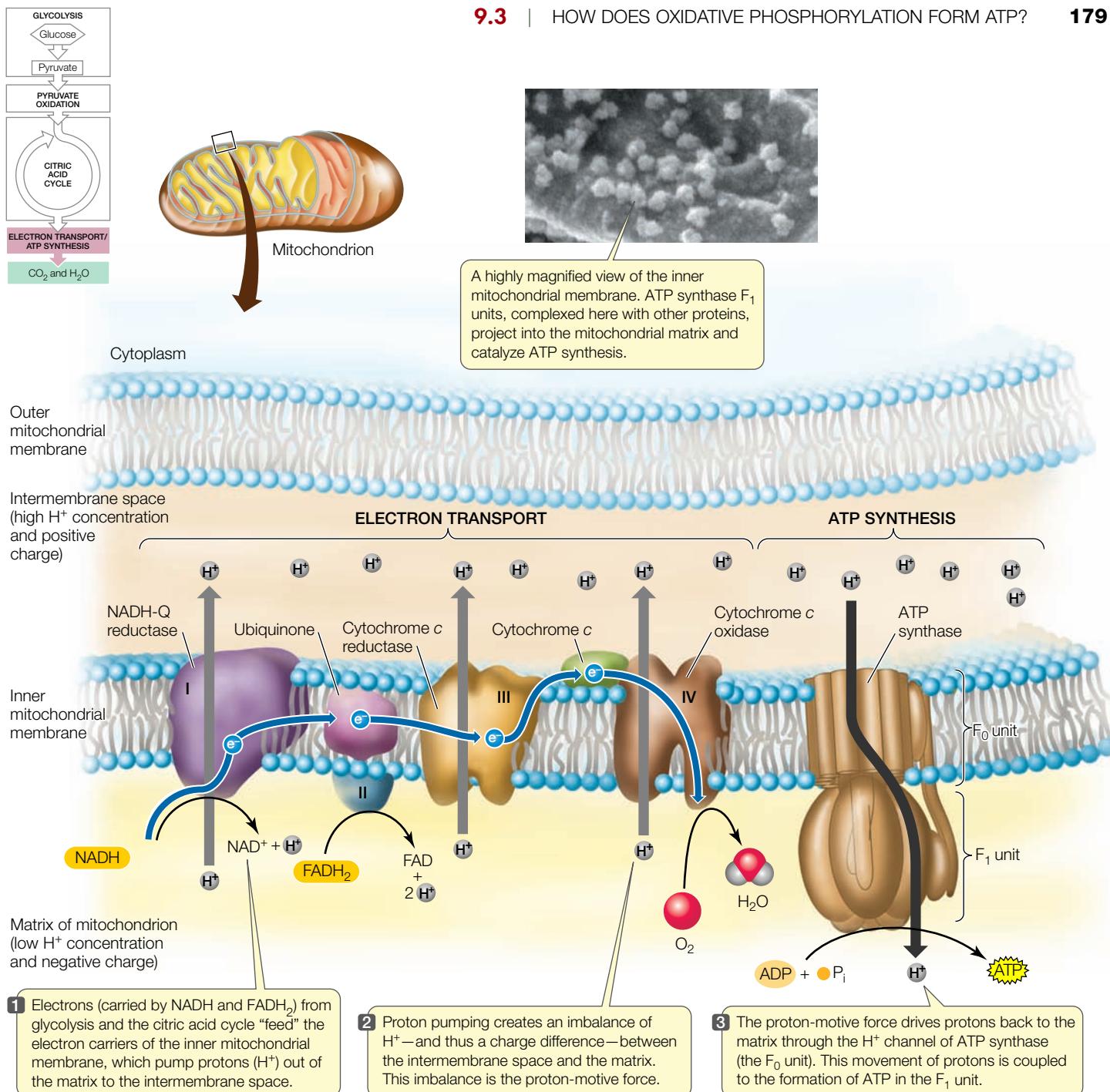
H<sub>2</sub>O

Free energy relative to O<sub>2</sub> (kcal/mol)

### Proton diffusion is coupled to ATP synthesis

All the electron carriers and enzymes of the respiratory chain, except cytochrome *c*, are embedded in the inner mitochondrial membrane. As we have just seen, the operation of the respiratory chain results in the active transport of protons from the mitochond-

**9.8 The Oxidation of NADH and FADH<sub>2</sub> in the Respiratory Chain** Electrons from NADH and FADH<sub>2</sub> are passed along the respiratory chain, a series of protein complexes in the inner mitochondrial membrane containing electron carriers and enzymes. The carriers gain free energy when they become reduced and release free energy when they are oxidized.



### 9.9 The Respiratory Chain and ATP Synthase Produce ATP by a Chemiosmotic Mechanism

**Chemiosmotic Mechanism** As electrons pass through the transmembrane protein complexes in the respiratory chain, protons are pumped from the mitochondrial matrix into the intermembrane space. As the protons return to the matrix through ATP synthase, ATP is formed.

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drial matrix to the intermembrane space. The transmembrane protein complexes (I, III, and IV) act as proton pumps, and as a result, the intermembrane space is more acidic than the matrix.

Because of the positive charge carried by a proton (H<sup>+</sup>), this pumping creates not only a concentration gradient but also a difference in electric charge across the inner mitochondrial

membrane, making the mitochondrial matrix more negative than the intermembrane space. Together, the proton concentration gradient and the electrical charge difference constitute a source of potential energy called the **proton-motive force**. This force tends to drive the protons back across the membrane, just as the charge on a battery drives the flow of electrons to discharge the battery.

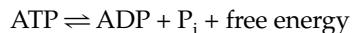
The hydrophobic lipid bilayer is essentially impermeable to protons, so the potential energy of the proton-motive force cannot be discharged by simple diffusion of protons across the membrane. However, protons can diffuse across the membrane by passing through a specific proton channel, called ATP synthase, which couples proton movement to the synthesis of ATP. This coupling of proton-motive force and ATP synthesis is called

the chemiosmotic mechanism (or **chemiosmosis**) and is found in all respiring cells.

**THE CHEMIOSMOTIC MECHANISM FOR ATP SYNTHESIS** The chemiosmotic mechanism involves transmembrane proteins, including a proton channel and the enzyme ATP synthase, that couple proton diffusion to ATP synthesis. The potential energy of the H<sup>+</sup>

gradient, or the proton-motive force (described above), is harnessed by ATP synthase. This protein complex has two roles: it acts as a channel allowing H<sup>+</sup> to diffuse back into the matrix, and it uses the energy of that diffusion to make ATP from ADP and P<sub>i</sub>.

ATP synthesis is a reversible reaction, and ATP synthase can also act as an ATPase, hydrolyzing ATP to ADP and P<sub>i</sub>:



If the reaction goes to the right, free energy is released and is used to pump H<sup>+</sup> out of the mitochondrial matrix—not the usual mode

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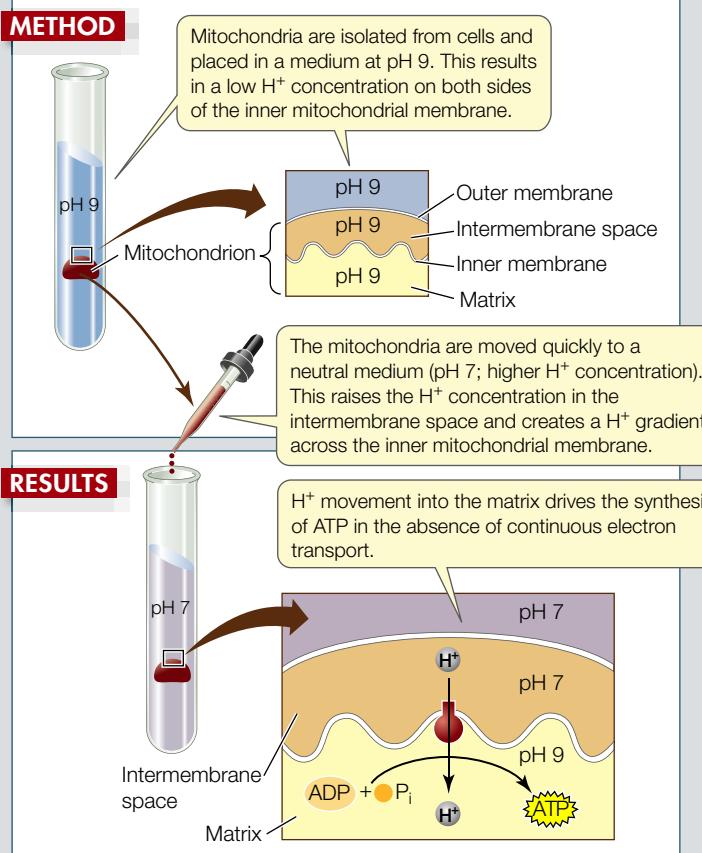
**GO TO** Animated Tutorial 9.2 • Two Experiments Demonstrate the Chemiosmotic Mechanism

## INVESTIGATING LIFE

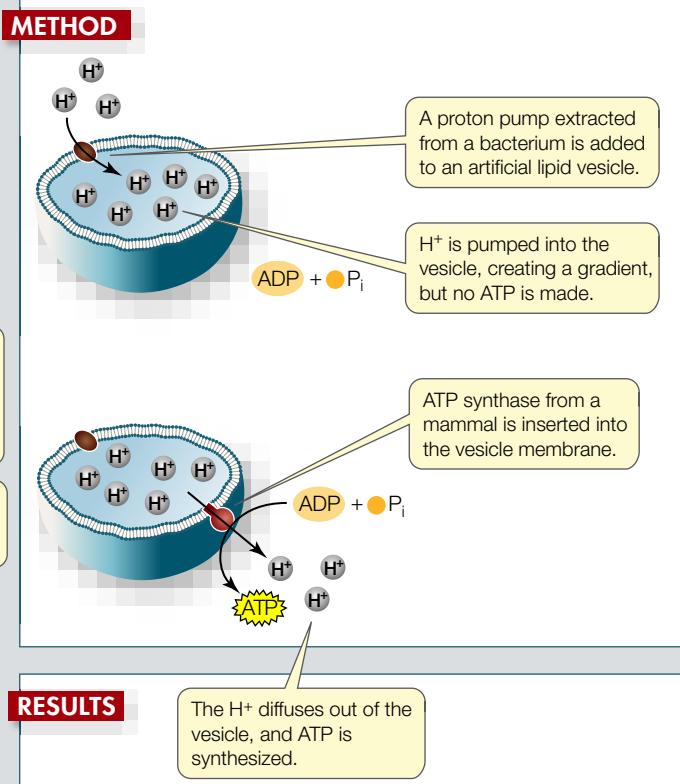
### 9.10 Two Experiments Demonstrate the Chemiosmotic Mechanism

The chemiosmosis hypothesis was a bold departure for the conventional scientific thinking of the time. It required an intact compartment separated by a membrane. Could a proton gradient drive the synthesis of ATP? And was this capacity entirely due to the ATP synthase enzyme?

**HYPOTHESIS** A H<sup>+</sup> gradient can drive ATP synthesis by isolated mitochondria.



**HYPOTHESIS** ATP synthase is needed for ATP synthesis.



**CONCLUSION** In the absence of electron transport, an artificial H<sup>+</sup> gradient is sufficient for ATP synthesis by mitochondria.

**CONCLUSION** ATP synthase, acting as a H<sup>+</sup> channel, is necessary for ATP synthesis.

**FURTHER INVESTIGATION:** What would happen in the experiment on the right if a second ATP synthase, oriented in the opposite way to the one originally inserted in the membrane, were added?

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of operation. If the reaction goes to the left, it uses the free energy from  $H^+$  diffusion into the matrix to make ATP. What makes it prefer ATP synthesis? There are two answers to this question:

- ATP leaves the mitochondrial matrix for use elsewhere in the cell as soon as it is made, keeping the ATP concentration in the matrix low, and driving the reaction toward the left.
- The  $H^+$  gradient is maintained by electron transport and proton pumping.

Every day a person hydrolyzes about  $10^{25}$  ATP molecules to ADP. This amounts to 9 kg, a significant fraction of almost everyone's entire body weight! The vast majority of this ADP is "recycled"—converted back to ATP—using free energy from the oxidation of glucose.

**EXPERIMENTS DEMONSTRATE CHEMIOSMOSIS** When it was first proposed almost a half-century ago, the idea that a proton gradient was the energy intermediate linking electron transport to ATP synthesis was a departure from the current conventional thinking. Scientists had been searching for a mitochondrial intermediate that they believed would carry energy in much the same way as the ATP produced by substrate level phosphorylation. The search for this intermediate was not successful, and this led to the idea that chemiosmosis was the mechanism of oxidative phosphorylation. Experimental evidence was needed to support this hypothesis. Two key experiments demonstrated (1) that a proton ( $H^+$ ) gradient across a membrane can drive ATP synthesis; and (2) that the enzyme ATP synthase is the catalyst for this reaction (Figure 9.10).

In the first experiment, mitochondria without a food source were "fooled" into making ATP by raising the  $H^+$  concentration in their environment. In the second experiment, a light-driven proton pump isolated from bacteria was inserted into artificial lipid vesicles. This generated a proton gradient, but since ATP synthase was absent, ATP was not made. Then, ATP synthase was inserted into the vesicles and ATP was generated.

**UNCOUPLING PROTON DIFFUSION FROM ATP PRODUCTION** The tight coupling between  $H^+$  diffusion and the formation of ATP provides further evidence for the chemiosmotic mechanism. If a second type of  $H^+$  diffusion channel (that does not synthesize ATP) is present in the mitochondrial membrane, the energy of the  $H^+$  gradient is released as heat rather than being coupled to ATP synthesis. Such uncoupling molecules actually exist in the mitochondria of some organisms to generate heat instead of ATP. For example, the natural uncoupling protein thermogenin plays an important role in regulating the temperatures of newborn human infants, who lack hair to keep warm, and in hibernating animals.

A popular weight loss drug in the 1930s was the uncoupler molecule, dinitrophenol. There were claims of dramatic weight loss when the drug was administered to obese patients. Unfortunately, the heat that was released caused fatally high fevers, and the effective dose and fatal dose were quite close. So the use of this drug was discontinued in 1938. However, the general strategy of using an uncoupler for weight loss remains a subject of research.

**HOW ATP SYNTHASE WORKS: A MOLECULAR MOTOR** Now that we have established that the  $H^+$  gradient is needed for ATP synthesis, a question remains: how does the enzyme actually make ATP from ADP and  $P_i$ ? This is certainly a fundamental question in biology, as it underlies energy harvesting in most cells. Look at the structure of ATP synthase in Figure 9.9. It is a molecular motor composed of two parts: the  $F_0$  unit, a transmembrane region that is the  $H^+$  channel, and the  $F_1$  unit, which contains the active sites for ATP synthesis.  $F_1$  consists of six subunits (three each of two polypeptide chains), arranged like the segments of an orange around a central polypeptide. ATP synthesis is coupled with conformational changes in the ATP synthase enzyme, which are induced by proton movement through the complex. The potential energy set up by the proton gradient across the inner membrane drives the passage of protons through the ring of polypeptides that make up the  $F_0$  component. This ring rotates as the protons pass through the membrane, causing the  $F_1$  unit to rotate as well. ADP and  $P_i$  bind to active sites that become exposed on the  $F_1$  unit as it rotates, and ATP is made. The structure and function of ATP synthase are shared by living organisms as diverse as bacteria and humans. These molecular motors make ATP at rates up to 100 molecules per second.

## 9.3 RECAP

The oxidation of reduced electron carriers in the respiratory chain drives the active transport of protons across the inner mitochondrial membrane, generating a proton-motive force. Diffusion of protons down their electrochemical gradient through ATP synthase is coupled to the synthesis of ATP.

- What are the roles of oxidation and reduction in the respiratory chain? See Figures 9.8 and 9.9
- What is the proton motive force and how does it drive chemiosmosis? See pp. 179–180
- Explain how the two experiments described in Figure 9.10 demonstrate the chemiosmotic mechanism. See p. 181

Oxidative phosphorylation captures a great deal of energy in ATP. But it does not occur if  $O_2$  is absent. We turn now to the metabolism of glucose in anaerobic conditions.

## 9.4 How Is Energy Harvested from Glucose in the Absence of Oxygen?

In the absence of  $O_2$  (anaerobic conditions), a small amount of ATP can be produced by glycolysis and fermentation. Like glycolysis, fermentation pathways occur in the cytoplasm. There are many different types of fermentation, but they all operate to regenerate  $NAD^+$  so that the NAD-requiring reaction of glycolysis can continue (see reaction 6 in Figure 9.5). Of course, if a necessary reactant such as  $NAD^+$  is not present, the reaction will not take place. How do fermentation reactions regenerate  $NAD^+$  and permit ATP formation to continue?

Prokaryotic organisms often live in O<sub>2</sub>-deficient environments and are known to use many different fermentation pathways. But the two best understood fermentation pathways are found in a wide variety of organisms including eukaryotes. These two short pathways are lactic acid fermentation, whose end product is lactic acid (lactate); and alcoholic fermentation, whose end product is ethyl alcohol (ethanol).

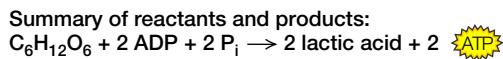
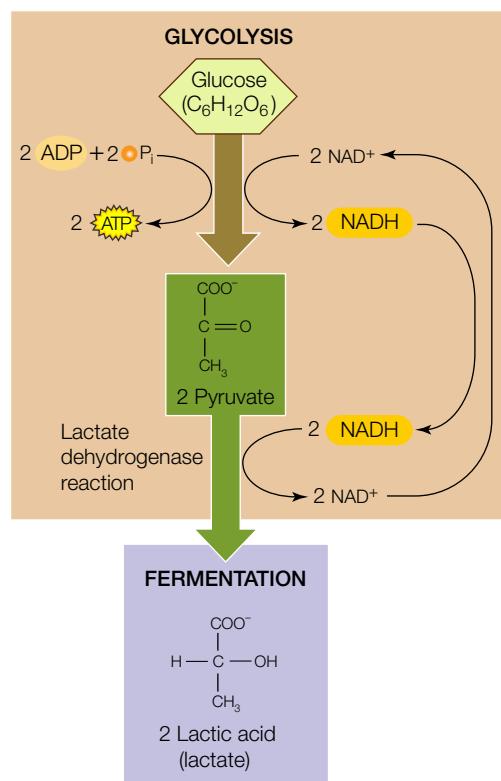
In lactic acid fermentation, pyruvate serves as the electron acceptor and lactate is the product (Figure 9.11). This process takes place in many microorganisms and complex organisms, including higher plants and vertebrates. A notable example of lactic acid fermentation occurs in vertebrate muscle tissue. Usually, vertebrates get their energy for muscle contraction aerobically, with the circulatory system supplying O<sub>2</sub> to muscles. In small vertebrates, this is almost always adequate: for example, birds can fly long distances without resting. But in larger vertebrates such as humans, the circulatory system is not up to the task of delivering enough O<sub>2</sub> when the need is great, such as during high activity. At this point, the muscle cells break down glycogen (a stored polysaccharide) and undergo lactic acid fermentation.

Lactic acid buildup becomes a problem after prolonged periods because the acid ionizes, forming H<sup>+</sup> and lowering the pH of the cell. This affects cellular activities and causes muscle

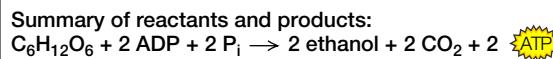
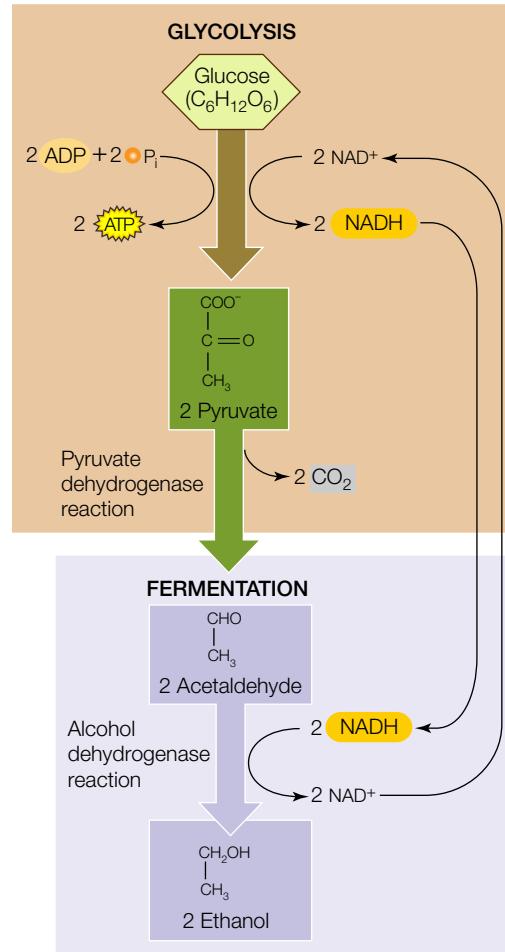
cramps, resulting in muscle pain, which abates upon resting. Lactate dehydrogenase, the enzyme that catalyzes the fermentation reaction, works in both directions. That is, it can catalyze the oxidation of lactate as well as the reduction of pyruvate. When lactate levels are decreased, muscle activity can resume.

Alcoholic fermentation takes place in certain yeasts (eukaryotic microbes) and some plant cells under anaerobic conditions. This process requires two enzymes, pyruvate dehydrogenase and alcohol dehydrogenase, which metabolize pyruvate to ethanol (Figure 9.12). As with lactic acid fermentation, the reactions are essentially reversible. For thousands of years, humans have used anaerobic fermentation by yeast cells to produce alcoholic beverages. The cells use sugars from plant sources (glucose from grapes or maltose from barley) to produce the end product, ethanol, in wine and beer.

By recycling NAD<sup>+</sup>, fermentation allows glycolysis to continue, thus producing small amounts of ATP through substrate-level phosphorylation. The net yield of two ATPs per glucose



**9.11 Lactic Acid Fermentation** Glycolysis produces pyruvate, ATP, and NADH from glucose. Lactic acid fermentation uses NADH as a reducing agent to reduce pyruvate to lactic acid (lactate), thus regenerating NAD<sup>+</sup> to keep glycolysis operating.



**9.12 Alcoholic Fermentation** In alcoholic fermentation, pyruvate from glycolysis is converted into acetaldehyde, and CO<sub>2</sub> is released. NADH from glycolysis is used to reduce acetaldehyde to ethanol, thus regenerating NAD<sup>+</sup> to keep glycolysis operating.

molecule is much lower than the energy yield from cellular respiration. For this reason, most organisms existing in anaerobic environments are small microbes that grow relatively slowly.

### Cellular respiration yields much more energy than fermentation

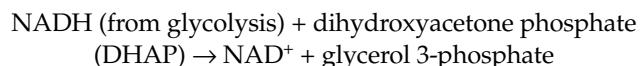
The total net energy yield from glycolysis plus fermentation is two molecules of ATP per molecule of glucose oxidized. The maximum yield of ATP that can be harvested from a molecule of glucose through glycolysis followed by cellular respiration is much greater—about 32 molecules of ATP (Figure 9.13). (Review Figures 9.5, 9.7, and 9.9 to see where all the ATP molecules come from.)

Why do the metabolic pathways that operate in aerobic environments produce so much more ATP? Glycolysis and fermentation only partially oxidize glucose, as does fermentation. Much more energy remains in the end products of fermentation (lactic acid and ethanol) than in  $\text{CO}_2$ , the end product of cellular respiration. In cellular respiration, carriers (mostly  $\text{NAD}^+$ ) are reduced in pyruvate oxidation and the citric acid cycle. Then the reduced carriers are oxidized by the respiratory chain, with the accompanying production of ATP by chemiosmosis (2.5 ATP for each NADH and 1.5 ATP for each  $\text{FADH}_2$ ). In an aerobic environment, a cell or organism capable of aerobic metabolism will have the advantage over one that is limited to fermentation, in terms of its ability to harvest chemical energy. Two key events in the evolution of multicellular organisms were the rise in atmospheric  $\text{O}_2$  levels (see Chapter 1) and the development of metabolic pathways to utilize that  $\text{O}_2$ .

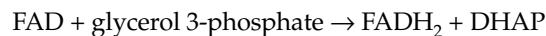
### The yield of ATP is reduced by the impermeability of some mitochondria to NADH

The total gross yield of ATP from the oxidation of one molecule of glucose to  $\text{CO}_2$  is 32. However, in some animal cells the inner mitochondrial membrane is impermeable to NADH, and a “toll” of one ATP must be paid for each NADH molecule that is produced in glycolysis and must be “shuttled” into the mitochondrial matrix. So in these animals, the net yield of ATP is 30.

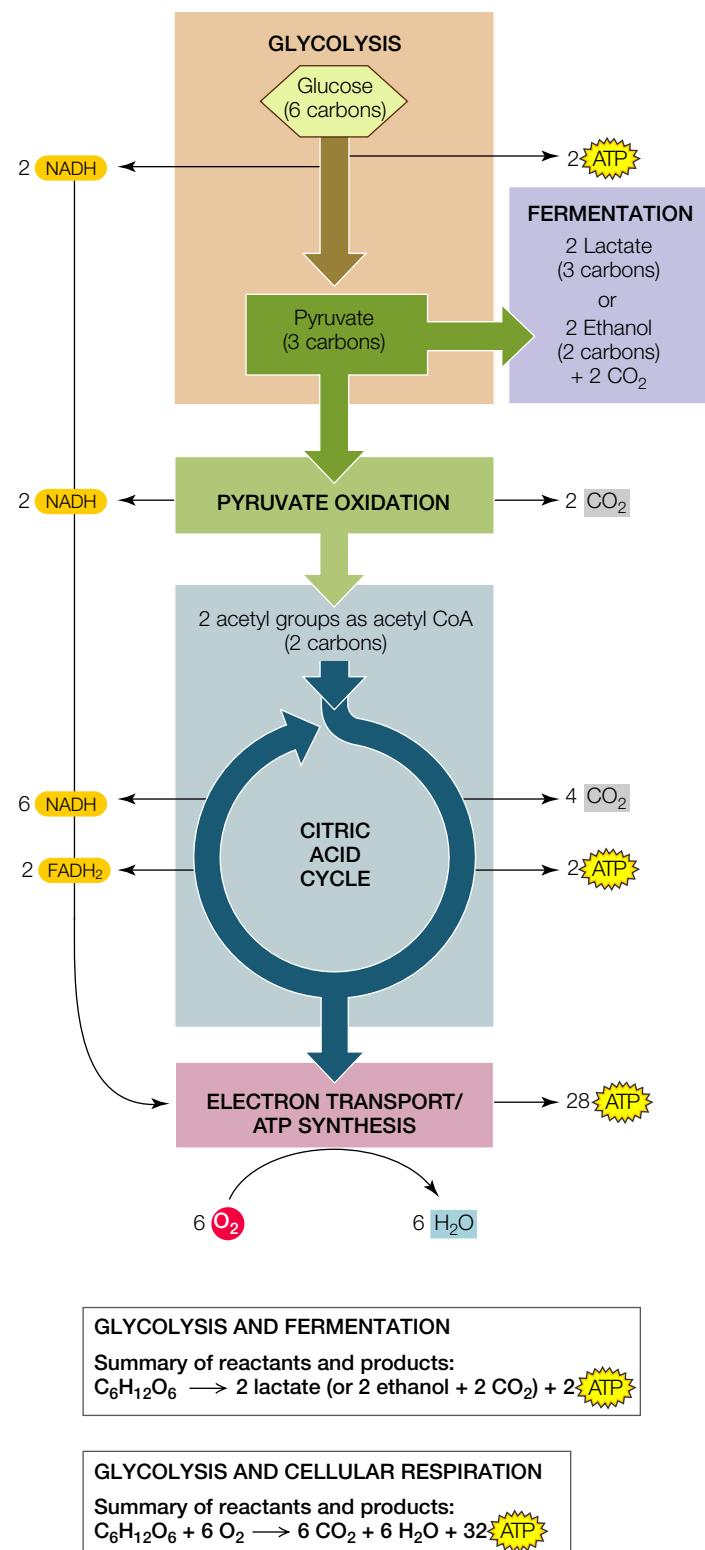
NADH shuttle systems transfer the electrons captured by glycolysis onto substrates that are capable of movement across the mitochondrial membranes. In muscle and liver tissues, an important shuttle involves glycerol 3-phosphate. In the cytosol,



Glycerol 3-phosphate crosses both mitochondrial membranes. In the mitochondrial matrix,



DHAP is able to move back to the cytosol, where it is available to repeat the process. Note that the reducing electrons are transferred from NADH outside the mitochondrion to  $\text{FADH}_2$  inside the mitochondrion. As you know from Figures 9.8 and 9.9, the energy yield in terms of ATP from  $\text{FADH}_2$  is lower than that from NADH. This lowers the overall energy yield.



### 9.13 Cellular Respiration Yields More Energy Than Fermentation

Electron carriers are reduced in pyruvate oxidation and the citric acid cycle, then oxidized by the respiratory chain. These reactions produce ATP via chemiosmosis.

## 9.4 RECAP

In the absence of  $O_2$ , fermentation pathways use NADH formed by glycolysis to reduce pyruvate and regenerate NAD<sup>+</sup>. The energy yield of fermentation is low because glucose is only partially oxidized. When  $O_2$  is present, the electron carriers of cellular respiration allow for the full oxidation of glucose, so the energy yield from glucose is much higher.

- Why is replenishing NAD<sup>+</sup> crucial to cellular metabolism?  
See pp. 182–183
- What is the total energy yield from glucose in human cells in the presence versus the absence of  $O_2$ ?  
See p. 183 and Figure 9.13

Now that you've seen how cells harvest energy, let's see how that energy moves through other metabolic pathways in the cell.

## 9.5 How Are Metabolic Pathways Interrelated and Regulated?

Glycolysis and the pathways of cellular respiration do not operate in isolation. Rather, there is an interchange of molecules into and out of these pathways, to and from the metabolic pathways for the synthesis and breakdown of amino acids, nucleotides, fatty acids, and other building blocks of life. Carbon skeletons can enter the catabolic pathways and be broken down to release their energy, or they can enter anabolic pathways to be used in the formation of the macromolecules that are the major constituents of the cell. These relationships are summarized in **Figure 9.14**. In this section we will explore how pathways are interrelated by the sharing of intermediate substances, and we will see how pathways are regulated by the inhibitors of key enzymes.

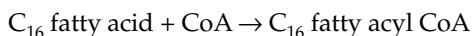
### Catabolism and anabolism are linked

A hamburger or veggie burger on a bun contains three major sources of carbon skeletons: carbohydrates, mostly in the form of starch (a polysaccharide); lipids, mostly as triglycerides (three fatty acids attached to glycerol); and proteins (polymers of amino acids). Look at Figure 9.14 to see how each of these three types of macromolecules can be hydrolyzed and used in catabolism or anabolism.

**9.14 Relationships among the Major Metabolic Pathways of the Cell** Note the central positions of glycolysis and the citric acid cycle in this network of metabolic pathways. Also note that many of the pathways can operate essentially in reverse.

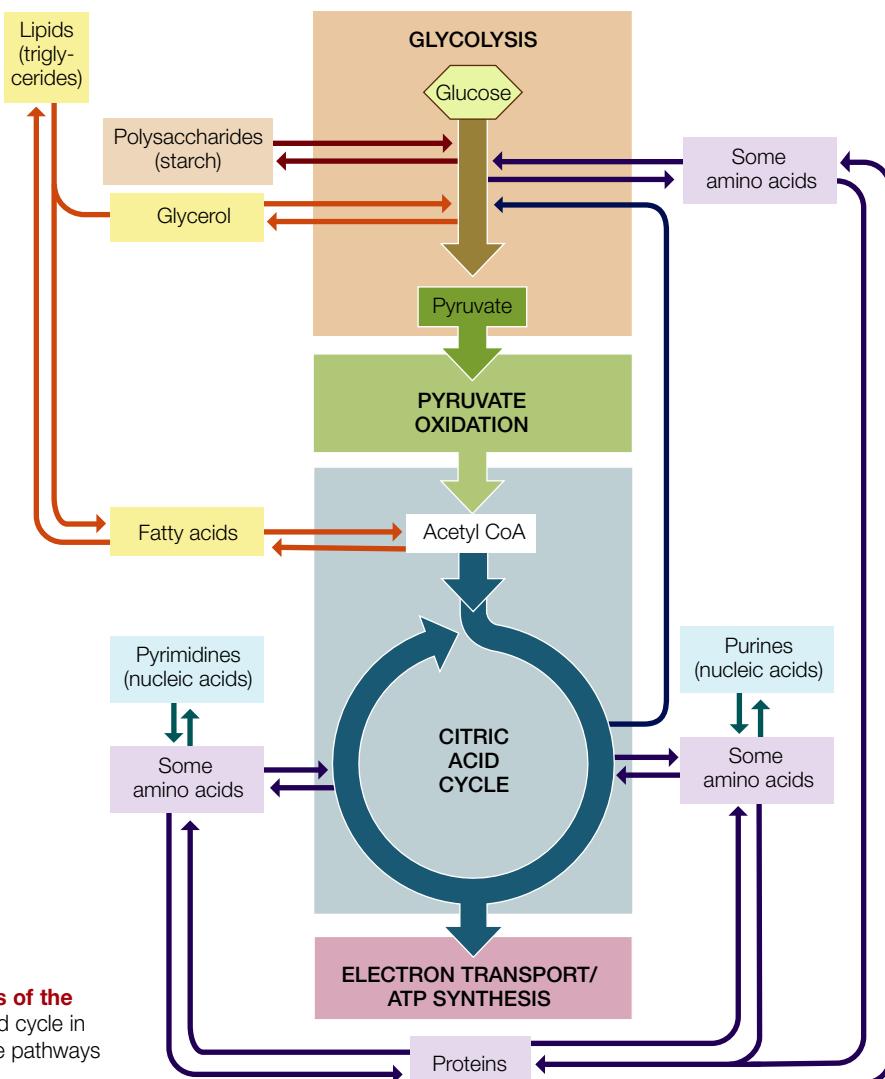
**CATABOLIC INTERCONVERSIONS** Polysaccharides, lipids, and proteins can all be broken down to provide energy:

- *Polysaccharides* are hydrolyzed to glucose. Glucose then passes through glycolysis and cellular respiration, where its energy is captured in ATP.
- *Lipids* are broken down into their constituents, glycerol and fatty acids. Glycerol is converted into dihydroxyacetone phosphate (DHAP), an intermediate in glycolysis. Fatty acids are highly reduced molecules that are converted to acetyl CoA inside the mitochondrion by a series of oxidation enzymes, in a process known as  $\beta$ -oxidation. For example, the  $\beta$ -oxidation of a C<sub>16</sub> fatty acid occurs in several steps:

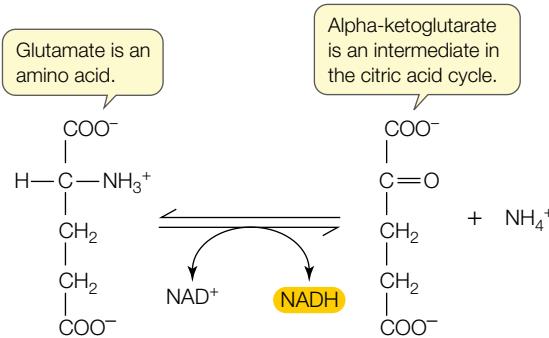


repeat 6 times  $\rightarrow$  8 acetyl CoA

The acetyl CoA can then enter the citric acid cycle and be catabolized to CO<sub>2</sub>.



- Proteins are hydrolyzed to their amino acid building blocks. The 20 different amino acids feed into glycolysis or the citric acid cycle at different points. For example, the amino acid glutamate is converted into  $\alpha$ -ketoglutarate, an intermediate in the citric acid cycle.



**ANABOLIC INTERCONVERSIONS** Many catabolic pathways can operate essentially in reverse, with some modifications. Glycolytic and citric acid cycle intermediates, instead of being oxidized to form CO<sub>2</sub>, can be reduced and used to form glucose in a process called **gluconeogenesis** (which means “new formation of glucose”). Likewise, acetyl CoA can be used to form fatty acids. The most common fatty acids have even numbers of carbons: 14, 16, or 18. These are formed by the addition of two-carbon acetyl CoA “units” one at a time until the appropriate chain length is reached. Acetyl CoA is also a building block for various pigments, plant growth substances, rubber, steroid hormones, and other molecules.

Some intermediates in the citric acid cycle are reactants in pathways that synthesize important components of nucleic acids. For example,  $\alpha$ -ketoglutarate is a starting point for purines, and oxaloacetate for pyrimidines. In addition,  $\alpha$ -ketoglutarate is a starting point for the synthesis of chlorophyll (used in photosynthesis; see Chapter 10) and the amino acid glutamate (used in protein synthesis).

### Catabolism and anabolism are integrated

A carbon atom from a protein in your burger can end up in DNA, fat, or CO<sub>2</sub>, among other fates. How does the organism “decide” which metabolic pathways to follow, in which cells? With all of the possible interconversions, you might expect that cellular concentrations of various biochemical molecules would vary widely. Remarkably, the levels of these substances in what is called the metabolic pool—the sum total of all the biochemical molecules in a cell—are quite constant. Organisms regulate the enzymes of catabolism and anabolism in various cells in order to maintain a balance. This metabolic homeostasis gets upset only in unusual circumstances. Let’s look one such unusual circumstance: undernutrition.

Glucose is an excellent source of energy, but lipids and proteins can also be broken down and their constituents used as energy sources. Any one or all three of these types of molecules could be used to provide the energy your body needs. But normally these substances are not equally available for energy me-

tabolism and ATP formation. Proteins, for example, have essential roles as enzymes and as structural elements, providing support and movement; they are not stored for energy, and using them for energy might deprive the body of other vital functions.

Fats (triglycerides) do not have catalytic roles. Because they are nonpolar, fats do not bind water, and they are therefore less dense than polysaccharides in aqueous environments. In addition, fats are more reduced than carbohydrates (have more C—H bonds and fewer C—OH bonds) and thus have more energy stored in their bonds (see Figure 9.2). So it is not surprising that fats are the preferred energy store in many organisms. The human body stores fats and carbohydrates; fats are stored in adipose tissue, and glucose is stored as the polysaccharide glycogen in muscles and the liver. A typical person has about one day’s worth of food energy stored as glycogen (a polysaccharide) and over a month’s food energy stored as fats.

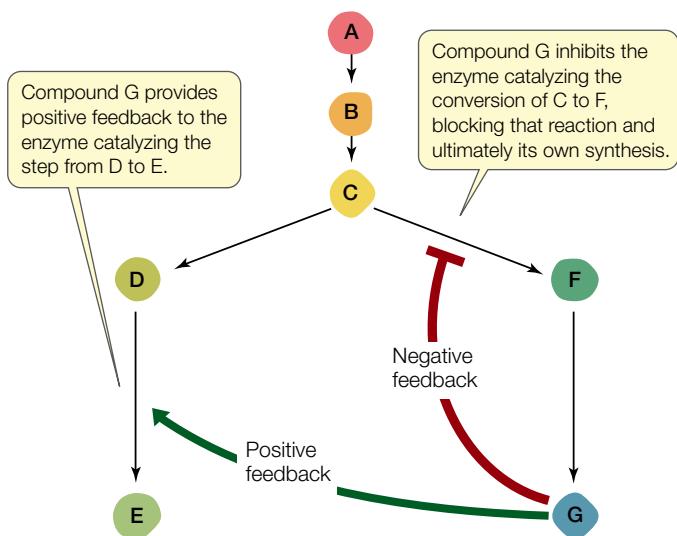
What happens if a person does not eat enough to produce sufficient ATP and NADH for anabolism and biological activities? This situation can be deliberate (to lose weight), but for too many people, it is forced upon them because not enough food is available, resulting in undernutrition and starvation. Initially, homeostasis can be maintained. The first energy stores to be used are the glycogen stores in muscle and liver cells. These stores do not last long, and next come the fats.

In cells that have access to fatty acids, their breakdown produces acetyl CoA for cellular respiration. However, a problem remains: because fatty acids cannot cross from the blood to the brain, the brain can use only glucose as its energy source. With glycogen already depleted, the body must convert something else to make glucose for the brain. This is accomplished by the breakdown of proteins and the conversion of their amino acids to glucose by gluconeogenesis. Without sufficient food intake, proteins and fats are used up. After several weeks of starvation, fat stores become depleted, and the only energy source left is protein. At this point, essential structural proteins, enzymes, and antibodies get broken down. The loss of such proteins can lead to severe illness and eventual death.

### Metabolic pathways are regulated systems

We have described the relationships between metabolic pathways and noted that these pathways work together to provide homeostasis in the cell and organism. But how does the cell regulate the interconversions between pathways to maintain constant metabolic pools? This is a problem of systems biology, which seeks to understand how biochemical pathways interact (see Figure 8.15). It is a bit like trying to predict traffic patterns in a city: if an accident blocks traffic on a major road, drivers take alternate routes, where the traffic volume consequently changes.

Consider what happens to the starch in your burger bun. In the digestive system, starch is hydrolyzed to glucose, which enters the blood for distribution to the rest of the body. But before the glucose is distributed, a regulatory check must be made: if there is already enough glucose in the blood to supply the body’s needs, the excess glucose is converted into glycogen and



### 9.15 Regulation by Negative and Positive Feedback

Allosteric feedback regulation plays an important role in metabolic pathways. The accumulation of some products can shut down their synthesis, or can stimulate other pathways that require the same raw materials.

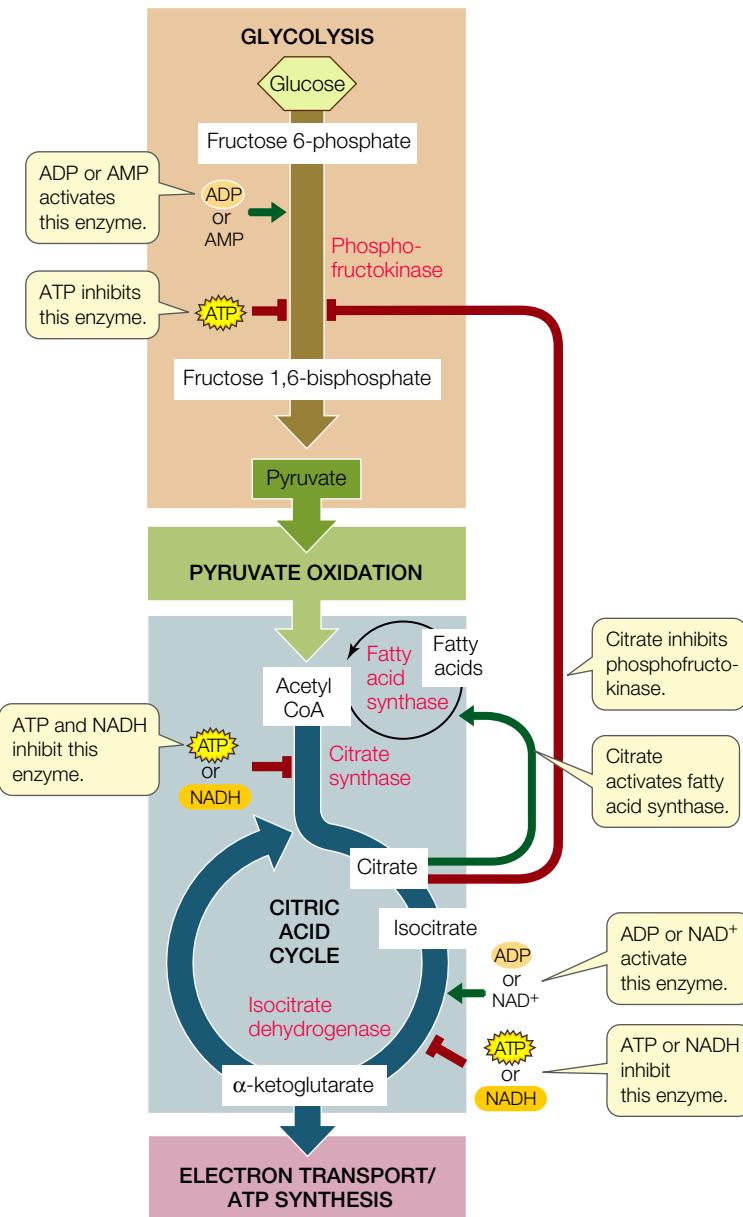
stored in the liver. If not enough glucose is supplied by food, glycogen is broken down, or other molecules are used to make glucose by gluconeogenesis.

The end result is that the level of glucose in the blood is remarkably constant. How does the body accomplish this?

Glycolysis, the citric acid cycle, and the respiratory chain are subject to *allosteric regulation* (see Section 8.5) of the enzymes involved. An example of allosteric regulation is feedback inhibition, illustrated in Figure 8.19. In a metabolic pathway, a high concentration of the final product can inhibit the action of an enzyme that catalyzes an earlier reaction. On the other hand, an excess of the product of one pathway can speed up reactions in another pathway, diverting raw materials away from synthesis of the first product (Figure 9.15). These negative and positive feedback mechanisms are used at many points in the energy-harvesting pathways, and are summarized in Figure 9.16.

- The main control point in glycolysis is the enzyme *phosphofructokinase* (reaction 3 in Figure 9.5). This enzyme is allosterically inhibited by ATP or citrate, and activated by ADP or AMP. Under anaerobic conditions, fermentation yields a relatively small amount of ATP, and phosphofructokinase operates at a high rate. However when conditions are aerobic, respiration makes 16 times more ATP than fermentation does, and the abundant ATP allosterically inhibits phosphofructokinase. Consequently, the conversion of fructose 6-phosphate to fructose 1,6-bisphosphate declines, and so does the rate of glucose utilization.
- The main control point in the citric acid cycle is the enzyme *isocitrate dehydrogenase*, which converts isocitrate to  $\alpha$ -ketoglutarate (reaction 3 in Figure 9.7). NADH and

ATP are feedback inhibitors of this reaction, while ADP and NAD<sup>+</sup> are activators. If too much ATP or NADH accumulates, the conversion of isocitrate is slowed, and the citric acid cycle shuts down. A shutdown of the citric acid cycle would cause large amounts of isocitrate and citrate to accumulate if the production of citrate were not also slowed. But, as mentioned above, an excess of citrate acts as a feedback inhibitor of phosphofructokinase. Thus, if the citric acid cycle has been slowed or shut down because of abun-



### 9.16 Allosteric Regulation of Glycolysis and the Citric Acid Cycle

Allosteric regulation controls glycolysis and the citric acid cycle at crucial early steps, increasing their efficiency and preventing the excessive buildup of intermediates.

dant ATP (and not because of a lack of oxygen), glycolysis is slowed as well. Both processes resume when the ATP level falls and they are needed again. Allosteric regulation keeps these processes in balance.

- Another control point involves *acetyl CoA*. If the level of ATP is high and the citric acid cycle shuts down, the accumulation of citrate activates fatty acid synthase, diverting acetyl CoA to the synthesis of fatty acids for storage. That is one reason why people who eat too much accumulate fat. These fatty acids may be metabolized later to produce more acetyl CoA.

## 9.5 RECAP

Glucose can be made from intermediates in glycolysis and the citric acid cycle by a process called gluconeogenesis. The metabolic pathways for the production and breakdown of lipids and amino acids are tied to those of glucose metabolism. Reaction products regulate key enzymes in the various pathways.

- Give examples of a catabolic interconversion of a lipid and of an anabolic interconversion of a protein. [See pp. 184–185 and Figure 9.14](#)
- How does phosphofructokinase serve as a control point for glycolysis? [See p. 186 and Figure 9.16](#)
- Describe what would happen if there was no allosteric mechanism for modulating the level of acetyl CoA.

## CHAPTER SUMMARY

### 9.1 How Does Glucose Oxidation Release Chemical Energy?

- As a material is **oxidized**, the electrons it loses are transferred to another material, which is thereby **reduced**. Such **redox reactions** transfer large amounts of energy. [Review Figure 9.2, WEB ACTIVITIES 9.1 and 9.2](#)
- The coenzyme **NAD<sup>+</sup>** is a key electron carrier in biological redox reactions. It exists in two forms, one oxidized (**NAD<sup>+</sup>**) and the other reduced (**NADH**).
- **Glycolysis** operates in the presence or absence of **O<sub>2</sub>**. Under **aerobic** conditions, **cellular respiration** continues the process of breaking down glucose. Under **anaerobic** conditions, **fermentation** occurs. [Review Figure 9.4](#)
- The pathways of cellular respiration after glycolysis are **pyruvate oxidation**, the **citric acid cycle**, and the **electron transport/ATP synthesis**.

### 9.2 What Are the Aerobic Pathways of Glucose Metabolism?

- Glycolysis consists of 10 enzyme-catalyzed reactions that occur in the cell cytoplasm. Two **pyruvate** molecules are produced for each partially oxidized molecule of glucose, providing the starting material for both cellular respiration and fermentation. [Review Figure 9.5](#)
- The first five reactions of glycolysis require an investment of energy; the last five produce energy. The net gain is two molecules of ATP. [Review Figure 9.6](#)
- The enzyme-catalyzed transfer of phosphate groups to ADP by enzymes other than ATPase is called **substrate-level phosphorylation** and produces ATP.
- Pyruvate oxidation follows glycolysis and links glycolysis to the citric acid cycle. This pathway converts pyruvate into **acetyl CoA**.
- Acetyl CoA is the starting point of the citric acid cycle. It reacts with oxaloacetate to produce citrate. A series of eight enzyme-catalyzed reactions oxidize citrate and regenerate oxaloacetate, continuing the cycle. [Review Figure 9.7, WEB ACTIVITY 9.3](#)

### 9.3 How Does Oxidative Phosphorylation Form ATP?

- Oxidation of electron carriers in the presence of **O<sub>2</sub>** releases energy that can be used to form ATP in a process called **oxidative phosphorylation**.
- The NADH and FADH<sub>2</sub> produced in glycolysis, pyruvate oxidation, and the citric acid cycle are oxidized by the respiratory

chain, regenerating NAD<sup>+</sup> and FAD. Oxygen (O<sub>2</sub>) is the final acceptor of electrons and protons, forming water (H<sub>2</sub>O). [Review Figure 9.8, WEB ACTIVITY 9.4](#)

- The respiratory chain not only transports electrons, but also pumps protons across the inner mitochondrial membrane, creating the **proton-motive force**.
- Protons driven by the proton-motive force can return to the mitochondrial matrix via **ATP synthase**, a molecular motor that couples this movement of protons to the synthesis of ATP. This process is called **chemiosmosis**. [Review Figure 9.9, ANIMATED TUTORIALS 9.1 and 9.2](#)

### 9.4 How Is Energy Harvested from Glucose in the Absence of Oxygen?

- In the absence of O<sub>2</sub>, glycolysis is followed by fermentation. Together, these pathways partially oxidize pyruvate and generate end products such as **lactic acid** or **ethanol**. In the process, NAD<sup>+</sup> is regenerated from NADH so that glycolysis can continue, thus generating a small amount of ATP. [Review Figures 9.11 and 9.12](#)
- For each molecule of glucose used, fermentation yields 2 molecules of ATP. In contrast, glycolysis operating with pyruvate oxidation, the citric acid cycle, and the respiratory chain/ATP synthase yields up to 32 molecules of ATP per molecule of glucose. [Review Figure 9.13, WEB ACTIVITY 9.5](#)

### 9.5 How Are Metabolic Pathways Interrelated and Regulated?

- The **catabolic pathways** for the breakdown of carbohydrates, fats, and proteins feed into the energy-harvesting metabolic pathways. [Review Figure 9.14](#)
- **Anabolic pathways** use intermediate components of the energy-harvesting pathways to synthesize fats, amino acids, and other essential building blocks.
- The formation of glucose from intermediates of glycolysis and the citric acid cycle is called **gluconeogenesis**.
- The rates of glycolysis and the citric acid cycle are controlled by **allosteric regulation** and by the diversion of excess acetyl CoA into fatty acid synthesis. Key regulated enzymes include phosphofructokinase, citrate synthase, isocitrate dehydrogenase, and fatty acid synthase. [See Figure 9.16, WEB ACTIVITY 9.6](#)

## SELF-QUIZ

1. The role of oxygen gas in our cells is to
  - a. catalyze reactions in glycolysis.
  - b. produce  $\text{CO}_2$ .
  - c. form ATP.
  - d. accept electrons from the respiratory chain.
  - e. react with glucose to split water.
2. Oxidation and reduction
  - a. entail the gain or loss of proteins.
  - b. are defined as the loss of electrons.
  - c. are both endergonic reactions.
  - d. always occur together.
  - e. proceed only under aerobic conditions.
3.  $\text{NAD}^+$  is
  - a. a type of organelle.
  - b. a protein.
  - c. present only in mitochondria.
  - d. a part of ATP.
  - e. formed in the reaction that produces ethanol.
4. Glycolysis
  - a. takes place in the mitochondrion.
  - b. produces no ATP.
  - c. has no connection with the respiratory chain.
  - d. is the same thing as fermentation.
  - e. reduces two molecules of  $\text{NAD}^+$  for every glucose molecule processed.
5. Fermentation
  - a. takes place in the mitochondrion.
  - b. takes place in all animal cells.
  - c. does not require  $\text{O}_2$ .
  - d. requires lactic acid.
  - e. prevents glycolysis.
6. Which statement about pyruvate is *not* true?
  - a. It is the end product of glycolysis.
  - b. It becomes reduced during fermentation.
  - c. It is a precursor of acetyl CoA.
  - d. It is a protein.
  - e. It contains three carbon atoms.
7. The citric acid cycle
  - a. has no connection with the respiratory chain.
  - b. is the same thing as fermentation.
  - c. reduces two  $\text{NAD}^+$  for every glucose processed.
  - d. produces no ATP.
  - e. takes place in the mitochondrion.
8. The respiratory chain
  - a. is located in the mitochondrial matrix.
  - b. includes only peripheral membrane proteins.
  - c. always produces ATP.
  - d. reoxidizes reduced coenzymes.
  - e. operates simultaneously with fermentation.
9. Compared with fermentation, the aerobic pathways of glucose metabolism produce
  - a. more ATP.
  - b. pyruvate.
  - c. fewer protons for pumping in the mitochondria.
  - d. less  $\text{CO}_2$ .
  - e. more oxidized coenzymes.
10. Which statement about oxidative phosphorylation is *not* true?
  - a. It forms ATP by the respiratory chain/ATP synthesis.
  - b. It is brought about by chemiosmosis.
  - c. It requires aerobic conditions.
  - d. It takes place in mitochondria.
  - e. Its functions can be served equally well by fermentation.

## FOR DISCUSSION

1. Trace the sequence of chemical changes that occurs in mammalian tissue when the oxygen supply is cut off. The first change is that the cytochrome *c* oxidase system becomes totally reduced, because electrons can still flow from cytochrome *c*, but there is no oxygen to accept electrons from cytochrome *c* oxidase. What are the remaining steps?
2. Some cells that use the aerobic pathways of glucose metabolism can also thrive by using fermentation under anaerobic conditions. Given the lower yield of ATP (per molecule

of glucose) in fermentation, how can these cells function so efficiently under anaerobic conditions?

3. The drug antimycin A blocks electron transport in mitochondria. Explain what would happen if the experiment on the left in Figure 9.10 were repeated in the presence of this drug.
4. You eat a burger that contains polysaccharides, proteins, and lipids. Using what you know of the integration of biochemical pathways, explain how the amino acids in the proteins and the glucose in the polysaccharides can end up as fats.

## ADDITIONAL INVESTIGATION

A protein in the fat of newborns uncouples the synthesis of ATP from electron transport and instead generates heat. How would

you investigate the hypothesis that this uncoupling protein adds a second proton channel to the mitochondrial membrane?

## WORKING WITH DATA (GO TO [yourBioPortal.com](http://yourBioPortal.com))

### Two Experiments Demonstrate the Chemiosmotic Mechanism

In this real-life exercise, you will examine the background and data from the original research paper by Jagendorf and Uribe in which they showed that an artificially induced  $\text{H}^+$  gradient

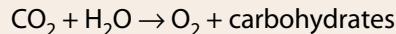
could drive ATP synthesis (Figure 9.10). You will see how they measured ATP by two different methods, and what control experiments they performed to confirm their interpretation.

# 10

# Photosynthesis: Energy from Sunlight

## Photosynthesis and global climate change

If all the carbohydrates produced by photosynthesis in a year were in the form of sugar cubes, there would be 300 quadrillion of them. Lined up, these cubes would extend from Earth to Pluto—a lot of photosynthesis! As you may have learned from previous courses, photosynthetic organisms use atmospheric carbon dioxide ( $\text{CO}_2$ ) to produce carbohydrates. The simplified equation says it all:



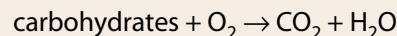
Given the role of  $\text{CO}_2$ , how will photosynthesis change with increasing levels of atmospheric  $\text{CO}_2$ ? Over the past 200 years, the concentration of atmospheric  $\text{CO}_2$  has increased—from 280 parts per million (ppm) in 1800 to 386 ppm in 2008. This increase is correlated with industrialization and the accompanying use of fossil fuels such as coal and oil, which release  $\text{CO}_2$  into the atmosphere when they

are burned. The Intergovernmental Panel of Climate Change, sponsored by the United Nations, estimates that atmospheric  $\text{CO}_2$  will continue to rise over the next century.

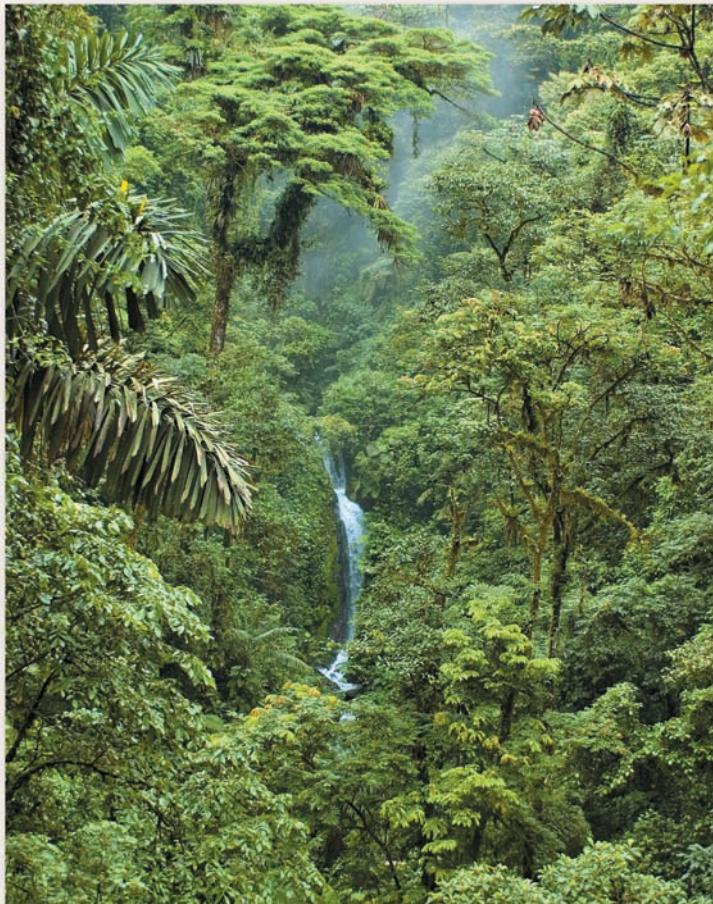
Carbon dioxide is a “greenhouse gas” that traps heat in the atmosphere, and the rising  $\text{CO}_2$  level is predicted to result in global climate change. Policy makers concerned about climate change are asking plant biologists to answer two questions about the rise in  $\text{CO}_2$ : will it lead to increased photosynthesis, and if so, will it lead to increased plant growth? To answer these questions, scientists initially measured the rate of photosynthesis of plants grown in greenhouses with elevated concentrations of  $\text{CO}_2$ . The results were surprising: at first, the rate of photosynthesis went up, but then it returned to near normal as the plants adapted to the higher  $\text{CO}_2$  levels.

To determine how plants might respond under more realistic conditions, scientists developed a way to expose plants to high levels of  $\text{CO}_2$  in the field. Free-air concentration enrichment (FACE) involves the use of rings of pipes that release  $\text{CO}_2$  to the air surrounding plants in fields or forests. Wind speed and direction are monitored by a computer, which constantly controls which pipes release  $\text{CO}_2$ . Data from these experiments confirm that photosynthetic rates increase as the concentration of  $\text{CO}_2$  rises—although generally the increase is not as high as that seen initially in the greenhouse experiments. Nevertheless, these measurements indicate that as atmospheric  $\text{CO}_2$  rises globally, there will be an increase in photosynthesis.

Will this increase in photosynthesis result in an increase in plant growth? Keep in mind that plants, like all organisms, use carbohydrates as an energy source. They perform cellular respiration with the general equation:



**Primary Producers** Covering less than 2 percent of Earth's surface, rainforests are photosynthetic dynamos. They may act as a “sink” for increasing atmospheric  $\text{CO}_2$ .





**FACE** Free-air carbon dioxide enrichment uses pipes to release CO<sub>2</sub> around plants in the field, to estimate the effects of rising atmospheric CO<sub>2</sub> on photosynthesis and plant growth.

The challenge facing plant biologists is to determine the balance between photosynthesis and respiration and how this affects the rate of plant growth. The FACE experiments indicate that crop yields increase under higher CO<sub>2</sub> concentrations, suggesting that the overall increase in photosynthesis is greater than the increase in respiration. But climate change alters rainfall patterns as well as temperatures. These changes affect where plants grow, and could shift the balance between plant growth and cellular respiration.

As with much in science, the initial questions at first appeared amenable to simple answers. Instead, they led to more questions, and more data are needed. An understanding of the processes of photosynthesis, described in this chapter, provides us with a foundation for asking and answering these urgent questions about climate change and its effects on our world.

**IN THIS CHAPTER** we begin with a consideration of light energy, and move on to describe how photosynthesis converts light energy into chemical energy, in the form of reduced electron carriers and ATP. Then, we show how these two sources of chemical energy are used to drive the synthesis of carbohydrates from CO<sub>2</sub>. Finally, we describe how these processes relate to plant metabolism and growth.

## CHAPTER OUTLINE

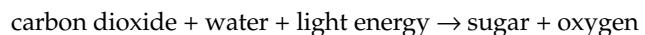
- 10.1** What Is Photosynthesis?
- 10.2** How Does Photosynthesis Convert Light Energy into Chemical Energy?
- 10.3** How Is Chemical Energy Used to Synthesize Carbohydrates?
- 10.4** How Do Plants Adapt to the Inefficiencies of Photosynthesis?
- 10.5** How Does Photosynthesis Interact with Other Pathways?

## 10.1 What Is Photosynthesis?

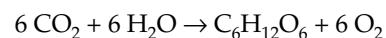
Photosynthesis (literally, “synthesis from light”) is a metabolic process by which the energy of sunlight is captured and used to convert carbon dioxide (CO<sub>2</sub>) and water (H<sub>2</sub>O) into carbohydrates (which we will represent as a six-carbon sugar, C<sub>6</sub>H<sub>12</sub>O<sub>6</sub>) and oxygen gas (O<sub>2</sub>). By early in the nineteenth century, scientists had grasped these broad outlines of photosynthesis and had established several facts about the way the process works:

- The water for photosynthesis in land plants comes primarily from the soil, and must travel from the roots to the leaves.
- Plants take in carbon dioxide, producing carbohydrates (sugars) for growth, and plants release O<sub>2</sub> (**Figure 10.1**).
- Light is absolutely necessary for the production of oxygen and sugars.

By 1804, scientists had summarized photosynthesis as follows:



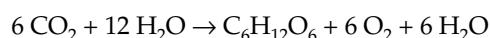
In molecular terms, this equation seems to be the reverse of the overall equation for cellular respiration (see Section 9.1). More precisely, photosynthesis can be written as:

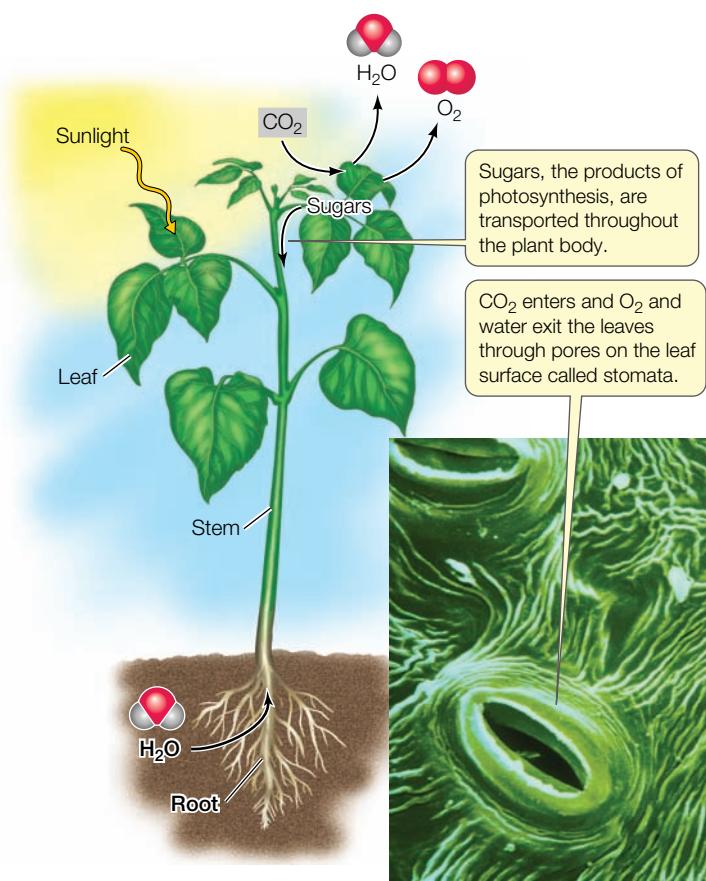


While this equation and the one for cellular respiration (given in the chapter opening story) are essentially correct, they are too general for a real understanding of the processes involved. A number of questions arise: What are the precise chemical reactions of photosynthesis? What role does light play in these reactions? How do carbons become linked to form carbohydrates? What carbohydrates are formed? And where does the oxygen gas come from: CO<sub>2</sub> or H<sub>2</sub>O?

### Experiments with isotopes show that in photosynthesis O<sub>2</sub> comes from H<sub>2</sub>O

In 1941 Samuel Ruben and Martin Kamen, at the University of California, Berkeley, performed experiments using the isotopes <sup>18</sup>O and <sup>16</sup>O to identify the source of the O<sub>2</sub> produced during photosynthesis (**Figure 10.2**). Their results showed that all the oxygen gas produced during photosynthesis comes from water, as is reflected in the revised balanced equation:

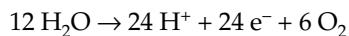




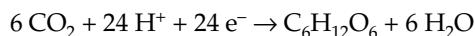
**10.1 The Ingredients for Photosynthesis** A typical terrestrial plant uses light from the sun, water from the soil, and carbon dioxide from the atmosphere to form organic compounds by photosynthesis.

Water appears on both sides of the equation because it is both used as a reactant (the twelve molecules on the left) and released as a product (the six new ones on the right). This revised equation accounts for all the water molecules needed for all the oxygen gas produced.

The realization that water was the source of photosynthetic  $\text{O}_2$  led to an understanding of photosynthesis in terms of *oxidation and reduction*. As we describe in Chapter 9, oxidation-reduction (redox) reactions are coupled: when one molecule becomes oxidized in a reaction, another gets reduced. In this case, oxygen atoms in the reduced state in  $\text{H}_2\text{O}$  get oxidized to  $\text{O}_2$ :



while carbon atoms in the oxidized state in  $\text{CO}_2$  get reduced to carbohydrate, with the simultaneous production of water:



Adding these two equations (chemistry students will recognize them as *half-cell reactions*) gives the overall equation shown above. As you will see, there is an intermediary carrier of the  $\text{H}^+$  and electrons between these two processes—the redox coenzyme, nicotinamide adenine dinucleotide phosphate ( $\text{NADP}^+$ ).

### Photosynthesis involves two pathways

The equations above summarize the overall process of photosynthesis, but not the stages by which it is completed. Like gly-

colysis and the other metabolic pathways that harvest energy in cells, photosynthesis is a process consisting of many reactions. These reactions are commonly divided into two main pathways:

- The **light reactions** convert light energy into chemical energy in the form of ATP and the reduced electron carrier NADPH. This molecule is similar to NADH (see Section 9.1) but with an additional phosphate group attached to the sugar of its adenosine. In general, NADPH acts as a reducing agent in photosynthesis and other anabolic reactions.
- The **light-independent reactions** (carbon-fixation reactions) do not use light directly, but instead use ATP, NADPH (*made by the light reactions*), and  $\text{CO}_2$  to produce carbohydrate.

## INVESTIGATING LIFE

### 10.2 The Source of the Oxygen Produced by Photosynthesis

Although it was clear that  $\text{O}_2$  was made during photosynthesis, its molecular source was not known. Two possibilities were the reactants,  $\text{CO}_2$  and  $\text{H}_2\text{O}$ . In two separate experiments, Samuel Ruben and Martin Kamen labeled the oxygen in these molecules with the isotope  $^{18}\text{O}$ , then tested the  $\text{O}_2$  produced by a green plant to find out which molecule contributed the oxygen.

**HYPOTHESIS** The oxygen released by photosynthesis comes from water rather than  $\text{CO}_2$ .

#### METHOD

Give plants isotope-labeled water and unlabeled  $\text{CO}_2$ .

#### Experiment 1

$\text{H}_2^{18}\text{O}$ ,  $\text{CO}_2$



#### Experiment 2

$\text{H}_2\text{O}$ ,  $\text{C}^{18}\text{O}_2$

Give plants isotope-labeled  $\text{CO}_2$  and unlabeled water.

#### RESULTS

The oxygen released is labeled.

$^{18}\text{O}_2$

The oxygen released is unlabeled.

#### CONCLUSION

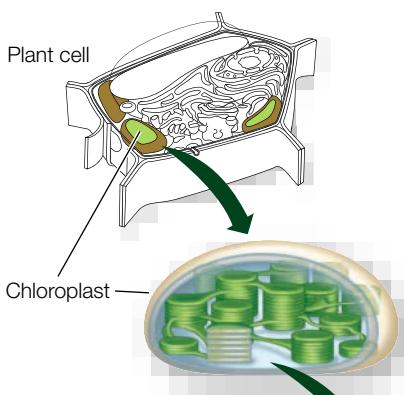
Water is the source of the  $\text{O}_2$  produced by photosynthesis.

**FURTHER INVESTIGATION:** How would you test for the source of oxygen atoms in the carbohydrates made by photosynthesis?

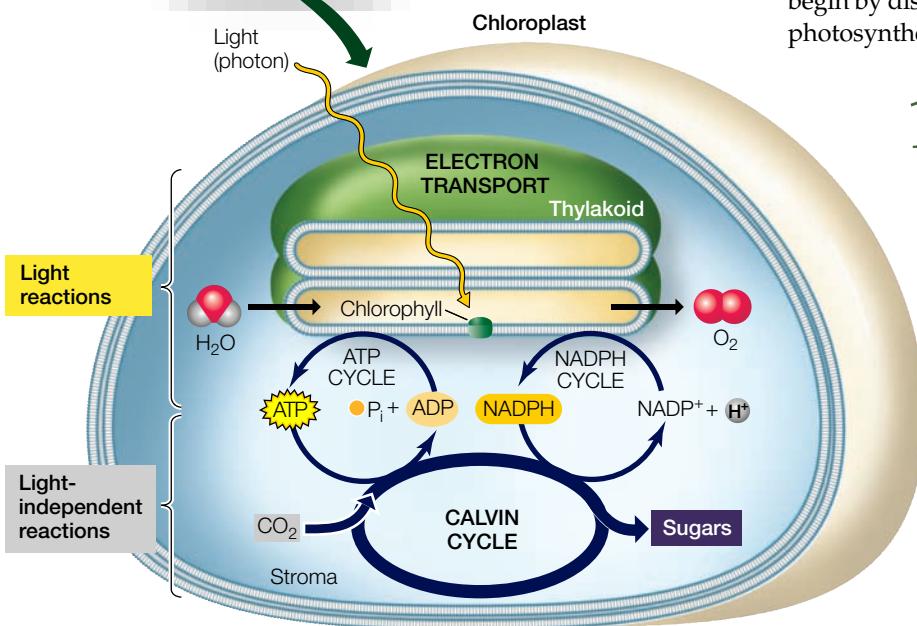
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GO TO Animated Tutorial 10.1 • The Source of the Oxygen Produced by Photosynthesis



**10.3 An Overview of Photosynthesis** Photosynthesis consists of two pathways: the light reactions and the light-independent reactions. These reactions take place in the thylakoids and the stroma of chloroplasts, respectively.



The light-independent reactions are sometimes called the *dark reactions* because they do not directly require light energy. They are also called the *carbon-fixation reactions*. However, both the light reactions and the light-independent reactions stop in the dark because ATP synthesis and NADP<sup>+</sup> reduction require light. The reactions of both pathways proceed within the chloroplast, but they occur in different parts of that organelle (Figure 10.3).

As we describe these two series of reactions in more detail, you will see that they conform to the principles of biochemistry that we discuss in Chapters 8 and 9: energy transformations, oxidation-reduction, and the stepwise nature of biochemical pathways.

## 10.1 RECAP

The light reactions of photosynthesis convert light energy into chemical energy. The light-independent reactions use that chemical energy to reduce CO<sub>2</sub> to carbohydrates.

- What is the experimental evidence that water is the source of the O<sub>2</sub> produced during photosynthesis? See pp. 190–191 and Figure 10.2
- What is the relationship between the light reactions and the light-independent reactions of photosynthesis? See pp. 191–192 and Figure 10.3

We will describe the light reactions and the light-independent reactions separately and in detail. But since these two photosynthetic pathways are powered by the energy of sunlight, let's begin by discussing the physical nature of light and the specific photosynthetic molecules that capture its energy.

## 10.2 How Does Photosynthesis Convert Light Energy into Chemical Energy?

Light is a form of energy, and it can be converted to other forms of energy such as heat or chemical energy. Our focus here will be on light as the source of energy to drive the formation of ATP (from ADP and P<sub>i</sub>) and NADPH (from NADP<sup>+</sup> and H<sup>+</sup>).

### Light is a form of energy with dual properties

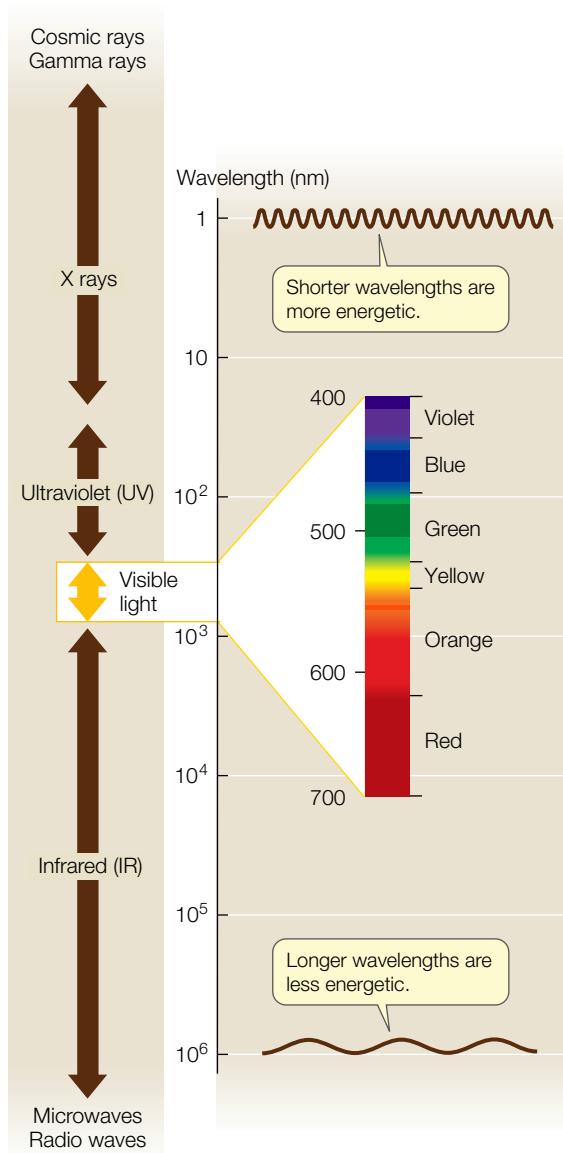
Light is a form of **electromagnetic radiation**. It is propagated in waves, and the amount of energy in light is inversely proportional to its **wavelength**—the shorter the wavelength, the greater the energy. The visible portion of the electromagnetic spectrum (Figure 10.4) encompasses a wide range of wavelengths and energy levels. In addition to traveling in waves, light also behaves as particles, called **photons**, which have no mass. In plants and other photosynthetic organisms, receptive molecules absorb photons in order to harvest their energy for biological processes. Because these receptive molecules absorb only specific wavelengths of light, the photons must have the correct amount of energy—they must be of the appropriate wavelength.

### Molecules become excited when they absorb photons

When a photon meets a molecule, one of three things can happen:

- The photon may bounce off the molecule—it may be scattered or reflected.
- The photon may pass through the molecule—it may be transmitted.
- The photon may be absorbed by the molecule, adding energy to the molecule.

Neither of the first two outcomes causes any change in the molecule. However, in the case of absorption, the photon disappears and its energy is absorbed by the molecule. The photon's energy cannot disappear, because according to the first law of thermodynamics, energy is neither created nor destroyed. When the molecule acquires the energy of the photon it is raised from a ground state (with lower energy) to an excited state (with higher energy) (Figure 10.5A).



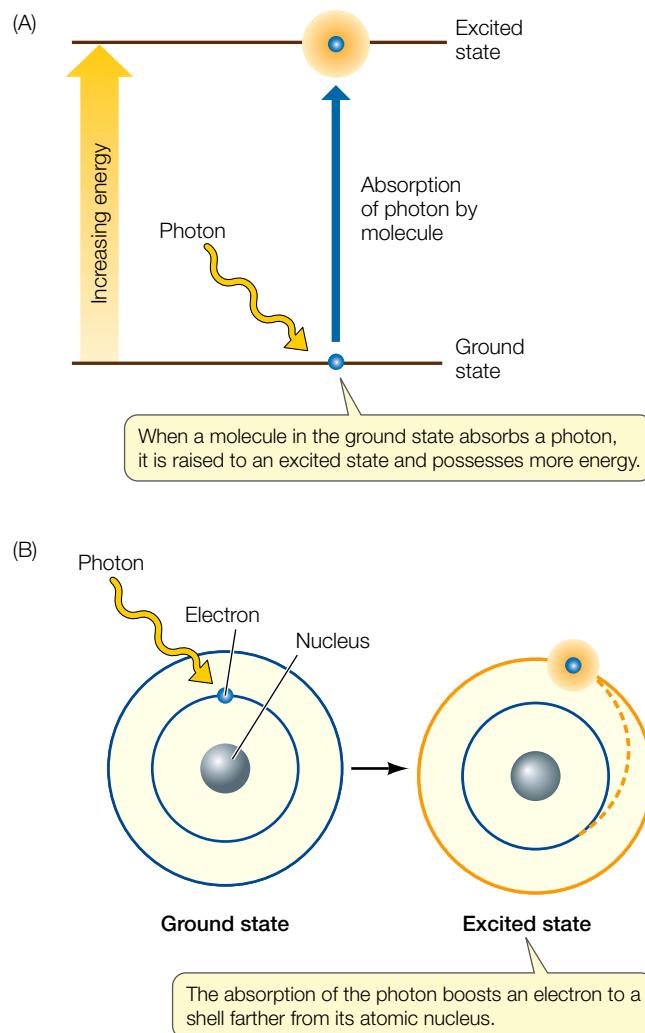
**10.4 The Electromagnetic Spectrum** The portion of the electromagnetic spectrum that is visible to humans as light is shown in detail at the right.

The difference in free energy between the molecule's excited state and its ground state is approximately equal to the free energy of the absorbed photon (a small amount of energy is lost to entropy). The increase in energy boosts one of the electrons within the molecule into a shell farther from its nucleus; this electron is now held less firmly (Figure 10.5B), making the molecule unstable and more chemically reactive.

### Absorbed wavelengths correlate with biological activity

The specific wavelengths absorbed by a particular molecule are characteristic of that type of molecule. Molecules that absorb wavelengths in the visible spectrum are called **pigments**.

When a beam of white light (containing all the wavelengths of visible light) falls on a pigment, certain wavelengths are absorbed. The remaining wavelengths, which are scattered or trans-

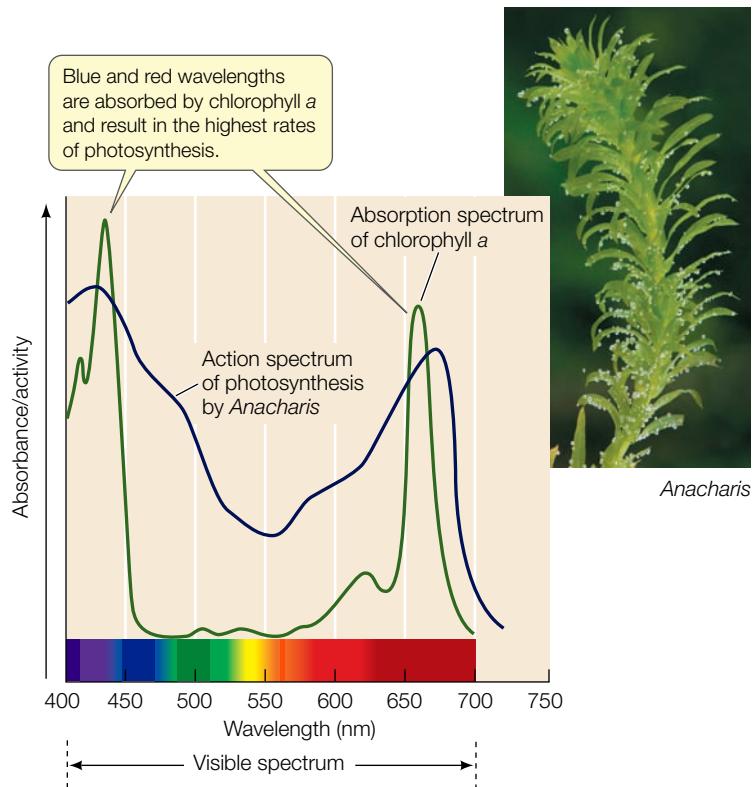


**10.5 Exciting a Molecule** (A) When a molecule absorbs the energy of a photon, it is raised from a ground state to an excited state. (B) In the excited state, an electron is boosted to a shell more distant from the atomic nucleus, where it is held less firmly.

mitted, make the pigment appear to us as colored. For example, if a pigment absorbs both blue and red light (as does chlorophyll) what we see is the remaining light, which is primarily green. If we plot light absorbed by a purified pigment against wavelength, the result is an **absorption spectrum** for that pigment.

In contrast to the absorption spectrum, an **action spectrum** is a plot of the *biological activity* of an organism as a function of the wavelengths of light to which it is exposed. The experimental determination of an action spectrum might be performed as follows:

1. Place a plant (a water plant with thin leaves is convenient) in a closed container.
2. Expose the plant to light of a certain wavelength for a period of time.
3. Measure photosynthesis by the amount of O<sub>2</sub> released.
4. Repeat with light of other wavelengths.



**10.6 Absorption and Action Spectra** The absorption spectrum of the purified pigment chlorophyll *a* from the aquatic plant *Anacharis* is similar to the action spectrum obtained when different wavelengths of light are shone on the intact plant and the rate of photosynthesis is measured. In the thicker leaves of land plants, the action spectra show less of a dip in the green region (500–650 nm).

**Figure 10.6** shows the absorption spectrum of the pigment chlorophyll *a*, which was isolated from the leaves of *Anacharis*, a common aquarium plant. Also shown is the action spectrum for photosynthetic activity by the same plant. A comparison of the two spectra shows that the wavelengths at which photosynthesis is highest are the same wavelengths at which chlorophyll *a* absorbs light.

### Several pigments absorb energy for photosynthesis

The light energy used for photosynthesis is not absorbed by just one type of pigment. Instead, several different pigments with different absorption spectra collect the energy that is eventually used for photosynthesis. In photosynthetic organisms as diverse as green algae, protists, and bacteria, these pigments include chlorophylls, carotenoids, and phycobilins.

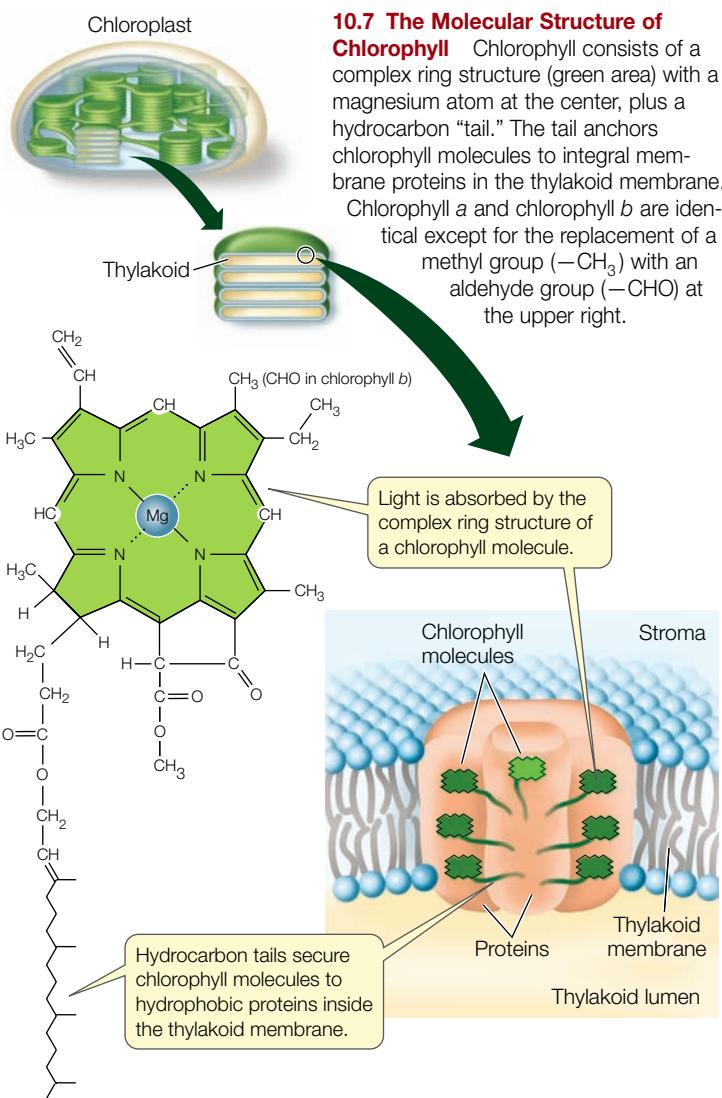
**CHLOROPHYLLS** In plants, two chlorophylls are responsible for absorbing the light energy that is used to drive the light reactions: **chlorophyll *a*** and **chlorophyll *b***. These two molecules differ only slightly in their molecular structures. Both have a complex ring structure similar to that of the heme group of hemoglobin (**Figure 10.7**). In the center of the chlorophyll ring is a magnesium atom. Attached at a peripheral location on the ring is a long hydrocarbon “tail,” which anchors the chlorophyll molecule to in-

tegral proteins in the thylakoid membrane of the chloroplast. (See Figure 5.13 to review the anatomy of a chloroplast.)

**ACCESSORY PIGMENTS** We saw in Figure 10.6 that chlorophyll absorbs blue and red light, which are near the two ends of the visible spectrum. Thus, if only chlorophyll were active in photosynthesis, much of the visible spectrum would go unused. This appears to be the case in higher plants. But lower plants (such as algae) and cyanobacteria possess accessory pigments, which absorb photons intermediate in energy between the red and the blue wavelengths and then transfer a portion of that energy to the chlorophylls. Among these accessory pigments are **carotenoids** such as  $\beta$ -carotene (see Figure 3.21), which absorb photons in the blue and blue-green wavelengths and appear deep yellow. The **phycobilins**, which are found in red algae and in cyanobacteria, absorb various yellow-green, yellow, and orange wavelengths.

### Light absorption results in photochemical change

Any pigment molecule can become excited when its absorption spectrum matches the energies of incoming photons. After a



pigment molecule absorbs a photon and enters an excited state (see Figure 10.5), there are several alternative fates for the absorbed energy:

- It can be released as heat and/or light.
- It may be rapidly transferred to a neighboring pigment molecule.
- It can be used as free energy to drive a chemical reaction.

When the excited molecule gives up the absorbed energy it returns to the ground state.

Sometimes the absorbed energy is given off as heat and light, in a process called *fluorescence*. Because some of the energy of the original absorbed photon is lost as heat, the photon that is released as fluorescence has less energy and a longer wavelength than the absorbed light. When there is fluorescence, there are no permanent chemical changes made or biological functions performed—no chemical work is done.

On the other hand, the excited pigment molecule may pass the absorbed energy along to another molecule—provided that the target molecule is very near, has the right orientation, and has the appropriate structure to receive the energy. This is what happens in photosynthesis.

The pigments in photosynthetic organisms are arranged into energy-absorbing **antenna systems**, also called *light-harvesting complexes*. These form part of a large multi-protein complex called a **photosystem**. The photosystem spans the thylakoid membrane, and consists of multiple antenna systems, with their associated pigment molecules, all surrounding a **reaction center**. The pigment molecules in the antenna systems are packed together in such a way that the excitation energy from an absorbed photon can be passed along from one pigment molecule to another (Figure 10.8). Excitation energy moves from pigments that absorb shorter wavelengths (higher energy) to pigments that absorb

longer wavelengths (lower energy). Thus the excitation ends up in the pigment molecules that absorb the longest wavelengths. These pigment molecules are in the reaction center of the photosystem, and form special associations with the photosystem proteins (see Figure 10.8). The ratio of antenna pigments to reaction center pigments can be quite high (over 300:1).

The reaction center converts the absorbed light energy into chemical energy. A pigment molecule in the reaction center absorbs sufficient energy that it actually gives up its excited electron (is chemically oxidized) and becomes positively charged. In plants, the reaction center contains a pair of chlorophyll *a* molecules. There are many other chlorophyll *a* molecules in the antenna systems, but because of their interactions with antenna proteins, all of them absorb light at shorter wavelengths than the pair in the reaction center.

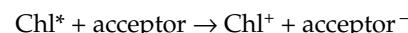
### Excited chlorophylls in the reaction center act as electron donors

Chlorophyll has two vital roles in photosynthesis:

- It absorbs light energy and transforms it into excited electrons.
- It transfers those electrons to other molecules, initiating chemical changes.

We have dealt with the first role; now we turn to the second.

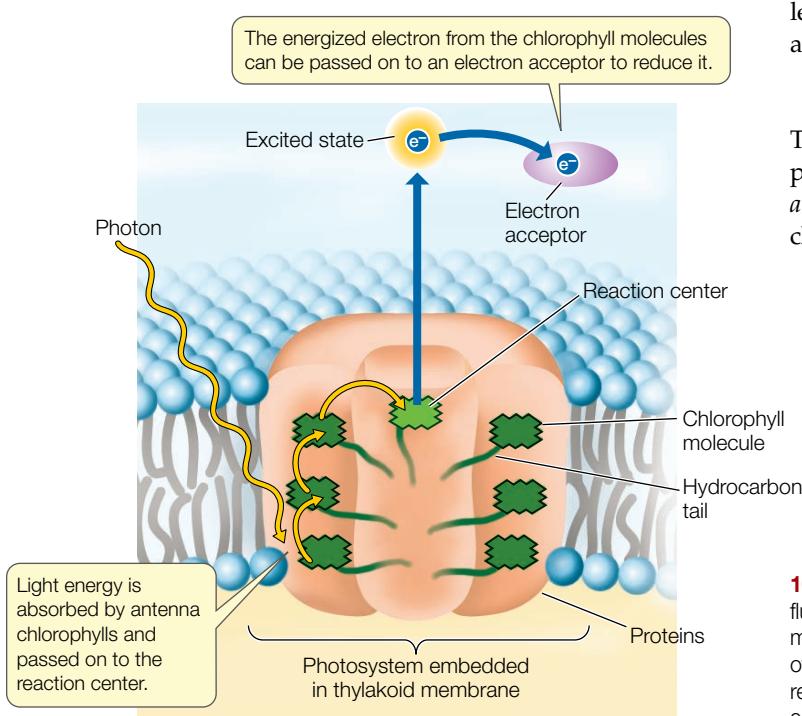
Photosynthesis harvests chemical energy by using the excited chlorophyll molecules in the reaction center as electron donors (reducing agents) to reduce a stable electron acceptor (see Figure 10.8). Ground-state chlorophyll (symbolized by Chl) is not much of a reducing agent, but excited chlorophyll (Chl\*) is a good one. This is because in the excited molecule, one of the electrons has moved to a shell that is farther away from the nucleus than the shell it normally occupies. This electron is held less tightly than in the normal state, and it can be transferred in a redox reaction to an electron acceptor (an oxidizing agent):



This, then, is the first consequence of light absorption by chlorophyll: a reaction center chlorophyll (Chl\*) loses its excited electron in a redox reaction and becomes Chl<sup>+</sup> (because it gives up a negative charge—it gets oxidized).

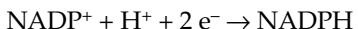
### Reduction leads to electron transport

The electron acceptor that is reduced by Chl\* is the first in a chain of electron carriers in the thylakoid membrane that participate in a process termed *electron transport*. This energetically “downhill” series of reductions and oxidations is similar to what occurs in the respiratory chain of



**10.8 Energy Transfer and Electron Transport** Rather than being lost as fluorescence, energy from a photon may be transferred from one pigment molecule to another. In a photosystem, energy is transferred through a series of molecules to one or more pigment molecules in the reaction center. If a reaction center molecule becomes sufficiently excited, it will give up its excited electron to an electron acceptor.

mitochondria (see Section 9.3). The final electron acceptor is NADP<sup>+</sup> (nicotinamide adenine dinucleotide phosphate), which gets reduced:



The energy-rich NADPH is a stable, reduced coenzyme.

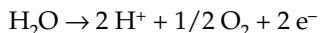
There are two different systems of electron transport in photosynthesis:

- **Noncyclic electron transport** produces NADPH and ATP. Essentially, the excited electron is “lost” from chlorophyll and the transport process ends up with a reduced coenzyme.
- **Cyclic electron transport** produces only ATP. Essentially, the transport process ends up with the excited electron returning to chlorophyll, after giving up energy to make ATP.

We'll consider these two systems before describing the production of ATP from ADP and P<sub>i</sub>.

### Noncyclic electron transport produces ATP and NADPH

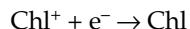
In noncyclic electron transport, light energy is used to oxidize water, forming O<sub>2</sub>, H<sup>+</sup>, and electrons. In quantitative terms this would be



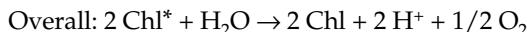
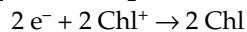
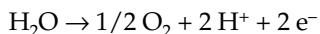
We saw above that a key reaction in photosynthesis occurs when chlorophyll that is excited by absorbing light (Chl\*) gives up its excited electron, becoming oxidized:



Because it lacks an electron, Chl<sup>+</sup> is very unstable; it has a very strong tendency to “grab” an electron from another molecule to replenish the one it lost:



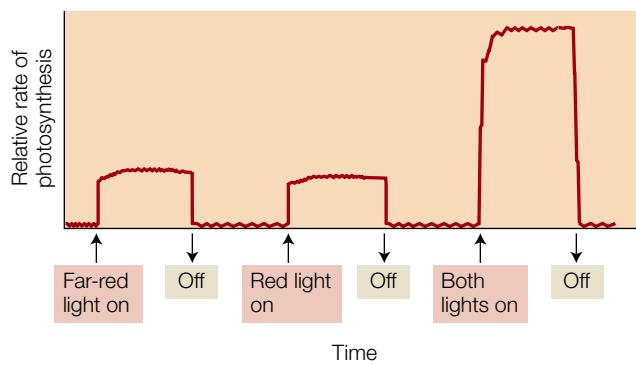
So in chemical terms, Chl<sup>+</sup> is a strong oxidizing agent. The replenishing electrons come from water, splitting the H–O–H bonds.



Notice that this is a more precise description of what Ruben and Kamen had found, namely that the source of O<sub>2</sub> in photosynthesis is H<sub>2</sub>O (see Figure 10.2).

The electrons are passed from chlorophyll to NADP<sup>+</sup> through a chain of electron carriers in the thylakoid membrane. These redox reactions are exergonic, and some of the released free energy is ultimately used to form ATP by *chemiosmosis* (see p. 180).

**TWO PHOTOSYSTEMS ARE REQUIRED** Noncyclic electron transport requires the participation of two different photosystems in the thylakoid membrane. What is the evidence of the existence of these two photosystems? In 1957, Robert Emerson at the University of Illinois shone light of various wavelengths onto cells of *Chlorella*, a freshwater protist. Both red light (wavelength 680 nm) and far-red light (700 nm) resulted in modest rates of photosynthesis, as measured by O<sub>2</sub> production. But when the two lights



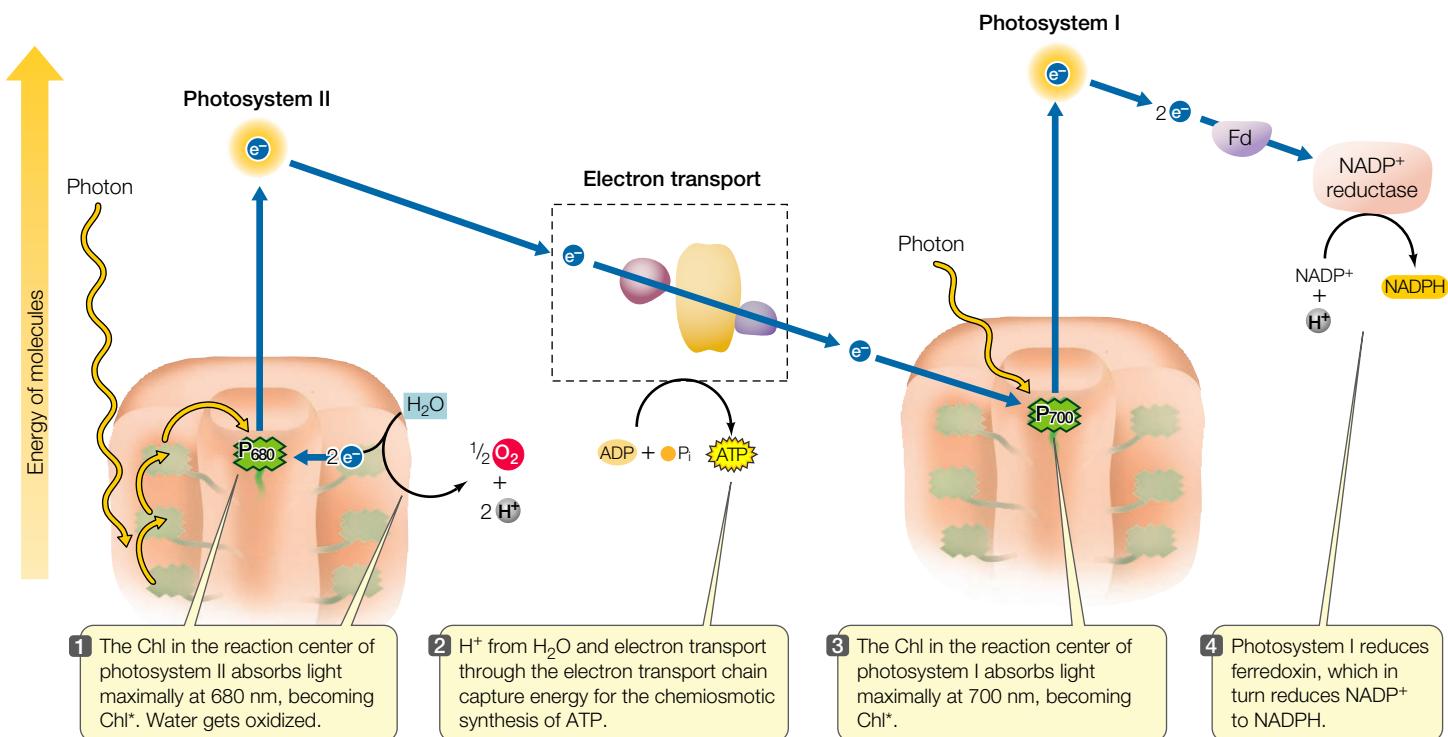
**10.9 Two Photosystems** The absorption and action spectra for chlorophyll and photosynthesis indicated that the rate of photosynthesis would increase in red light. Robert Emerson shone red (660 nm) and far-red (>700 nm) light both separately and together on algal cells to look for cooperative effects.

were combined, the rate of photosynthesis was much greater than the rates under either red light or far red light. In fact it was greater than the two rates added together. This phenomenon was termed photo enhancement (Figure 10.9). A few years later, photo enhancement was explained by the existence of *not one but two reaction centers*, which act together to enhance photosynthesis.

- **Photosystem I** uses light energy to pass an excited electron to NADP<sup>+</sup>, reducing it to NADPH.
- **Photosystem II** uses light energy to oxidize water molecules, producing electrons, protons (H<sup>+</sup>), and O<sub>2</sub>.

The reaction center for photosystem I contains a pair of chlorophyll *a* molecules called P<sub>700</sub> because it can best absorb light with a wavelength of 700 nm. Similarly, the pair of chlorophyll *a* molecules in the photosystem II reaction center is called P<sub>680</sub> because it absorbs light maximally at 680 nm. Thus photosystem II requires photons that are somewhat more energetic (i.e., have shorter wavelengths) than those required by photosystem I. To keep noncyclic electron transport going, both photosystems must be constantly absorbing light, thereby boosting electrons to higher shells from which they may be captured by specific electron acceptors. A model for the way photosystems I and II interact and complement each other is called the “Z scheme,” because when the path of the electrons is placed along an axis of rising energy level, it resembles a sideways letter Z (Figure 10.10).

**ELECTRON TRANSPORT: THE Z SCHEME** In the Z scheme model, which describes the reactions of noncyclic electron transport from water to NADP<sup>+</sup>, photosystem II comes before photosystem I. When photosystem II absorbs photons, electrons pass from P<sub>680</sub> to the primary electron acceptor and P<sub>680</sub>\* is oxidized to P<sub>680</sub><sup>+</sup>. Then an electron from the oxidation of water is passed to P<sub>680</sub><sup>+</sup>, reducing it to P<sub>680</sub> once again, so that it can receive more energy from neighboring chlorophyll molecules in the antenna systems. The electrons from photosystem II pass through a series of transfer reactions, one of which is directly responsible for the physical movement of protons from the stroma (the matrix outside the thylakoids) across the thylakoid membrane and into the lumen (see Figure 10.12). In addition to these protons, the protons derived from the splitting of water are deposited into the thylakoid lumen. Furthermore, protons in the stroma are



consumed during the reduction of  $\text{NADP}^+$ , and together these reactions create a proton gradient across the thylakoid membrane, which provides the energy for ATP synthesis.

In photosystem I, the  $\text{P}_{700}$  molecules in the reaction center become excited to  $\text{P}_{700}^*$ , leading to the reduction of an electron carrier called ferredoxin (Fd) and the production of  $\text{P}_{700}^+$ .  $\text{P}_{700}^+$  returns to the reduced state by accepting electrons passed through the electron transport system from photosystem II. Having identified the role of the electrons produced by photosystem II, we can now ask, "What is the role of the electrons transferred to Fd from photosystem I?" These electrons are used in the last step of noncyclic electron transport, in which two electrons and a proton are used to reduce a molecule of  $\text{NADP}^+$  to  $\text{NADPH}$ .

In summary:

- Noncyclic electron transport extracts electrons from water and passes them ultimately to  $\text{NADPH}$ , utilizing energy absorbed by photosystems I and II, and resulting in ATP synthesis.
- Noncyclic electron transport yields  $\text{NADPH}$ , ATP, and  $\text{O}_2$ .

### Cyclic electron transport produces ATP but no $\text{NADPH}$

Noncyclic electron transport results in the production of ATP and  $\text{NADPH}$ . However, as we will see, the light-independent reactions of photosynthesis require more ATP than  $\text{NADPH} + \text{H}^+$ . If only the noncyclic pathway is operating, there is the possibility that there will not be enough ATP formed. **Cyclic electron transport** makes up for the imbalance. This pathway, which produces only ATP, is called *cyclic* because an electron passed from an excited chlorophyll molecule at the outset cycles back to the same chlorophyll molecule at the end of the chain of reactions (Figure 10.11).

### 10.10 Noncyclic Electron Transport Uses Two Photosystems

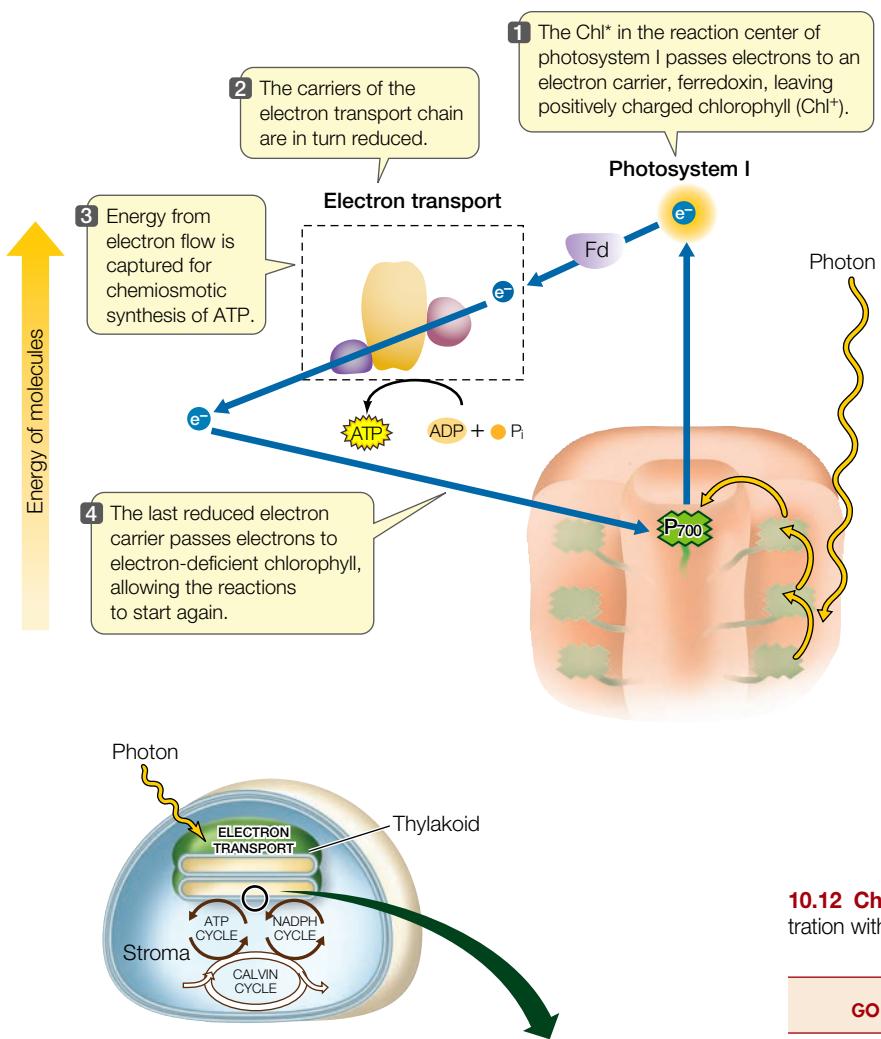
Absorption of light energy by chlorophyll molecules in the reaction centers of photosystems I and II allows them to pass electrons into a series of redox reactions. The term "Z scheme" describes the path (blue arrows) of electrons as they travel through the two photosystems. On this scheme the vertical positions represent the energy levels of the molecules in the electron transport system.

Cyclic electron transport begins and ends in photosystem I. A  $\text{P}_{700}$  chlorophyll molecule in the reaction center absorbs a photon and enters the excited state,  $\text{P}_{700}^*$ . The excited electron is passed from  $\text{P}_{700}^*$  to a primary acceptor, and then to oxidized ferredoxin ( $\text{Fd}_{\text{ox}}$ ), producing reduced ferredoxin ( $\text{Fd}_{\text{red}}$ ).  $\text{Fd}_{\text{red}}$  passes its added electron to a different oxidizing agent, plastocyanin (PQ, a small organic molecule), resulting in the transfer of two  $\text{H}^+$  from the stroma to the thylakoid lumen. The electron passes from reduced PQ through the electron transport system until it completes its cycle by returning to  $\text{P}_{700}^+$ , restoring it to its uncharged form,  $\text{P}_{700}$ . This electron transport is carried out by plastocyanin (PC) and cytochromes that are similar to those of the mitochondrial respiratory chain.

By the time the electron from  $\text{P}_{700}^*$  travels through the electron transport system and comes back to reduce  $\text{P}_{700}^+$ , all the energy from the original photon has been released. The released energy is stored in the form of a proton gradient that can be used to produce ATP.

### Chemiosmosis is the source of the ATP produced in photophosphorylation

In Chapter 9 we describe the chemiosmotic mechanism for ATP formation in the mitochondrion. A similar mechanism, called **photophosphorylation**, operates in the chloroplast, where electron transport is coupled to the transport of protons ( $\text{H}^+$ ) across



### 10.11 Cyclic Electron Transport Traps Light Energy as ATP

Cyclic electron transport produces ATP, but no NADPH.

the thylakoid membrane, resulting in a proton gradient across the membrane (**Figure 10.12**).

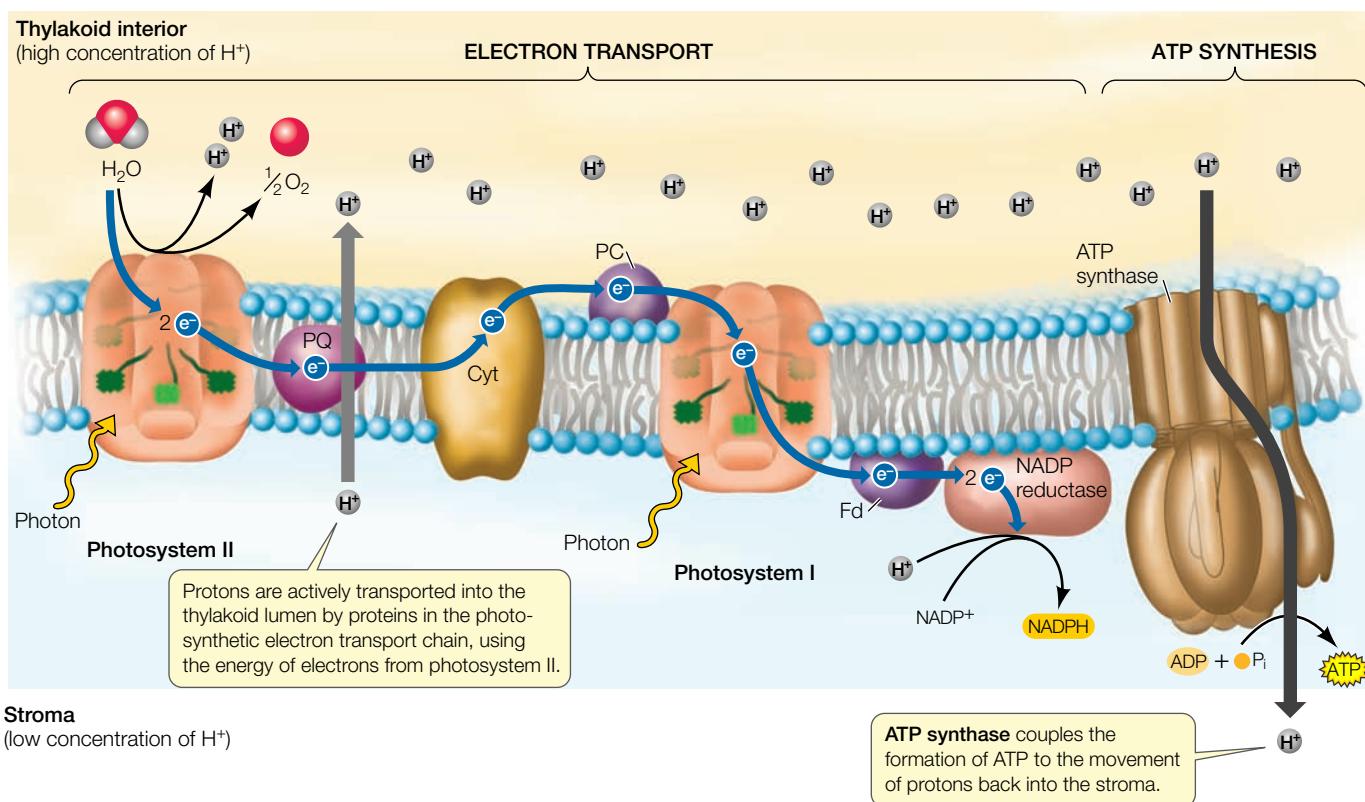
The electron carriers in the thylakoid membrane are oriented so that protons are actively pumped from the stroma into the lumen of the thylakoid. Thus the lumen becomes acidic with respect to the stroma, resulting in an electrochemical gradient across the thylakoid membrane, whose bilayer is not permeable to H<sup>+</sup>. Water oxidation and NADP<sup>+</sup> reduction also contribute to this gradient, which drives the movement of protons back out of the thylakoid lumen through specific protein channels in the thylakoid membrane. These channels are enzymes—ATP synthases—that couple the movement of protons to the formation of ATP, as they do in mitochondria (see Figure 9.9). Indeed, chloroplast ATP synthase is about 60 percent identical to human mitochondrial ATP synthase—a remarkable similarity, given that plants and animals had their most recent

### 10.12 Chloroplasts Form ATP Chemiosmotically

Compare this illustration with Figure 9.9, where a similar process is depicted in mitochondria.

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common ancestor more than a billion years ago. This is testimony to the evolutionary unity of life.

The mechanisms of the two enzymes are similar, but their orientations differ. In chloroplasts, protons flow through the ATP synthase out of the thylakoid lumen into the stroma (where the ATP is synthesized) but in mitochondria they flow out of the cytosol into the mitochondrial matrix.

## 10.2 RECAP

Conversion of light energy into chemical energy occurs when pigments absorb photons. Light energy is used to drive a series of protein-associated redox reactions in the thylakoid membranes of the chloroplast.

- How does chlorophyll absorb and transfer light energy? See pp. 194–195 and Figure 10.8
- How are electrons produced in photosystem II and how do they flow to photosystem I? See pp. 196–197 and Figure 10.10
- How does cyclic electron transport in photosystem I result in the production of ATP? See p. 197 and Figure 10.11

We have seen how light energy drives the synthesis of ATP and NADPH in the stroma of chloroplasts. We now turn to the light-independent reactions of photosynthesis, which use energy-rich ATP and NADPH to reduce  $\text{CO}_2$  and form carbohydrates.

## 10.3 How Is Chemical Energy Used to Synthesize Carbohydrates?

Most of the enzymes that catalyze the reactions of  $\text{CO}_2$  fixation are dissolved in the stroma of the chloroplast, where those reactions take place. These enzymes use the energy in ATP and NADPH to reduce  $\text{CO}_2$  to carbohydrates. Therefore, with some exceptions,  $\text{CO}_2$  fixation occurs only in the light, when ATP and NADPH are being generated.

### Radioisotope labeling experiments revealed the steps of the Calvin cycle

To identify the reactions by which the carbon from  $\text{CO}_2$  ends up in carbohydrates, scientists found a way to label  $\text{CO}_2$  so that they could isolate and identify the compounds formed from it during photosynthesis. In the 1950s, Melvin Calvin, Andrew Benson, and their colleagues used radioactively labeled  $\text{CO}_2$  in which some of the carbon atoms were the radioisotope  $^{14}\text{C}$  rather than the normal  $^{12}\text{C}$ . Although  $^{14}\text{C}$  emits radiation, its chemical behavior is virtually identical to that of nonradioactive  $^{12}\text{C}$ .

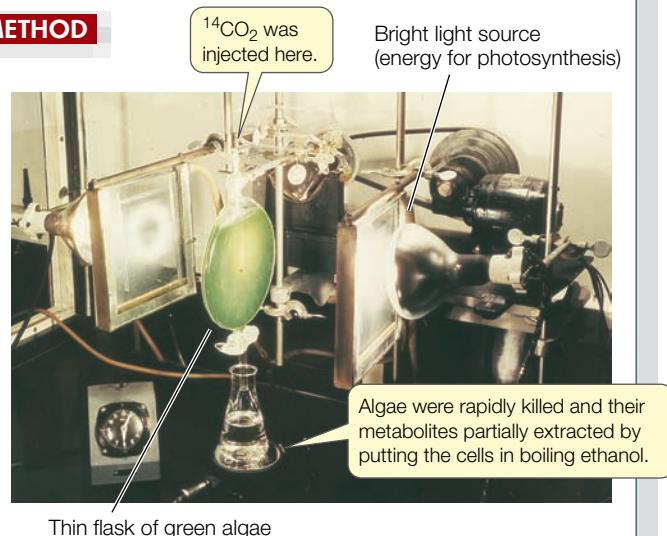
Calvin and his colleagues exposed cultures of the unicellular green alga *Chlorella* to  $^{14}\text{CO}_2$  for various lengths of time. Then they rapidly killed the cells and extracted the organic compounds. They separated the different compounds from one another by paper chromatography and exposed the paper to X-ray film (Figure 10.13). When the film was developed, dark

### 10.13 Tracing the Pathway of $\text{CO}_2$

How is  $\text{CO}_2$  incorporated into carbohydrate during photosynthesis? What is the first stable covalent linkage that forms with the carbon of  $\text{CO}_2$ ? Short exposures to  $^{14}\text{CO}_2$  were used to identify the first compound formed from  $\text{CO}_2$ .

**HYPOTHESIS** The first product of  $\text{CO}_2$  fixation is a 3-carbon molecule.

#### METHOD



Thin flask of green algae

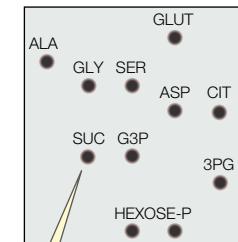
The algal extract was spotted here and run in two directions to separate compounds from one another.

After separation of the compounds, the chromatogram was overlaid with X-ray film.

#### RESULTS



A chromatogram made after 3 seconds of exposure to  $^{14}\text{CO}_2$  shows  $^{14}\text{C}$  only in 3PG (3-phosphoglycerate).



A chromatogram made after 30 seconds of exposure to  $^{14}\text{CO}_2$  shows  $^{14}\text{C}$  in many molecules.

#### CONCLUSION

The initial product of  $\text{CO}_2$  fixation is 3PG. Later, the carbon from  $\text{CO}_2$  ends up in many molecules.

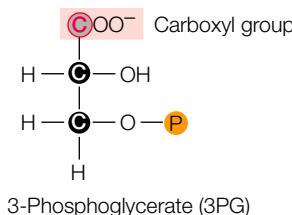
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spots indicated the locations of compounds containing  $^{14}\text{C}$  in the paper.

To discover the first compound in the pathway of  $\text{CO}_2$  fixation, Calvin and his team exposed the algae to  $^{14}\text{CO}_2$  for shorter and shorter periods of time. The 3-second exposure revealed that only one compound was labeled—a 3-carbon sugar phosphate called 3-phosphoglycerate (3PG) (the  $^{14}\text{C}$  is shown in red):



With successive exposures longer than 3 seconds, Calvin and his colleagues were able to trace the route of  $^{14}\text{C}$  as it moved through a series of compounds, including monosaccharides and amino acids. It turned out that the pathway the  $^{14}\text{C}$  moved through was a cycle. In this cycle, the  $\text{CO}_2$  initially bonds covalently to a larger five-carbon acceptor molecule, which then breaks into two three-carbon molecules. As the cycle repeats a carbohydrate is produced and the initial  $\text{CO}_2$  acceptor is regenerated. This was appropriately named the **Calvin cycle**.

The initial reaction in the Calvin cycle adds the 1-carbon  $\text{CO}_2$  to an acceptor molecule, the 5-carbon compound ribulose 1,5-bisphosphate (RuBP). The product is an intermediate 6-carbon compound, which quickly breaks down and forms two molecules of 3PG (Figure 10.14). The intermediate compound is broken down so rapidly that Calvin did not observe radioactive label appearing in it first. But the enzyme that catalyzes its formation, **ribulose bisphosphate carboxylase/oxygenase (rubisco)**, is the most abundant protein in the world! It constitutes up to 50 percent of all the protein in every plant leaf.

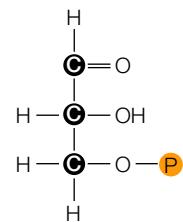
### The Calvin cycle is made up of three processes

The Calvin cycle uses the ATP and NADPH made in the light to reduce  $\text{CO}_2$  in the stroma to a carbohydrate. Like all biochem-

ical pathways, each reaction is catalyzed by a specific enzyme. The cycle is composed of three distinct processes (Figure 10.15):

- *Fixation* of  $\text{CO}_2$ . As we have seen, this reaction is catalyzed by rubisco, and its stable product is 3PG.
- *Reduction* of 3PG to form glyceraldehyde 3-phosphate (G3P). This series of reactions involves a phosphorylation (using the ATP made in the light reactions) and a reduction (using the NADPH made in the light reactions).
- *Regeneration* of the  $\text{CO}_2$  acceptor, RuBP. Most of the G3P ends up as ribulose monophosphate (RuMP), and ATP is used to convert this compound into RuBP. So for every “turn” of the cycle, with one  $\text{CO}_2$  fixed, the  $\text{CO}_2$  acceptor is regenerated.

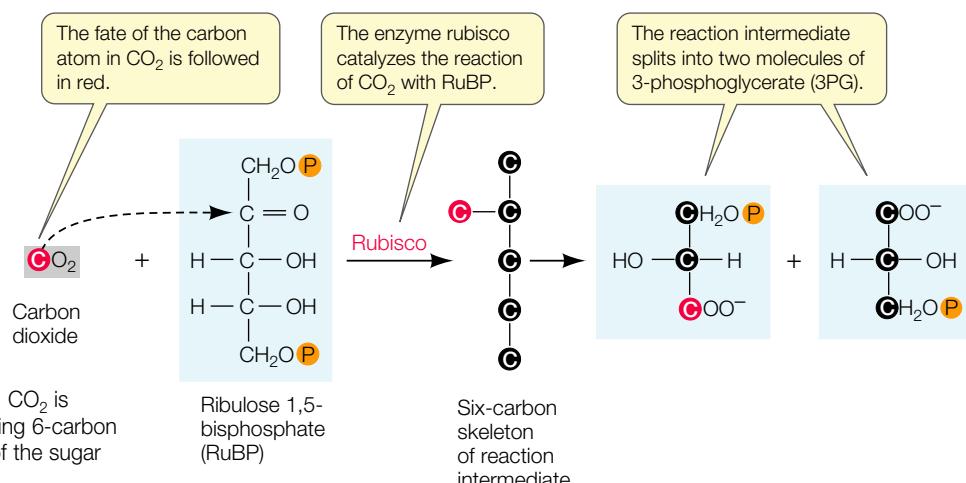
The product of this cycle is **glyceraldehyde 3-phosphate (G3P)**, which is a 3-carbon sugar phosphate, also called triose phosphate:



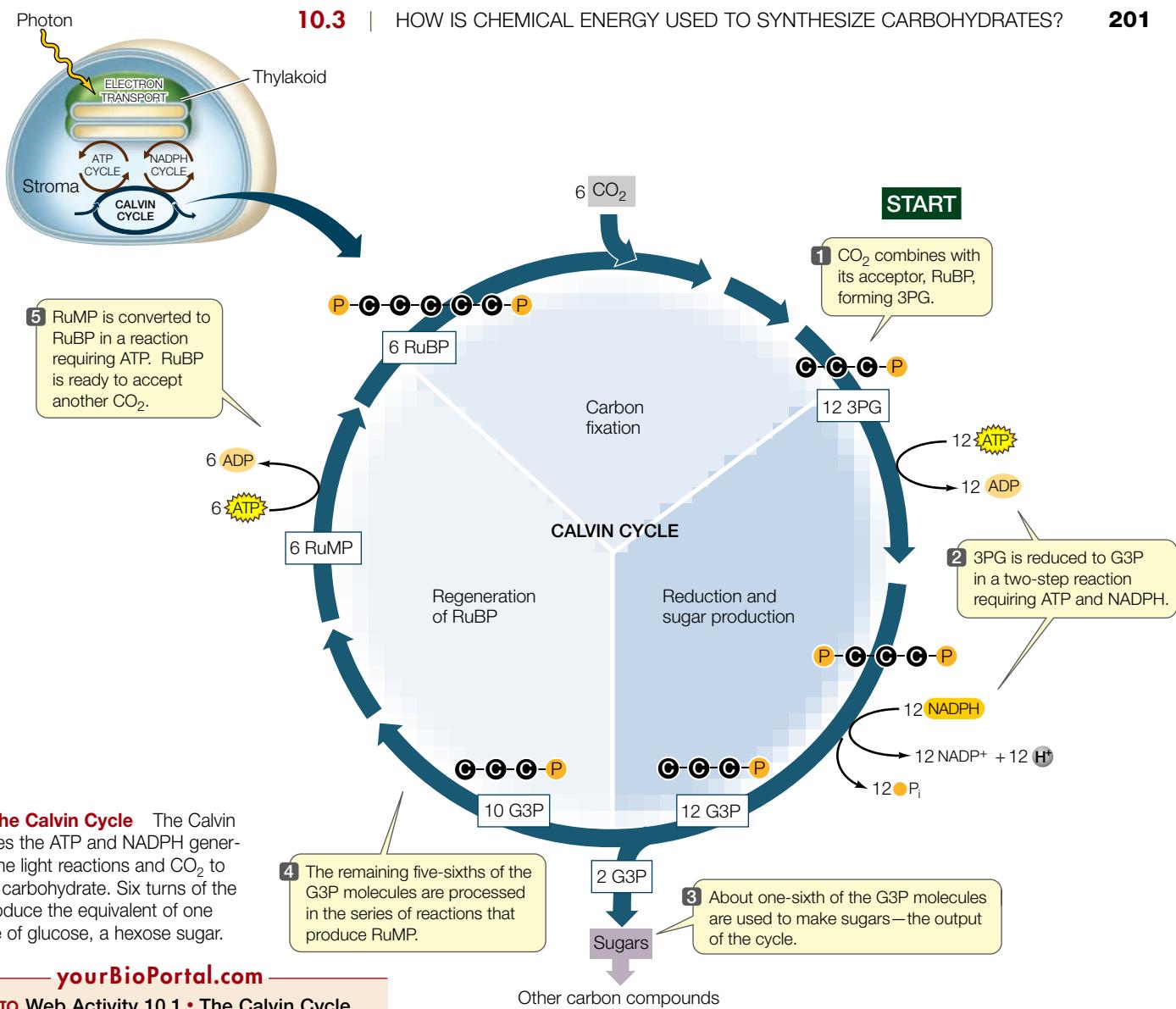
Glyceraldehyde 3-phosphate (G3P)

In a typical leaf, five-sixths of the G3P is recycled into RuBP. There are two fates for the remaining G3P, depending on the time of day and the needs of different parts of the plant:

- Some of it is exported out of the chloroplast to the cytosol, where it is converted to hexoses (glucose and fructose). These molecules may be used in glycolysis and mitochondrial respiration to power the activities of photosynthetic cells (see Chapter 9) or they may be converted into the disaccharide sucrose, which is transported out of the leaf to other organs in the plant. There it is hydrolyzed to its constituent monosaccharides, which can be used as sources of energy or as building blocks for other molecules.



**10.14 RuBP Is the Carbon Dioxide Acceptor**  $\text{CO}_2$  is added to a 5-carbon compound, RuBP. The resulting 6-carbon compound immediately splits into two molecules of the sugar phosphate 3PG.



- As the day wears on, glucose accumulates inside of the chloroplast, and these glucose units are linked to form the polysaccharide starch. This stored carbohydrate can then be drawn upon during the night so that the photosynthetic tissues can continue to export sucrose to the rest of the plant, even when photosynthesis is not taking place. In addition, starch is abundant in nonphotosynthetic organs such as roots, underground stems and seeds, where it provides a ready supply of glucose to fuel cellular activities, including plant growth.

The carbohydrates produced in photosynthesis are used by the plant to make other compounds. The carbon molecules are incorporated into amino acids, lipids, and the building blocks of nucleic acids—in fact all the organic molecules in the plant.

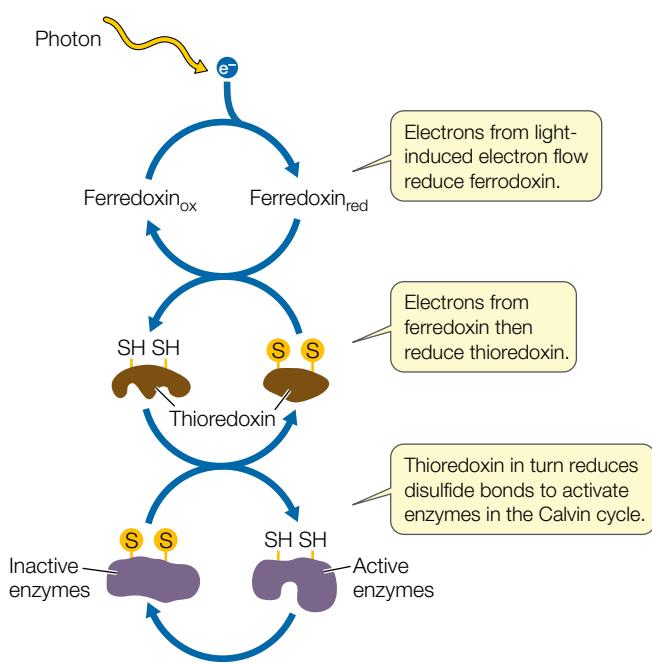
The products of the Calvin cycle are of crucial importance to the Earth's entire biosphere. For the majority of living organisms on Earth, the C—H covalent bonds generated by the cycle provide almost all of the energy for life. Photosynthetic organisms, which are also called **autotrophs** ("self-feeders"), release most of this energy by glycolysis and cellular respiration, and use it to support their own growth, development, and repro-

duction. But plants are also the source of energy for other organisms. Much plant matter ends up being consumed by **heterotrophs** ("other-feeders"), such as animals, which cannot photosynthesize. Heterotrophs depend on autotrophs for both raw materials and energy. Free energy is released from food by glycolysis and cellular respiration in heterotroph cells.

### Light stimulates the Calvin cycle

As we have seen, the Calvin cycle uses NADPH and ATP, which are generated using energy from light. Two other processes connect the light reactions with this CO<sub>2</sub> fixation pathway. Both connections are indirect but significant:

- Light-induced pH changes in the stroma activate some Calvin cycle enzymes. Proton pumping from the stroma into the thylakoid lumen causes an increase in the pH of the stroma from 7 to 8 (a tenfold decrease in H<sup>+</sup> concentration). This favors the activation of rubisco.
- The light-induced electron transport reduces disulfide bonds in four of the Calvin cycle enzymes, thereby activat-



**10.16 The Photochemical Reactions Stimulate the Calvin Cycle**  
By reducing (breaking) disulfide bridges, electrons from the light reactions activate enzymes in CO<sub>2</sub> fixation.

ing them (Figure 10.16). When ferredoxin is reduced in photosystem I (see Figure 10.10), it passes some electrons to a small, soluble protein called thioredoxin, and this protein passes electrons to four enzymes in the CO<sub>2</sub> fixation pathway. Reduction of the sulfurs in the disulfide bridges of these enzymes (see Figure 3.5) forms SH groups and breaks the bridges. The resulting changes in their three-dimensional shapes activate the enzymes and increase the rate at which the Calvin cycle operates.

### 10.3 RECAP

ATP and NADPH produced in the light reactions power the synthesis of carbohydrates by the Calvin cycle. This cycle fixes CO<sub>2</sub>, reduces it, and regenerates the acceptor, RuBP, for further fixation.

- Describe the experiments that led to the identification of RuBP as the initial CO<sub>2</sub> acceptor in photosynthesis.  
**See pp. 199–200 and Figure 10.13**
- What are the three processes of the Calvin cycle?  
**See pp. 200–201 and Figure 10.15**
- In what ways does light stimulate the Calvin cycle?  
**See pp. 201–202 and Figure 10.16**

Although all green plants carry out the Calvin cycle, some plants have evolved variations on, or additional steps in, the light-independent reactions. These variations and additions have permitted plants to adapt to and thrive in certain environmental conditions. Let's look at these environmental limitations and the metabolic bypasses that have evolved to circumvent them.

## 10.4 How Do Plants Adapt to the Inefficiencies of Photosynthesis?

In addition to fixing CO<sub>2</sub> during photosynthesis, rubisco can react with O<sub>2</sub>. This reaction leads to a process called photorespiration, which lowers the overall rate of CO<sub>2</sub> fixation in some plants. After examining this problem, we'll look at some biochemical pathways and features of plant anatomy that compensate for the limitations of rubisco.

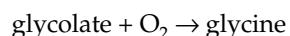
### Rubisco catalyzes the reaction of RuBP with O<sub>2</sub> or CO<sub>2</sub>

As its full name indicates, rubisco is an **oxygenase** as well as a **carboxylase**—it can add O<sub>2</sub> to the acceptor molecule RuBP instead of CO<sub>2</sub>. The affinity of rubisco for CO<sub>2</sub> is about ten times stronger than its affinity for O<sub>2</sub>. This means that inside a leaf with a normal exchange of air with the outside, CO<sub>2</sub> fixation is favored even though the concentration of CO<sub>2</sub> in the air is far less than that of O<sub>2</sub>. But if there is an even higher concentration of O<sub>2</sub> in the leaf, it acts as a competitive inhibitor, and RuBP reacts with O<sub>2</sub> rather than CO<sub>2</sub>. This reduces the overall amount of CO<sub>2</sub> that is converted into carbohydrates, and may play a role in limiting plant growth.

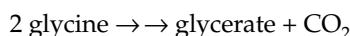
When O<sub>2</sub> is added to RuBP, one of the products is a 2-carbon compound, phosphoglycolate:



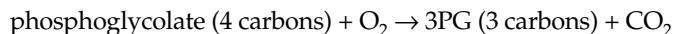
The 3PG formed by oxygenase activity enters the Calvin cycle but the phosphoglycolate does not. Plants have evolved a metabolic pathway that can partially recover the carbon in phosphoglycolate. The phosphoglycolate is hydrolyzed to glycolate, which diffuses into membrane-enclosed organelles called peroxisomes (Figure 10.17). There, a series of reactions converts it into the amino acid glycine:



The glycine then diffuses into a mitochondrion, where two glycine molecules are converted in a series of reactions into the amino acid serine, which goes back to the peroxisome and is converted into glycerate (a 3-carbon molecule) and CO<sub>2</sub>:

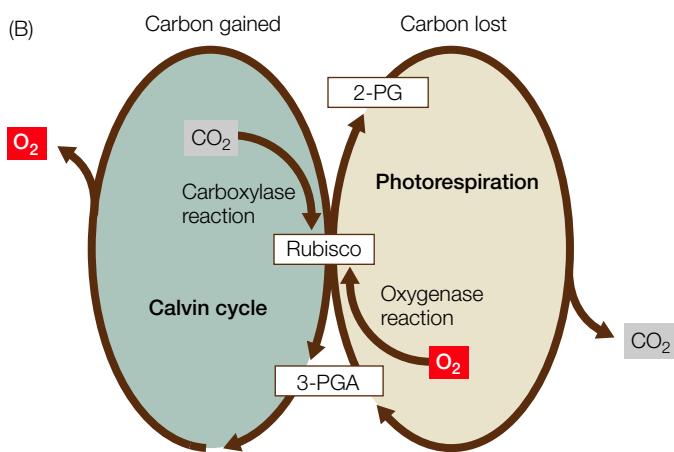
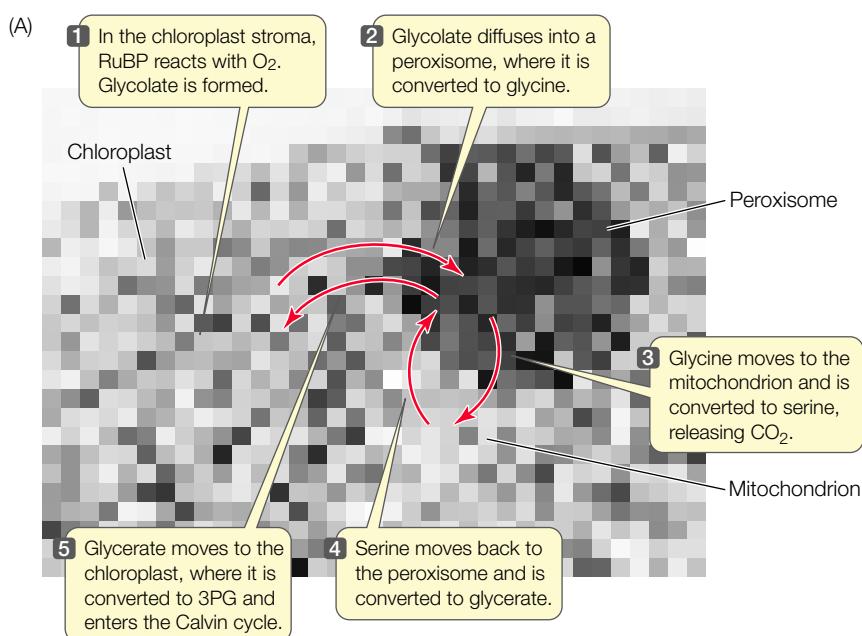


The glycerate moves into the chloroplast, where it is phosphorylated to make 3PG, which enters the Calvin cycle. So overall:



This pathway thus reclaims 75 percent of the carbons from phosphoglycolate for the Calvin cycle. In other words, the reaction of RuBP with O<sub>2</sub> instead of CO<sub>2</sub> reduces the net carbon fixed by the Calvin cycle by 25 percent. The pathway is called **photorespiration** because it consumes O<sub>2</sub> and releases CO<sub>2</sub> and because it occurs only in the light (due to the same enzyme activation processes that were mentioned above with regard to the Calvin cycle).

Why does rubisco act as an oxygenase as well as a carboxylase? Several factors are involved: active site affinities, concentrations of CO<sub>2</sub> and O<sub>2</sub>, and temperature.



**10.17 Organelles of Photorespiration** (A) The reactions of photorespiration take place in the chloroplasts, peroxisomes, and mitochondria. (B) Overall, photorespiration consumes O<sub>2</sub> and releases CO<sub>2</sub>.

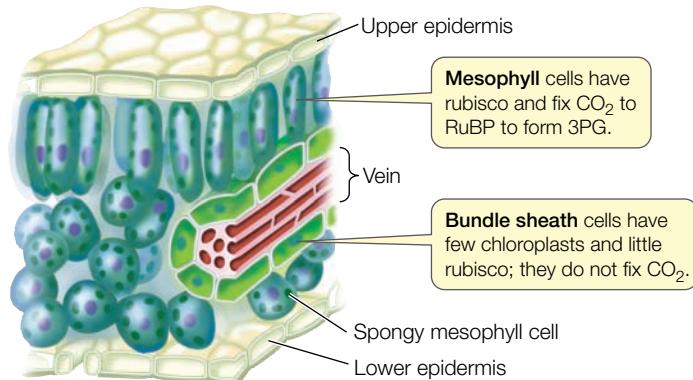
- As noted above, rubisco has a ten times higher affinity for CO<sub>2</sub> than for O<sub>2</sub>, and this favors CO<sub>2</sub> fixation.
- In the leaf, the relative concentrations of CO<sub>2</sub> and O<sub>2</sub> vary. If O<sub>2</sub> is relatively abundant, rubisco acts as an oxygenase and photorespiration ensues. If CO<sub>2</sub> predominates, rubisco fixes it for the Calvin cycle.
- Photorespiration is more likely at high temperatures. On a hot, dry day, small pores in the leaf surface called **stomata** close to prevent water from evaporating from the leaf (see Figure 10.1). But this also prevents gases from entering and leaving the leaf. The CO<sub>2</sub> concentration in the leaf falls as CO<sub>2</sub> is used up in photosynthetic reactions, and the O<sub>2</sub> concentration rises because of these same reactions. As the ratio of CO<sub>2</sub> to O<sub>2</sub> falls, the oxygenase activity of rubisco is favored, and photorespiration proceeds.

### C<sub>3</sub> plants undergo photorespiration but C<sub>4</sub> plants do not

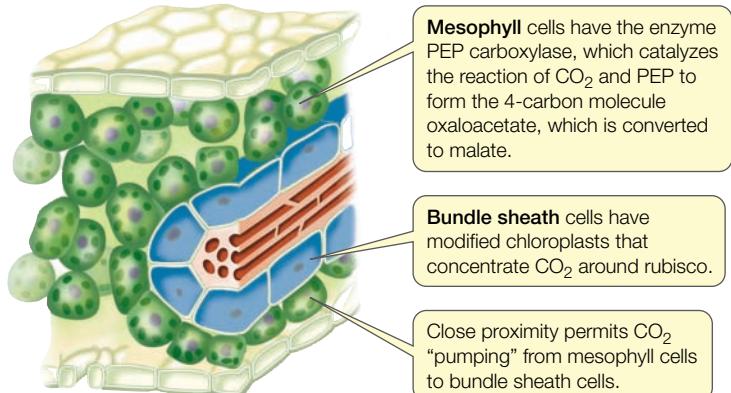
Plants differ in how they fix CO<sub>2</sub>, and can be distinguished as C<sub>3</sub> or C<sub>4</sub> plants, based on whether the first product of CO<sub>2</sub> fixation is a 3- or 4-carbon molecule. In **C<sub>3</sub> plants** such as roses, wheat, and rice, the first product is the 3-carbon molecule 3PG—as we have just described for the Calvin cycle. In these plants the cells of the mesophyll, which makes up the main body of the leaf, are full of chloroplasts containing rubisco (Figure 10.18A). On a hot day, these leaves close their stomata to conserve water, and as a result, rubisco acts as an oxygenase as well as a carboxylase, and photorespiration occurs.

**C<sub>4</sub> plants**, which include corn, sugarcane, and tropical grasses, make the 4-carbon molecule **oxaloacetate** as the first product of CO<sub>2</sub> fixation (Figure 10.18B). On a hot day, they partially close their stomata to conserve water, but their rate of photosynthesis does not fall, nor does photorespiration occur. What do they do differently?

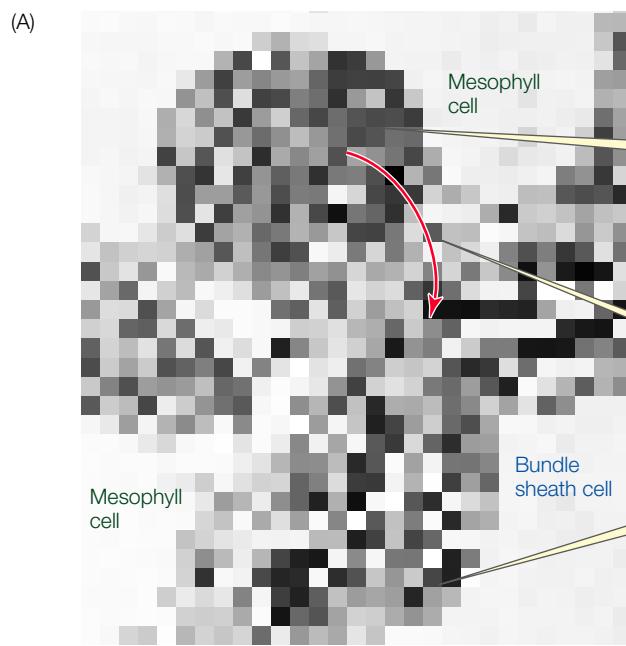
#### (A) Arrangement of cells in a C<sub>3</sub> leaf



#### (B) Arrangement of cells in a C<sub>4</sub> leaf



**10.18 Leaf Anatomy of C<sub>3</sub> and C<sub>4</sub> Plants** Carbon dioxide fixation occurs in different organelles and cells of the leaves in (A) C<sub>3</sub> plants and (B) C<sub>4</sub> plants. Cells that are tinted blue have rubisco.

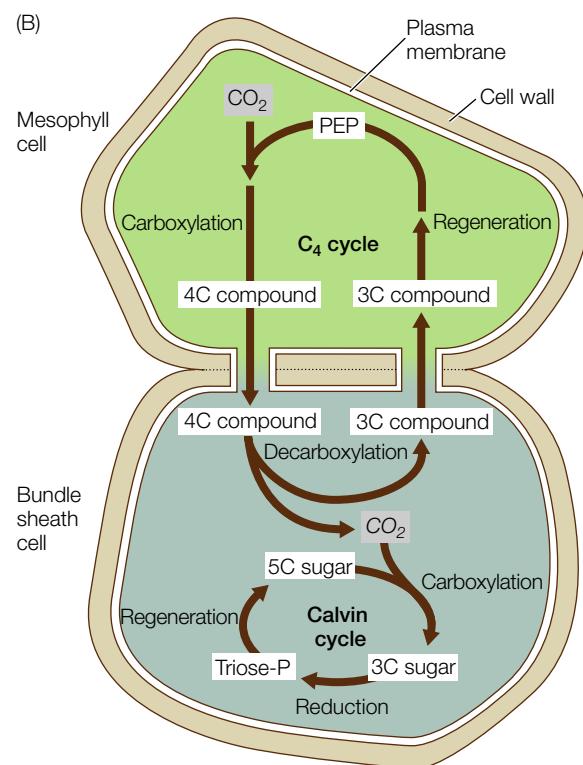


**10.19 The Anatomy and Biochemistry of C<sub>4</sub> Carbon Fixation** (A) Carbon dioxide is fixed initially in the mesophyll cells, but enters the Calvin cycle in the bundle sheath cells. (B) The two cell types share an interconnected biochemical pathway for CO<sub>2</sub> assimilation.

surface of the leaf. It fixes CO<sub>2</sub> to a 3-carbon acceptor compound, **phosphoenolpyruvate (PEP)**, to produce the 4-carbon fixation product, oxaloacetate. PEP carboxylase has two advantages over rubisco:

- It does not have oxygenase activity.
- It fixes CO<sub>2</sub> even at very low CO<sub>2</sub> levels.

So even on a hot day when the stomata are partially closed and the ratio of O<sub>2</sub> to



C<sub>4</sub> plants perform the normal Calvin cycle, but they have an additional early reaction that fixes CO<sub>2</sub> without losing carbon to photorespiration. Because this initial CO<sub>2</sub> fixation step can function even at low levels of CO<sub>2</sub> and high temperatures, C<sub>4</sub> plants very effectively optimize photosynthesis under conditions that inhibit it in C<sub>3</sub> plants. C<sub>4</sub> plants have *two separate enzymes for CO<sub>2</sub> fixation, located in different parts of the leaf* (Figure 10.19; see also Figure 10.18B). The first enzyme, called **PEP carboxylase**, is present in the cytosols of mesophyll cells near the

CO<sub>2</sub> rises, PEP carboxylase just keeps on fixing CO<sub>2</sub>.

Oxaloacetate is converted to malate, which diffuses out of the mesophyll cells and into the **bundle sheath cells** (see Figure 10.18B), located in the interior of the leaf. (Some C<sub>4</sub> plants convert the oxaloacetate to aspartate instead of malate, but we will only discuss the malate pathway here.) The bundle sheath cells contain modified chloroplasts that are designed to concentrate CO<sub>2</sub> around the rubisco. There, the 4-carbon malate loses one carbon (is decarboxylated), forming CO<sub>2</sub> and pyruvate. The latter moves back to the mesophyll cells where the 3-carbon acceptor compound, PEP, is regenerated at the expense of ATP. Thus the role of PEP is to bind CO<sub>2</sub> from the air in the leaf so that it can be transferred to the bundle sheath cells, where it is delivered to rubisco. This process essentially “pumps up” the CO<sub>2</sub> concentration around rubisco, so that it acts as a carboxylase and begins the Calvin cycle.

C<sub>3</sub> plants have an advantage over C<sub>4</sub> plants in that they don't expend extra ATP to “pump up” the concentration of CO<sub>2</sub> near rubisco. But this advantage begins to be outweighed under conditions that favor photorespiration, such as warmer seasons and climates. Under these conditions C<sub>4</sub> plants have the advantage. For example, Kentucky bluegrass is a C<sub>3</sub> plant that thrives on lawns in April and May. But in the heat of summer it does not do as well and Bermuda grass, a C<sub>4</sub> plant, takes over the lawn. The same is true on a global scale for crops: C<sub>3</sub> plants such as soybean, wheat, and barley have been adapted for human food production in temperate climates, while C<sub>4</sub> plants such as corn and sugarcane originated and are grown in the tropics.

**THE EVOLUTION OF CO<sub>2</sub> FIXATION PATHWAYS** C<sub>3</sub> plants are certainly more ancient than C<sub>4</sub> plants. While C<sub>3</sub> photosynthesis appears to have begun about 3.5 billion years ago, C<sub>4</sub> plants appeared about 12 million years ago. A possible factor in the emergence of the C<sub>4</sub> pathway is the decline in atmospheric CO<sub>2</sub>. When dinosaurs dominated Earth 100 million years ago, the concentration of CO<sub>2</sub> in the atmosphere was four times what it is now. As CO<sub>2</sub> levels declined thereafter, the more efficient C<sub>4</sub>

**TABLE 10.1**  
**Comparison of Photosynthesis in C<sub>3</sub>, C<sub>4</sub>, and CAM Plants**

	C <sub>3</sub> PLANTS	C <sub>4</sub> PLANTS	CAM PLANTS
Calvin cycle used?	Yes	Yes	Yes
Primary CO <sub>2</sub> acceptor	RuBP	PEP	PEP
CO <sub>2</sub> -fixing enzyme	Rubisco	PEP carboxylase	PEP carboxylase
First product of CO <sub>2</sub> fixation	3PG (3-carbon)	Oxaloacetate (4-carbon)	Oxaloacetate (4-carbon)
Affinity of carboxylase for CO <sub>2</sub>	Moderate	High	High
Photosynthetic cells of leaf	Mesophyll	Mesophyll and bundle sheath	Mesophyll with large vacuoles
Photorespiration	Extensive	Minimal	Minimal

plants would have gained an advantage over their C<sub>3</sub> counterparts.

As we described in the opening essay of this chapter, CO<sub>2</sub> levels have been increasing over the past 200 years. Currently, the level of CO<sub>2</sub> is not enough for maximal CO<sub>2</sub> fixation by rubisco, so photorespiration occurs, reducing the growth rates of C<sub>3</sub> plants. Under hot conditions, C<sub>4</sub> plants are favored. But if CO<sub>2</sub> levels in the atmosphere continue to rise, the reverse will occur and C<sub>3</sub> plants will have a comparative advantage. The overall growth rates of crops such as rice and wheat should increase. This may or may not translate into more food, given that other effects of the human-spurred CO<sub>2</sub> increase (such as global warming) will also alter Earth's ecosystems.

#### CAM plants also use PEP carboxylase

Other plants besides the C<sub>4</sub> plants use PEP carboxylase to fix and accumulate CO<sub>2</sub>. They include some water-storing plants (called succulents) of the family Crassulaceae, many cacti, pineapples, and several other kinds of flowering plants. The CO<sub>2</sub> metabolism of these plants is called **crassulacean acid metabolism**, or **CAM**, after the family of succulents in which it was discovered. CAM is much like the metabolism of C<sub>4</sub> plants in that CO<sub>2</sub> is initially fixed into a 4-carbon compound. But in CAM plants the initial CO<sub>2</sub> fixation and the Calvin cycle are separated in time rather than space.

- At night, when it is cooler and water loss is minimized, the stomata open. CO<sub>2</sub> is fixed in mesophyll cells to form the 4-carbon compound oxaloacetate, which is converted into malate and stored in the vacuole.
- During the day, when the stomata close to reduce water loss, the accumulated malate is shipped to the chloroplasts, where its decarboxylation supplies the CO<sub>2</sub> for the Calvin cycle and the light reactions supply the necessary ATP and NADPH.

CAM benefits the plant by allowing it to close its stomata during the day. As you will learn in Chapter 35, plants lose most of the water that they take up in their roots by evaporation through the leaves (transpiration). In dry climates, closing stomata is a key to water conservation and survival.

**Table 10.1** compares photosynthesis in C<sub>3</sub>, C<sub>4</sub>, and CAM plants.

#### 10.4 RECAP

Rubisco catalyzes the carboxylation of RuBP to form two 3PG, and the oxygenation of RuBP to form one 3PG and one phosphoglycolate. The diversion of rubisco to its oxygenase function decreases net CO<sub>2</sub> fixation. C<sub>4</sub> photosynthesis and CAM allow plants to adapt to environmental conditions that result in a limited availability of CO<sub>2</sub> inside the leaf.

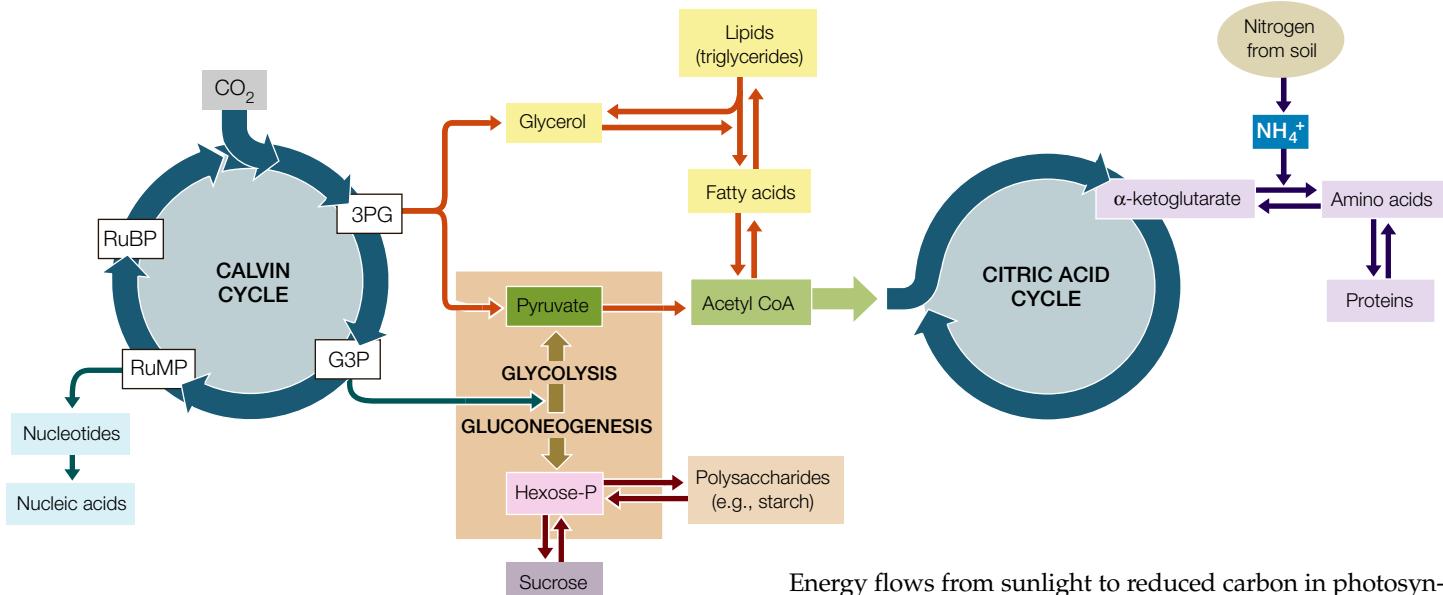
- Explain how photorespiration recovers some of the carbon that is channeled away from the Calvin cycle.  
**See pp. 202–203 and Figure 10.17**
- What do C<sub>4</sub> plants do to keep the concentration of CO<sub>2</sub> around rubisco high, and why? **See pp. 203–204 and Figure 10.19**
- What is the pathway for CO<sub>2</sub> fixation in CAM plants?  
**See p. 205**

Now that we understand how photosynthesis produces carbohydrates, let's see how the pathways of photosynthesis are connected to other metabolic pathways.

## 10.5 How Does Photosynthesis Interact with Other Pathways?

Green plants are autotrophs and can synthesize all the molecules they need from simple starting materials: CO<sub>2</sub>, H<sub>2</sub>O, phosphate, sulfate, ammonium ions (NH<sub>4</sub><sup>+</sup>), and small quantities of other mineral nutrients. The NH<sub>4</sub><sup>+</sup> is needed to synthesize amino acids and nucleotides, and it comes from either the conversion of nitrogen-containing molecules in soil water or the conversion of N<sub>2</sub> gas from the atmosphere by bacteria, as we will see in Chapter 36.

Plants use the carbohydrates generated in photosynthesis to provide energy for processes such as active transport and anabolism. Both cellular respiration and fermentation can occur in plants, although the former is far more common. Unlike photosynthesis, plant cellular respiration takes place both in the light and in the dark.



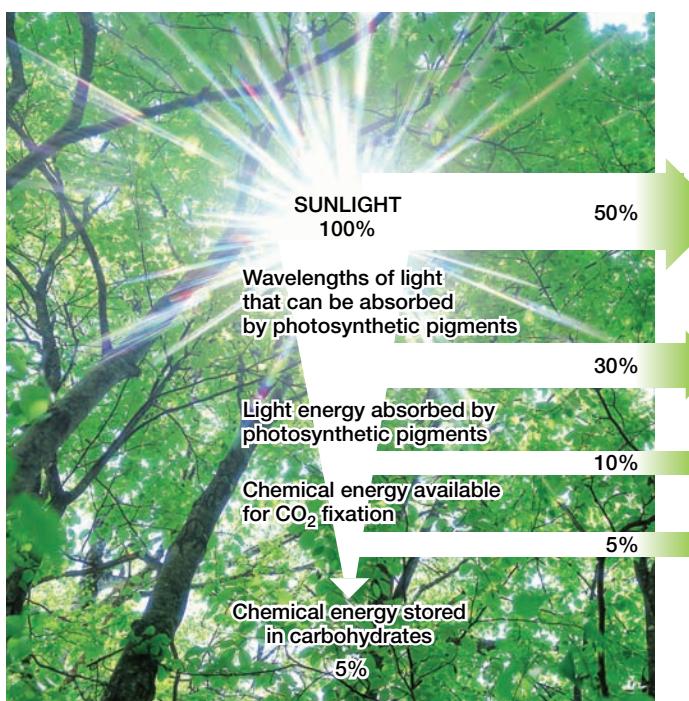
**10.20 Metabolic Interactions in a Plant Cell** The products of the Calvin cycle are used in the reactions of cellular respiration (glycolysis and the citric acid cycle).

Photosynthesis and respiration are closely linked through the Calvin cycle (**Figure 10.20**). The partitioning of G3P is particularly important:

- Some G3P from the Calvin cycle takes part in the glycolysis pathway and is converted into pyruvate in the cytosol. This pyruvate can be used in cellular respiration for energy, or its carbon skeletons can be used in anabolic reactions to make lipids, proteins, and other carbohydrates (see Figure 9.14).
- Some G3P can enter a pathway that is the reverse of glycolysis (gluconeogenesis; see Section 9.5). In this case, hexose-phosphates and then sucrose are formed and transported to the nonphotosynthetic tissues of the plant (such as the root).

Energy flows from sunlight to reduced carbon in photosynthesis, then to ATP in respiration. Energy can also be stored in the bonds of macromolecules such as polysaccharides, lipids, and proteins. For a plant to grow, energy storage (as body structures) must exceed energy release; that is, overall carbon fixation by photosynthesis must exceed respiration. This principle is the basis of the ecological food chain, as we will see in later chapters.

Photosynthesis provides most of the energy that we need for life. Given the uncertainties about the future of photosynthesis (due to changes in CO<sub>2</sub> levels and climate change), it would be wise to seek ways to improve photosynthetic efficiency. **Figure 10.21** shows the various ways in which solar energy is utilized by plants or lost. In essence, only about 5 percent of the sunlight that reaches Earth is converted into plant growth. The inefficiencies of photosynthesis involve basic chemistry and physics (some light energy is not absorbed by photosynthetic pigments) as well as biology (plant anatomy and leaf exposure, photorespiration, and inefficiencies in metabolic pathways). While it is hard to change chemistry and physics, biologists might be able to use their knowledge of plants to improve on the basic biology of photosynthesis. This could result in a more efficient use of resources and better food production.



## 10.5 RECAP

The products of photosynthesis are utilized in glycolysis and the citric acid cycle, as well as in the synthesis of lipids, proteins, and other large molecules.

- How do common intermediates link the pathways of glycolysis, the citric acid cycle, and photosynthesis? See p. 206 and Figure 10.20

**10.21 Energy Losses During Photosynthesis** As we face an increasingly uncertain future for photosynthesis on Earth, understanding its inefficiencies becomes increasingly important. Photosynthetic pathways preserve at most about 5 percent of the sun's energy input as chemical energy in carbohydrates.

## CHAPTER SUMMARY

### 10.1 What Is Photosynthesis?

- In the process of **photosynthesis**, plants and other organisms take in CO<sub>2</sub>, water, and light energy, producing O<sub>2</sub> and carbohydrates. **SEE ANIMATED TUTORIAL 10.1**
- The **light reactions** of photosynthesis convert light energy into chemical energy. They produce ATP and reduce NADP<sup>+</sup> to NADPH. **Review Figure 10.3**
- The **light-independent reactions** do not use light directly but instead use ATP and NADPH to reduce CO<sub>2</sub>, forming carbohydrates.

### 10.2 How Does Photosynthesis Convert Light Energy into Chemical Energy?

- Light is a form of electromagnetic radiation. It is emitted in particle-like packets called **photons** but has wavelike properties.
- Molecules that absorb light in the visible spectrum are called **pigments**. Photosynthetic organisms have several pigments, most notably **chlorophylls**, but also accessory pigments such as carotenoids and phycobilins.
- Absorption of a photon puts a pigment molecule in an excited state that has more energy than its ground state. **Review Figure 10.5**
- Each compound has a characteristic **absorption spectrum**. An **action spectrum** reflects the biological activity of a photosynthetic organism for a given wavelength of light. **Review Figure 10.6**
- The pigments in photosynthetic organisms are arranged into **antenna systems** that absorb energy from light and funnel this energy to a pair of chlorophyll *a* molecules in the reaction center of the **photosystem**. Chlorophyll can act as a reducing agent, transferring excited electrons to other molecules. **Review Figure 10.8**
- Noncyclic electron transport** uses photosystems I and II to produce ATP, NADPH and O<sub>2</sub>. **Cyclic electron transport** uses only photosystem I and produces only ATP. **Review Figures 10.10 and 10.11**
- Chemiosmosis is the mechanism of ATP production in **photophosphorylation**. **Review Figure 10.12, ANIMATED TUTORIAL 10.2**

### 10.3 How Is Chemical Energy Used to Synthesize Carbohydrates?

- The **Calvin cycle** makes carbohydrates from CO<sub>2</sub>. The cycle consists of three processes: fixation of CO<sub>2</sub>, reduction and carbohydrate production, and regeneration of RuBP. **SEE ANIMATED TUTORIAL 10.3**
- RuBP** is the initial CO<sub>2</sub> acceptor, and **3PG** is the first stable product of CO<sub>2</sub> fixation. The enzyme **rubisco** catalyzes the reaction of CO<sub>2</sub> and RuBP to form 3PG. **Review Figure 10.14, WEB ACTIVITY 10.1**
- ATP and NADPH formed by the light reactions are used in the reduction of 3PG to form **G3P**. **Review Figure 10.15**
- Light stimulates enzymes in the Calvin cycle, further integrating the light-dependent and light-independent pathways.

### 10.4 How Do Plants Adapt to the Inefficiencies of Photosynthesis?

- Rubisco can catalyze a reaction between O<sub>2</sub> and RuBP in addition to the reaction between CO<sub>2</sub> and RuBP. At high temperatures and low CO<sub>2</sub> concentrations, the **oxygenase** function of rubisco is favored over its **carboxylase** function.
- When rubisco functions as an oxygenase, the result is **photo-respiration**, which significantly reduces the efficiency of photosynthesis.
- In **C<sub>4</sub> plants**, CO<sub>2</sub> reacts with **PEP** to form a 4-carbon intermediate in mesophyll cells. The 4-carbon product releases its CO<sub>2</sub> to rubisco in the **bundle sheath** cells in the interior of the leaf. **Review Figure 10.18, WEB ACTIVITY 10.2**
- CAM** plants operate much like C<sub>4</sub> plants, but their initial CO<sub>2</sub> fixation by PEP carboxylase is temporally separated from the Calvin cycle, rather than spatially separated as in C<sub>4</sub> plants.

### 10.5 How Does Photosynthesis Interact with Other Pathways?

- Photosynthesis and cellular respiration are linked through the **Calvin cycle**, the **citric acid cycle**, and **glycolysis**. **Review Figure 10.20**
- To survive, a plant must photosynthesize more than it respires.
- Photosynthesis utilizes only a small portion of the energy of sunlight. **Review Figure 10.21**

## SELF-QUIZ

- In noncyclic photosynthetic electron transport, water is used to
  - excite chlorophyll.
  - hydrolyze ATP.
  - reduce P<sub>i</sub>.
  - oxidize NADPH.
  - reduce chlorophyll.
- Which statement about light is true?
  - An absorption spectrum is a plot of biological effectiveness versus wavelength.
  - An absorption spectrum may be a good means of identifying a pigment.
  - Light need not be absorbed to produce a biological effect.
  - A given kind of molecule can occupy any energy level.
  - A pigment loses energy as it absorbs a photon.
- Which statement about chlorophylls is *not* true?
  - Chlorophylls absorb light near both ends of the visible spectrum.
  - Chlorophylls can accept energy from other pigments, such as carotenoids.
  - Excited chlorophyll can either reduce another substance or release light energy.
  - Excited chlorophyll cannot be an oxidizing agent.
  - Chlorophylls contain magnesium.

4. In cyclic electron transport,
  - a. oxygen gas is released.
  - b. ATP is formed.
  - c. water donates electrons and protons.
  - d. NADPH forms.
  - e.  $\text{CO}_2$  reacts with RuBP.
5. Which of the following does *not* happen in noncyclic electron transport?
  - a. Oxygen gas is released.
  - b. ATP forms.
  - c. Water donates electrons and protons.
  - d. NADPH forms.
  - e.  $\text{CO}_2$  reacts with RuBP.
6. In chloroplasts,
  - a. light leads to the flow of protons out of the thylakoids.
  - b. ATP is formed when protons flow into the thylakoid lumen.
  - c. light causes the thylakoid lumen to become less acidic than the stroma.
  - d. protons return passively to the stroma through protein channels.
  - e. proton pumping requires ATP.
7. Which statement about the Calvin cycle is *not* true?
  - a.  $\text{CO}_2$  reacts with RuBP to form 3PG.
  - b. RuBP forms by the metabolism of 3PG.
8. In  $\text{C}_4$  photosynthesis,
  - a. 3PG is the first product of  $\text{CO}_2$  fixation.
  - b. rubisco catalyzes the first step in the pathway.
  - c. 4-carbon acids are formed by PEP carboxylase in bundle sheath cells.
  - d. photosynthesis continues at lower  $\text{CO}_2$  levels than in  $\text{C}_3$  plants.
  - e.  $\text{CO}_2$  released from RuBP is transferred to PEP.
9. Photosynthesis in green plants occurs only during the day. Respiration in plants occurs
  - a. only at night.
  - b. only when there is enough ATP.
  - c. only during the day.
  - d. all the time.
  - e. in the chloroplast after photosynthesis.
10. Photorespiration
  - a. takes place only in  $\text{C}_4$  plants.
  - b. includes reactions carried out in peroxisomes.
  - c. increases the yield of photosynthesis.
  - d. is catalyzed by PEP carboxylase.
  - e. is independent of light intensity.

## FOR DISCUSSION

1. Both photosynthetic electron transport and the Calvin cycle stop in the dark. Which specific reaction stops first? Which stops next? Continue answering the question “Which stops next?” until you have explained why both pathways have stopped.
2. In what principal ways are the reactions of electron transport in photosynthesis similar to the reactions of oxidative phosphorylation discussed in Section 9.3?
3. Differentiate between cyclic and noncyclic electron transport in terms of (1) the products and (2) the source of electrons for the reduction of oxidized chlorophyll.
4. If water labeled with  $^{18}\text{O}$  is added to a suspension of photosynthesizing chloroplasts, which of the following compounds will first become labeled with  $^{18}\text{O}$ : ATP, NADPH,  $\text{O}_2$ , or 3PG? If water labeled with  $^3\text{H}$  is added, which of the

same compounds will first become radioactive? Which will be first if  $\text{CO}_2$  labeled with  $^{14}\text{C}$  is added?

5. The Viking lander was sent to Mars in 1976 to detect signs of life. Explain the rationale behind the following experiments this unmanned probe performed:
  - a. A scoop of dirt was inserted into a container and  $^{14}\text{CO}_2$  was added. After a while during the Martian day, the  $^{14}\text{CO}_2$  was removed and the dirt was heated to a high temperature. Scientists monitoring the experiment back on Earth looked for the release of  $^{14}\text{CO}_2$  as a sign of life.
  - b. The same experiment was performed, except that the dirt was heated to a high temperature for 30 minutes and then allowed to cool to Martian temperature right after scooping, and before the  $^{14}\text{CO}_2$  was added. If living things were present, then  $^{14}\text{CO}_2$  would be released in experiment (a), but not this one.

## ADDITIONAL INVESTIGATION

Calvin’s experiment (see Figure 10.13) laid the foundations for a full description of the pathway of  $\text{CO}_2$  fixation. Given the interrelationships between metabolic pathways in plants, how

would you do an experiment to follow the pathway of fixed carbon from photosynthesis to proteins?

## WORKING WITH DATA (GO TO [yourBioPortal.com](http://yourBioPortal.com))

### Water is the Source of the Oxygen Produced by Photosynthesis

The proposal that the source of  $\text{O}_2$  in photosynthesis was  $\text{H}_2\text{O}$  rather than  $\text{CO}_2$  was first made in 1932. But it took the invention of isotope tracing a decade later to prove this. In this exercise, you will examine the methods that Ruben and Kamen used (Figure 10.2) to identify the isotopes of oxygen and the data they obtained.

**Tracing the Pathway of  $\text{CO}_2$**  Studies of radioactive isotopes were intensified during World War II as an offshoot of the development of nuclear weapons. This led Calvin and his colleagues to perform the experiments designed to trace the path of carbon in photosynthesis (Figure 10.13). In this hands-on exercise, you will examine their data and see the reasoning that led to the  $\text{CO}_2$  fixation pathway.

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# Answers to Self-Quizzes

## Chapter 2

1. b      6. a  
2. d      7. d  
3. c      8. a  
4. c      9. c  
5. d      10. b

## Chapter 3

1. e      6. a  
2. e      7. c  
3. c      8. e  
4. d      9. b  
5. b      10. d

## Chapter 4

1. c      6. c  
2. c      7. e  
3. c      8. b  
4. d      9. c  
5. e      10. b

## Chapter 5

1. b      6. e  
2. d      7. a  
3. c      8. d  
4. e      9. b  
5. a      10. d

## Chapter 6

1. e      6. c  
2. c      7. c  
3. a      8. b  
4. d      9. e  
5. c      10. c

## Chapter 7

1. d      6. a  
2. d      7. e  
3. c      8. d  
4. c      9. c  
5. d      10. a

## Chapter 8

1. c      6. c  
2. e      7. d  
3. b      8. b  
4. c      9. d  
5. c      10. e

## Chapter 9

1. d      6. d  
2. d      7. e  
3. e      8. d  
4. e      9. a  
5. c      10. e

## Chapter 12\*

1. e      6. d  
2. a      7. b  
3. d      8. b  
4. d      9. b  
5. d      10. b

## Chapter 13

1. c      6. b  
2. a      7. d  
3. c      8. d  
4. b      9. c  
5. e      10. c

## Chapter 14

1. c      6. d  
2. d      7. b  
3. e      8. d  
4. b      9. d  
5. a      10. c

## Chapter 15

1. a      6. b  
2. c      7. d  
3. b      8. d  
4. b      9. d  
5. d      10. b

## Chapter 16

1. b      6. c  
2. e      7. c  
3. a      8. d  
4. e      9. b  
5. b      10. a

## Chapter 17

1. c      6. e  
2. c      7. b  
3. a      8. b  
4. e      9. b  
5. e      10. a

## Chapter 18

1. b      6. b  
2. b      7. c  
3. a      8. a  
4. c      9. e  
5. e      10. d

## Chapter 19

1. c      6. c  
2. b      7. e  
3. a      8. b  
4. b      9. a  
5. d      10. b

## Chapter 20

1. c      6. b  
2. a      7. a  
3. c      8. e  
4. b      9. d  
5. c      10. b

## Chapter 21

1. d      6. d  
2. e      7. a  
3. d      8. e  
4. c      9. b  
5. d      10. c

## Chapter 22

1. b      6. b  
2. e      7. e  
3. a      8. a  
4. b      9. e  
5. e      10. d

## Chapter 23

1. c      6. c  
2. e      7. a  
3. d      8. e  
4. c      9. c  
5. a      10. e

## Chapter 24

1. a      6. e  
2. a      7. e  
3. d      8. e  
4. a      9. b  
5. b      10. e

## Chapter 25

1. d      6. a  
2. b      7. c  
3. e      8. b  
4. c      9. c  
5. a      10. d

## Chapter 26

1. e      6. b  
2. e      7. d  
3. a      8. d  
4. c      9. b  
5. e      10. d

## \*Answers to Chapter 12 Genetics Problems

- $BB \times bb; bb \times bb; Bb \times bb; Bb \times Bb$
- 1/32
- Autosomal dominant
- 1/4
- Males (XY) contain only one allele and will show only one color, black ( $X^B Y$ ) or yellow ( $X^b Y$ ). Females can be heterozygous ( $X^B X^b$ ).
- $X^b Y$ , yellow
- The body color ( $G/g$ ) and wing size ( $A/a$ ) genes are linked; eye color ( $R/r$ ) is unlinked to the other two genes. The map distance is 18.5 units.
- Yellow, blue, and white in a 1:2:1 ratio
- $F_1$  all wild-type,  $PpSws$ ;  $F_2$  will have phenotypes in the ratio 9:3:3:1. See Figure 12.7 (p. 244) for analogous genotypes.
- Ratio of phenotypes in  $F_2$  is 3:1 (double dominant to double recessive).
- The  $F_1$  are  $PpByby$ ; they produce just two kinds of gametes ( $Pby$  and  $pBy$ ). Combine them carefully and see the 1:2:1 phenotypic ratio fall out in the  $F_2$ .
- Pink-blistery
- See Figures 11.17 and 11.19 (pp. 224–226). Crossing over took place in the  $F_1$  generation.
- $Rraa$  and  $RrAa$
- $w^+ > w^e > w$
- Parents are  $w^w$  and  $w^+Y$ . Progeny are  $w^+w^e$ ,  $w^+w$ ,  $w^eY$ , and  $wY$ .
- $BX^a$ ,  $BY$ ,  $bX^a$ ,  $bY$
- Mother  $bbX^AX^a$ , father  $BbX^aY$ , son  $BbX^aY$ , daughter  $bbX^aX^a$
- 75 percent
- Because the gene is carried on mitochondrial DNA, it is passed through the mother only. Thus if the woman does not have the disease but her husband does, their child will not be affected. On the other hand, if the woman has the disease but her husband does not, their child will have the disease.

**A-2 ANSWERS TO SELF-QUIZZES****Chapter 27**

1. a 6. b  
2. e 7. d  
3. c 8. b  
4. d 9. a  
5. c 10. d

**Chapter 28**

1. d 6. e  
2. c 7. c  
3. e 8. b  
4. b 9. b  
5. b 10. d

**Chapter 29**

1. d 6. c  
2. c 7. a  
3. d 8. e  
4. a 9. c  
5. d 10. a

**Chapter 30**

1. b 6. a  
2. d 7. e  
3. e 8. a  
4. c 9. e  
5. d 10. c

**Chapter 31**

1. c 6. b  
2. d 7. c  
3. c 8. d  
4. d 9. e  
5. e 10. d

**Chapter 32**

1. b 6. e  
2. e 7. b  
3. c 8. d  
4. d 9. d  
5. a 10. e

**Chapter 33**

1. d 6. e  
2. a 7. a  
3. c 8. e  
4. d 9. c  
5. d 10. b

**Chapter 34**

1. c 6. b  
2. b 7. b  
3. e 8. c  
4. e 9. a  
5. a 10. d

**Chapter 35**

1. c 6. d  
2. d 7. d  
3. b 8. e  
4. b 9. e  
5. b 10. a

**Chapter 36**

1. d 6. c  
2. d 7. e  
3. c 8. d  
4. a 9. d  
5. c 10. e

**Chapter 37**

1. a 6. c  
2. e 7. b  
3. c 8. c  
4. d 9. a  
5. b 10. b

**Chapter 38**

1. d 6. e  
2. b 7. a  
3. e 8. c  
4. b 9. c  
5. d 10. d

**Chapter 39**

1. e 6. a  
2. b 7. b  
3. c 8. c  
4. c 9. e  
5. d 10. a

**Chapter 40**

1. c 6. b  
2. c 7. e  
3. a 8. a  
4. d 9. e  
5. b 10. b

**Chapter 41**

1. b 6. b  
2. a 7. d  
3. b 8. e  
4. e 9. c  
5. e 10. c

**Chapter 42**

1. a 6. a  
2. b 7. d  
3. e 8. d  
4. e 9. a  
5. c 10. d

**Chapter 43**

1. c 6. d  
2. e 7. d  
3. a 8. d  
4. d 9. d  
5. d 10. a

**Chapter 44**

1. a 6. c  
2. c 7. b  
3. e 8. b  
4. a 9. b  
5. d 10. c

**Chapter 45**

1. d 6. e  
2. d 7. c  
3. c 8. c  
4. c 9. d  
5. e 10. d

**Chapter 46**

1. d 6. e  
2. d 7. b  
3. a 8. c  
4. e 9. c  
5. e 10. d

**Chapter 47**

1. c 6. c  
2. a 7. a  
3. e 8. c  
4. d 9. a  
5. d 10. c

**Chapter 48**

1. e 6. d  
2. a 7. e  
3. b 8. a  
4. c 9. a  
5. b 10. e

**Chapter 49**

1. e 6. b  
2. d 7. c  
3. a 8. c  
4. b 9. a  
5. c 10. d

**Chapter 50**

1. d 6. d  
2. a 7. b  
3. c 8. d  
4. d 9. c  
5. c 10. e

**Chapter 51**

1. b 6. d  
2. e 7. a  
3. c 8. b  
4. a 9. d  
5. b 10. d

**Chapter 52**

1. d 6. b  
2. a 7. e  
3. d 8. a  
4. a 9. c  
5. d 10. e

**Chapter 53**

1. b 6. d  
2. e 7. e  
3. c 8. e  
4. a 9. a  
5. d 10. e

**Chapter 54**

1. d 6. c  
2. a 7. c  
3. a 8. c  
4. d 9. d  
5. a 10. b

**Chapter 55**

1. c 6. b  
2. c 7. e  
3. a 8. c  
4. d 9. e  
5. c 10. d

**Chapter 56**

1. a 6. a  
2. c 7. b  
3. b 8. d  
4. c 9. e  
5. d 10. b

**Chapter 57**

1. a 6. b  
2. a 7. e  
3. b 8. b  
4. d 9. d  
5. e 10. e

**Chapter 58**

1. e 6. e  
2. d 7. a  
3. b 8. e  
4. c 9. d  
5. c 10. b

**Chapter 59**

1. b 6. a  
2. d 7. d  
3. e 8. c  
4. e 9. a  
5. b 10. c

# Glossary

## - A -

**abiotic** (uh' bye ah tick) [Gk. *a*: not + *bios*: life] Nonliving. (Contrast with biotic.)

**abscisic acid (ABA)** (ab sighs' ik) A plant growth substance with growth-inhibiting action. Causes stomata to close; involved in a plant's response to salt and drought stress.

**abscission** (ab sizh' un) [L. *abscissio*: break off] The process by which leaves, petals, and fruits separate from a plant.

**absorption** (1) Of light: complete retention, without reflection or transmission. (2) Of water or other molecules: soaking up (taking in through pores or by diffusion).

**absorption spectrum** A graph of light absorption versus wavelength of light; shows how much light is absorbed at each wavelength.

**absorptive heterotroph** An organism (usually a fungus) that obtains its food by secreting digestive enzymes into the environment to break down large food molecules, then absorbing the breakdown products.

**abyssal plain** (uh biss' ul) [Gk. *abyssos*: bottomless] The deep ocean floor.

**accessory pigments** Pigments that absorb light and transfer energy to chlorophylls for photosynthesis.

**acetylcholine (ACh)** A neurotransmitter that carries information across vertebrate neuromuscular junctions and some other synapses. It is then broken down by the enzyme acetylcholinesterase (AChE).

**acetyl coenzyme A (acetyl CoA)** A compound that reacts with oxaloacetate to produce citrate at the beginning of the citric acid cycle; a key metabolic intermediate in the formation of many compounds.

**acid** [L. *acidus*: sharp, sour] A substance that can release a proton in solution. (Contrast with base.)

**acid growth hypothesis** The hypothesis that auxin increases proton pumping, thereby lowering the pH of the cell wall and activating enzymes that loosen polysaccharides. Proposed to explain auxin-induced cell expansion in plants.

**acid precipitation** Precipitation that has a lower pH than normal as a result of acid-forming precursor molecules introduced into the atmosphere by human activities.

**acidic** Having a pH of less than 7.0 (a hydrogen ion concentration greater than  $10^{-7}$  molar). (Contrast with basic.)

**acoelomate** An animal that does not have a coelom.

**acrosome** (uh' krow soam) [Gk. *akros*: highest + *soma*: body] The structure at the forward tip of an animal sperm which is the first to fuse with the egg membrane and enter the egg cell.

**ACTH** See corticotropin.

**actin** [Gk. *aktis*: ray] A protein that makes up the cytoskeletal microfilaments in eukaryotic cells and is one of the two contractile proteins in muscle.

**action potential** An impulse in a neuron taking the form of a wave of depolarization or hyperpolarization.

**action spectrum** A graph of a biological process versus light wavelength; shows which wavelengths are involved in the process.

**activation energy ( $E_a$ )** The energy barrier that blocks the tendency for a chemical reaction to occur.

**active site** The region on the surface of an enzyme or ribozyme where the substrate binds, and where catalysis occurs.

**active transport** The energy-dependent transport of a substance across a biological membrane against a concentration gradient—that is, from a region of low concentration (of that substance) to one of high concentration. (See also primary active transport, secondary active transport; contrast with facilitated diffusion, passive transport.)

**adaptation** (uh dap' tay' shun) (1) In evolutionary biology, a particular structure, physiological process, or behavior that makes an organism better able to survive and reproduce. Also, the evolutionary process that leads to the development or persistence of such a trait. (2) In sensory neurophysiology, a sensory cell's loss of sensitivity as a result of repeated stimulation.

**adaptive radiation** An evolutionary radiation that results in an array of related species that live in a variety of environments and differ in the characteristics they use to exploit those environments.

**adenine (A)** (uh' den een) A nitrogen-containing base found in nucleic acids, ATP, NAD, and other compounds.

**adenosine triphosphate** See ATP.

**adrenal gland** (uh dreel' nal) [L. *ad*: toward + *renes*: kidneys] An endocrine gland located near the kidneys of vertebrates, consisting of two glandular parts, the cortex and medulla.

**adrenaline** See epinephrine.

**adrenocorticotrophic hormone** See corticotropin.

**adsorption** Binding of a gas or a solute to the surface of a solid.

**adventitious roots** (uh ven ti' shus) [L.

*adventitius*: arriving from outside] Roots originating from the stem at ground level or below; typical of the fibrous root system of monocots.

**aerenchyma** In plants, parenchymal tissue containing air spaces.

**aerobic** (air oh' bic) [Gk. *aer*: air + *bios*: life] In the presence of oxygen; requiring oxygen. (Contrast with anaerobic.)

**afferent** (uh' ur unt) [L. *ad*: toward + *ferre*: to carry] Carrying to, as in a neuron that carries impulses to the central nervous system (afferent neuron), or a blood vessel that carries blood to a structure. (Contrast with efferent.)

**age structure** The distribution of the individuals in a population across all age groups.

**AIDS** Acquired immune deficiency syndrome, a condition caused by human immunodeficiency virus (HIV) in which the body's T-helper cells are

reduced, leaving the victim subject to opportunistic diseases.

**air sacs** Structures in the respiratory system of birds that receive inhaled air; they keep fresh air flowing unidirectionally through the lungs, but are not themselves gas exchange surfaces.

**aldosterone** (al dohs' ter own) A steroid hormone produced in the adrenal cortex of mammals. Promotes secretion of potassium and reabsorption of sodium in the kidney.

**aleurone layer** In some seeds, a tissue that lies beneath the seed coat and surrounds the endosperm. Secretes digestive enzymes that break down macromolecules stored in the endosperm.

**allantoic membrane** In animal development, an outgrowth of extraembryonic endoderm plus adjacent mesoderm that forms the allantois, a saclike structure that stores metabolic wastes produced by the embryo.

**allantois** (al lun twah') [Gk. *allant*: sausage] An extraembryonic membrane enclosing a sausage-shaped sac that stores the embryo's nitrogenous wastes.

**allele** (uh leel') [Gk. *allos*: other] The alternate form of a genetic character found at a given locus on a chromosome.

**allele frequency** The relative proportion of a particular allele in a specific population.

**allergic reaction** [Ger. *allergie*: altered] An overreaction of the immune system to amounts of an antigen that do not affect most people; often involves IgE antibodies.

**allometric growth** A pattern of growth in which some parts of the body of an organism grow faster than others, resulting in a change in body proportions as the organism grows.

**allopatric speciation** (al' lo pat' rick) [Gk. *allos*: other + *patria*: homeland] The formation of two species from one when reproductive isolation occurs because of the interposition of (or crossing of) a physical geographic barrier such as a river. Also called geographic speciation. (Contrast with sympatric speciation.)

**allopolyploidy** The possession of more than two chromosome sets that are derived from more than one species.

**allosteric regulation** (al lo steer' ik) [Gk. *allos*: other + *stereos*: structure] Regulation of the activity of a protein (usually an enzyme) by the binding of an effector molecule to a site other than the active site.

**alpha diversity** Species diversity within a single community or habitat. (Contrast with beta diversity, gamma diversity.)

**$\alpha$  (alpha) helix** A prevalent type of secondary protein structure; a right-handed spiral.

**alternation of generations** The succession of multicellular haploid and diploid phases in some sexually reproducing organisms, notably plants.

**alternative splicing** A process for generating different mature mRNAs from a single gene by splicing together different sets of exons during RNA processing.

**altruism** Pertaining to behavior that benefits other individuals at a cost to the individual who performs it.

**alveolus** (al've'ō lus) (plural: alveoli) [L. *alveus*: cavity] A small, baglike cavity, especially the blind sacs of the lung.

**amensalism** (a men'sul ism) Interaction in which one animal is harmed and the other is unaffected. (Contrast with commensalism, mutualism.)

**amine** An organic compound containing an amino group ( $\text{NH}_2$ ).

**amino acid** An organic compound containing both  $\text{NH}_2$  and  $\text{COOH}$  groups. Proteins are polymers of amino acids.

**amino acid replacement** A change in the nucleotide sequence that results in one amino acid being replaced by another.

**ammonotelic** (am moan'ō teel'ik) [Gk. *telos*: end] Pertaining to an organism in which the final product of breakdown of nitrogen-containing compounds (primarily proteins) is *ammonia*. (Contrast with ureotelic, uricotelic.)

**amnion** (am'nee on) The fluid-filled sac within which the embryos of reptiles (including birds) and mammals develop.

**amniote egg** A shelled egg surrounding four extraembryonic membranes and embryo-nourishing yolk. This evolutionary adaptation permitted mammals and reptiles to live and reproduce in drier environments than can most amphibians.

**amphipathic** (am'fi path'ik) [Gk. *amphi*: both + *pathos*: emotion] Of a molecule, having both hydrophilic and hydrophobic regions.

**amplitude** The magnitude of change over the course of a regular cycle.

**amygdala** A component of the limbic system that is involved in fear and fear memory.

**amylase** (am'il ase) An enzyme that catalyzes the hydrolysis of starch, usually to maltose or glucose.

**anabolic reaction** (an uh bah'lik) [Gk. *ana*: upward + *ballein*: to throw] A synthetic reaction in which simple molecules are linked to form more complex ones; requires an input of energy and captures it in the chemical bonds that are formed. (Contrast with catabolic reaction.)

**anaerobic** (an ur row'bic) [Gk. *an*: not + *aer*: air + *bios*: life] Occurring without the use of molecular oxygen,  $\text{O}_2$ . (Contrast with aerobic.)

**analogy** (a nal'ō jee) [Gk. *analogia*: resembling] A resemblance between two features that is due to convergent evolution rather than to common ancestry. The structures are said to be *analogous*, and each is an *analog* of the others. (Contrast with homology.)

**anaphase** (an'ā phase) [Gk. *ana*: upward] The stage in cell nuclear division at which the first separation of sister chromatids (or, in the first meiotic division, of paired homologs) occurs.

**ancestral trait** The trait originally present in the ancestor of a given group; may be retained or changed in the descendants of that ancestor.

**androgen** (an'dro jen) Any of the several male sex steroids (most notably testosterone).

**aneuploidy** (an'you ploy dee) A condition in which one or more chromosomes or pieces of chromosomes are either lacking or present in excess.

**angiotensin** (an'jee oh ten'sin) A peptide hormone that raises blood pressure by causing pe-

ripheral vessels to constrict. Also maintains glomerular filtration by constricting efferent vessels and stimulates thirst and the release of aldosterone.

**angular gyrus** A part of the human brain believed to be essential for integrating spoken and written language.

**animal hemisphere** The metabolically active upper portion of some animal eggs, zygotes, and embryos; does not contain the dense nutrient yolk. (Contrast with vegetal hemisphere.)

**anion** (an'ē eye on) [Gk. *ana*: upward progress] A negatively charged ion. (Contrast with cation.)

**anisogamous** (an eye sog'ā muss) [Gk. *aniso*: unequal + *gamos*: marriage] Having morphologically dissimilar male and female gametes. (Contrast with isogamous.)

**annual** A plant whose life cycle is completed in one growing season. (Contrast with biennial, perennial.)

**antagonistic interactions** Interactions between two species in which one species benefits and the other is harmed. Includes predation, herbivory, and parasitism.

**antenna system** In photosynthesis, a group of different molecules that cooperate to absorb light energy and transfer it to a reaction center.

**anterior** Toward or pertaining to the tip or headward region of the body axis. (Contrast with posterior.)

**anterior pituitary** The portion of the vertebrate pituitary gland that derives from gut epithelium and produces tropic hormones.

**anther** (an'thur) [Gk. *anthos*: flower] A pollen-bearing portion of the stamen of a flower.

**antheridium** (an'thur id'ee um) [Gk. *antheros*: blooming] The multicellular structure that produces the sperm in nonvascular land plants and ferns.

**antibody** One of the myriad proteins produced by the immune system that specifically binds to a foreign substance in blood or other tissue fluids and initiates its removal from the body.

**anticodon** The three nucleotides in transfer RNA that pair with a complementary triplet (a codon) in messenger RNA.

**antidiuretic hormone (ADH)** A hormone that promotes water reabsorption by the kidney. ADH is produced by neurons in the hypothalamus and released from nerve terminals in the posterior pituitary. Also called vasopressin.

**antigen** (an'ti jun) Any substance that stimulates the production of an antibody or antibodies in the body of a vertebrate.

**antigenic determinant** The specific region of an antigen that is recognized and bound by a specific antibody. Also called an epitope.

**antiparallel** Pertaining to molecular orientation in which a molecule or parts of a molecule have opposing directions.

**antiporter** A membrane transport protein that moves one substance in one direction and another in the opposite direction. (Contrast with symporter, uniporter.)

**antisense RNA** A single-stranded RNA molecule complementary to, and thus targeted against, an mRNA of interest to block its translation.

**anus** (a' nus) An opening through which solid digestive wastes are expelled, located at the posterior end of a tubular gut.

**aorta** (a'ōrətah) [Gk. *aorte*: aorta] The main trunk of the arteries leading to the systemic (as opposed to the pulmonary) circulation.

**aortic body** A chemosensor in the aorta that senses a decrease in blood supply or a dramatic decrease in partial pressure of oxygen in the blood.

**aortic valve** A one-way valve between the left ventricle of the heart and the aorta that prevents backflow of blood into the ventricle when it relaxes.

**apex** (a'peks) The tip or highest point of a structure, as of a growing stem or root.

**aphasia** a deficit in the ability to use or understand words.

**apical** (a'pi kül) Pertaining to the *apex*, or tip, usually in reference to plants.

**apical dominance** In plants, inhibition by the apical bud of the growth of axillary buds.

**apical hook** A form taken by the stems of many eudicot seedlings that protects the delicate shoot apex while the stem grows through the soil.

**apical meristem** The meristem at the tip of a shoot or root; responsible for a plant's primary growth.

**apomixis** (ap oh mix'is) [Gk. *apo*: away from + *mixis*: sexual intercourse] The asexual production of seeds.

**apoplast** (ap'oh plast) In plants, the continuous meshwork of cell walls and extracellular spaces through which material can pass without crossing a plasma membrane. (Contrast with symplast.)

**apoptosis** (ap uh toh' sis) A series of genetically programmed events leading to cell death.

**aposematism** Warning coloration; bright colors or striking patterns of toxic or mimetic prey species that act as a warning to predators.

**appendix** In the human digestive system, the vestigial equivalent of the cecum, which serves no digestive function.

**aquaporin** A transport protein in plant and animal cell membranes through which water passes in osmosis.

**aquatic** (a kwa'tic) [L. *aqua*: water] Pertaining to or living in water. (Contrast with marine, terrestrial.)

**aqueous** (a'kwee us) Pertaining to water or a watery solution.

**aquifer** A large pool of groundwater.

**archegonium** (ar'ke go'nee um) The multicellular structure that produces eggs in nonvascular land plants, ferns, and gymnosperms.

**archenteron** (ark en'ter on) [Gk. *archos*: first + *enteron*: bowel] The earliest primordial animal digestive tract.

**area phylogenies** Phylogenies in which the names of the taxa are replaced with the names of the places where those taxa live or lived.

**arms race** A series of reciprocal adaptations between species involved in antagonistic interactions, in which adaptations that increase the fitness of a consumer species exert selection pressure on its resource species to counter the consumer's adaptation, and vice versa.

**arteriole** A small blood vessel arising from an artery that feeds blood into a capillary bed.

**artery** A muscular blood vessel carrying oxygenated blood away from the heart to other parts of the body. (Contrast with vein.)

**artificial selection** The selection by plant and animal breeders of individuals with certain desirable traits.

**ascus** (ass' cus) (plural: asci) [Gk. *askos*: bladder] In sac fungi, the club-shaped sporangium within which spores (ascospores) are produced by meiosis.

**asexual reproduction** Reproduction without sex.

**assisted reproductive technologies (ARTs)** Any of several procedures that remove unfertilized eggs from the ovary, combine them with sperm outside the body, and then place fertilized eggs or egg–sperm mixtures in the appropriate location in a female's reproductive tract for development.

**association cortex** In the vertebrate brain, the portion of the cortex involved in higher-order information processing, so named because it integrates, or associates, information from different sensory modalities and from memory.

**associative learning** A form of learning in which two unrelated stimuli become linked to the same response.

**astrocyte** [Gk. *astron*: star] A type of glial cell that contributes to the blood–brain barrier by surrounding the smallest, most permeable blood vessels in the brain.

**atherosclerosis** (ath' er oh sklair oh' sis) [Gk. *athero*: gruel, porridge + *skleros*: hard] A disease of the lining of the arteries characterized by fatty, cholesterol-rich deposits in the walls of the arteries. When fibroblasts infiltrate these deposits and calcium precipitates in them, the disease becomes arteriosclerosis, or “hardening of the arteries.”

**atom** [Gk. *atomos*: indivisible] The smallest unit of a chemical element. Consists of a nucleus and one or more electrons.

**atomic mass** See atomic weight.

**atomic number** The number of protons in the nucleus of an atom; also equals the number of electrons around the neutral atom. Determines the chemical properties of the atom.

**atomic weight** The average of the mass numbers of a representative sample of atoms of an element, with all the isotopes in their normally occurring proportions. Also called atomic mass.

**ATP (adenosine triphosphate)** An energy-storage compound containing adenine, ribose, and three phosphate groups. When it is formed from ADP, useful energy is stored; when it is broken down (to ADP or AMP), energy is released to drive endergonic reactions.

**ATP synthase** An integral membrane protein that couples the transport of protons with the formation of ATP.

**atrial natriuretic peptide** A hormone released by the atrial muscle fibers of the heart when they are overly stretched, which decreases reabsorption of sodium by the kidney and thus blood volume.

**atrioventricular node** A modified node of cardiac muscle that organizes the action potentials that control contraction of the ventricles.

**atrium** (ā tree' um) [L. *atrium*: central hall] An internal chamber. In the hearts of vertebrates, the thin-walled chamber(s) entered by blood on its way to the ventricle(s). Also, the outer ear.

**auditory system** A sensory system that uses mechanoreceptors to convert pressure waves into receptor potentials; includes structures that gather sound waves, direct them to a sensory or-

gan, and amplify their effect on the mechanoreceptors.

**autocatalysis** [Gk. *autos*: self + *kata*: to break down] A positive feedback process in which an activated enzyme acts on other inactive molecules of the same enzyme to activate them.

**autocrine** A chemical signal that binds to and affects the cell that makes it. (Contrast with paracrine.)

**autoimmunity** An immune response by an organism to its own molecules or cells.

**autonomic nervous system (ANS)** The portion of the peripheral nervous system that controls such involuntary functions as those of guts and glands. Also called the involuntary nervous system.

**autopolyploidy** The possession of more than two entire chromosomes sets that are derived from a single species.

**autosome** Any chromosome (in a eukaryote) other than a sex chromosome.

**autotroph** (au' tow trowf') [Gk. *autos*: self + *trophē*: food] An organism that is capable of living exclusively on inorganic materials, water, and some energy source such as sunlight (photoautotrophs) or chemically reduced matter (see chemolithotrophs). (Contrast with heterotroph.)

**auxin** (awk' sin) [Gk. *auxein*: to grow] In plants, a substance (the most common being indoleacetic acid) that regulates growth and various aspects of development.

**avirulence (Avr) genes** Genes in a pathogen that may trigger defenses in plants. See gene-for-gene resistance.

**Avogadro's number** The number of atoms or molecules in a mole (weighed out in grams) of a substance, calculated to be  $6.022 \times 10^{23}$ .

**axillary bud** A bud that forms in the angle (axil) where a leaf meets a stem.

**axon** [Gk. axle] The part of a neuron that conducts action potentials away from the cell body.

**axon hillock** The junction between an axon and its cell body, where action potentials are generated.

**axon terminals** The endings of an axon; they form synapses and release neurotransmitter.

## - B -

**B cell** A type of lymphocyte involved in the humoral immune response of vertebrates. Upon recognizing an antigenic determinant, a B cell develops into a plasma cell, which secretes an antibody. (Contrast with T cell.)

**bacillus** (bah sil' us) [L: little rod] Any of various rod-shaped bacteria.

**bacterial artificial chromosome (BAC)** A DNA cloning vector used in bacteria that can carry up to 150,000 base pairs of foreign DNA.

**bacteriophage** (bak teer' ee o fayj) [Gk. *bakterion*: little rod + *phagein*: to eat] Any of a group of viruses that infect bacteria. Also called phage.

**bacteroids** Nitrogen-fixing organelles that develop from endosymbiotic bacteria.

**bark** All tissues external to the vascular cambium of a plant.

**baroreceptor** [Gk. *baros*: weight] A pressure-sensing cell or organ. Sometimes called a stress receptor.

**basal body** A centriole found at the base of a eukaryotic flagellum or cilium.

**basal metabolic rate (BMR)** The minimum rate of energy turnover in an awake (but resting) bird or mammal that is not expending energy for thermoregulation.

**base** (1) A substance that can accept a hydrogen ion in solution. (Contrast with acid.) (2) In nucleic acids, the purine or pyrimidine that is attached to each sugar in the sugar-phosphate backbone.

**base pair (bp)** In double-stranded DNA, a pair of nucleotides formed by the complementary base pairing of a purine on one strand and a pyrimidine on the other.

**basic** Having a pH greater than 7.0 (i.e., having a hydrogen ion concentration lower than  $10^{-7}$  molar). (Contrast with acidic.)

**basidiocarp** A fruiting structure produced by club fungi.

**basidium** (bass id' ee yum) In club fungi, the characteristic sporangium in which four spores are formed by meiosis and then borne externally before being shed.

**basilar membrane** A membrane in the human inner ear whose flexion in response to sound waves activates hair cells; flexes at different locations in response to different pitches of sound.

**basophil** A type of phagocytic white blood cell that releases histamine and may promote T cell development.

**Batesian mimicry** The convergence in appearance of an edible species (mimic) with an unpalatable species (model).

**benefit** An improvement in survival and reproductive success resulting from performing a behavior or having a trait. (Contrast with cost.)

**benthic zone** [Gk. *benthos*: bottom] The bottom of the ocean.

**beta diversity** Between-habitat diversity; a measure of the change in species composition from one community or habitat to another. (Contrast with alpha diversity, gamma diversity.)

**β (beta) pleated sheet** A type of protein secondary structure; results from hydrogen bonding between polypeptide regions running antiparallel to each other.

**biennial** A plant whose life cycle includes vegetative growth in the first year and flowering and senescence in the second year. (Contrast with annual, perennial.)

**bilateral symmetry** The condition in which only the right and left sides of an organism, divided by a single plane through the midline, are mirror images of each other.

**bilayer** A structure that is two layers in thickness. In biology, most often refers to the phospholipid bilayer of membranes. (See phospholipid bilayer.)

**bile** A secretion of the liver made up of bile salts synthesized from cholesterol, various phospholipids, and bilirubin (the breakdown product of hemoglobin). Emulsifies fats in the small intestine.

**binary fission** Reproduction of a prokaryote by division of a cell into two comparable progeny cells.

**binocular vision** Overlapping visual fields of an animal's two eyes; allows the animal to see in three dimensions.

**binomial nomenclature** A taxonomic naming system in which each species is given two names (a genus name followed by a species name).

**biofilm** A community of microorganisms embedded in a polysaccharide matrix, forming a highly resistant coating on almost any moist surface.

**biogeochemical cycle** Movement of inorganic elements such as nitrogen, phosphorus, and carbon through living organisms and the physical environment.

**biogeographic region** One of several defined, continental-scale regions of Earth, each of which has a biota distinct from that of the others. (Contrast with biome.)

**biogeography** The scientific study of the patterns of distribution of populations, species, and ecological communities across Earth.

**bioinformatics** The use of computers and/or mathematics to analyze complex biological information, such as DNA sequences.

**biological species concept** The definition of a species as a group of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups. (Contrast with lineage species concept; morphological species concept.)

**biology** [Gk. *bios*: life + *logos*: study] The scientific study of living things.

**bioluminescence** The production of light by biochemical processes in an organism.

**biomass** The total weight of all the organisms, or some designated group of organisms, in a given area.

**biome** (bye' ome) A major division of the ecological communities of Earth, characterized primarily by distinctive vegetation. A given biogeographic region contains many different biomes.

**bioremediation** The use by humans of other organisms to remove contaminants from the environment.

**biosphere** (bye' oh sphere) All regions of Earth (terrestrial and aquatic) and Earth's atmosphere in which organisms can live.

**biota** (bye oh' tah) All of the organisms—animals, plants, fungi, and microorganisms—found in a given area. (Contrast with flora, fauna.)

**biotechnology** The use of cells or living organisms to produce materials useful to humans.

**biotic** (bye ah' tick) [Gk. *bios*: life] Alive. (Contrast with abiotic.)

**biotic interchange** The dispersal of species from two different biotas into the region they had not previously inhabited, as when two formerly separated land masses fuse.

**blade** The thin, flat portion of a leaf.

**blastocoel** (blass' toe seal) [Gk. *blastos*: sprout + *koilos*: hollow] The central, hollow cavity of a blastula.

**blastocyst** (blass' toe cist) An early embryo formed by the first divisions of the fertilized egg (zygote). In mammals, a hollow ball of cells.

**blastodisc** (blass' toe disk) An embryo that forms as a disk of cells on the surface of a large yolk mass; comparable to a blastula, but occurring in animals such as birds and reptiles, in which the massive yolk restricts incomplete cleavage.

**blastomere** Any of the cells produced by the early divisions of a fertilized animal egg.

**blastula** (blass' chu luuh) An early stage of the animal embryo; in many species, a hollow sphere of cells surrounding a central cavity, the blastocoel. (Contrast with blastodisc.)

**block to polyspermy** Any of several responses to entry of a sperm into an egg that prevent more than one sperm from entering the egg.

**blood** A fluid tissue that is pumped around the body; a component of the circulatory system.

**blood-brain barrier** A property of blood vessels in the brain that prevents most chemicals from diffusing from the blood into the brain.

**blue-light receptors** Pigments in plants that absorb blue light (400–500 nm). These pigments mediate many plant responses including phototropism, stomatal movements, and expression of some genes.

**body plan** The general structure of an animal, the arrangement of its organ systems, and the integrated functioning of its parts.

**bond** See chemical bond.

**bottleneck** See population bottleneck.

**bone** A rigid component of vertebrate skeletal systems that contains an extracellular matrix of insoluble calcium phosphate crystals as well as collagen fibers.

**Bowman's capsule** An elaboration of the renal tubule, composed of podocytes, that surrounds and collects the filtrate from the glomerulus.

**brain** The centralized integrative center of a nervous system.

**brainstem** The portion of the vertebrate brain between the spinal cord and the forebrain, made up of the medulla, pons, and midbrain.

**brassinosteroids** Plant steroid hormones that mediate light effects promoting the elongation of stems and pollen tubes.

**Broca's area** A portion of the human brain essential for speech. Located in the frontal lobe just in front of the primary motor cortex.

**bronchioles** The smallest airways in a vertebrate lung, branching off the bronchi.

**bronchus** (plural: bronchi) The major airway(s) branching off the trachea into the vertebrate lung.

**brown fat** In mammals, fat tissue that is specialized to produce heat. It has many mitochondria and capillaries, and a protein that uncouples oxidative phosphorylation.

**budding** Asexual reproduction in which a more or less complete new organism grows from the body of the parent organism, eventually detaching itself.

**buffer** A substance that can transiently accept or release hydrogen ions and thereby resist changes in pH.

**bulbourethral glands** Secretory structures of the human male reproductive system that produce a small volume of an alkaline, mucoid secretion that helps neutralize acidity in the urethra and lubricate it to facilitate the passage of semen.

**bulk flow** The movement of a solution from a region of higher pressure potential to a region of lower pressure potential.

**bundle of His** Fibers of modified cardiac muscle that conduct action potentials from the atria to the ventricular muscle mass.

**bundle sheath cell** Part of a tissue that surrounds the veins of plants; contains chloroplasts in C<sub>4</sub> plants.

## - C -

**C3 plants** Plants that produce 3PG as the first stable product of carbon fixation in photosynthesis and use ribulose bisphosphate as a CO<sub>2</sub> receptor.

**C4 plants** Plants that produce oxaloacetate as the first stable product of carbon fixation in photosynthesis and use phosphoenolpyruvate as CO<sub>2</sub> acceptor. C<sub>4</sub> plants also perform the reactions of C<sub>3</sub> photosynthesis.

**calcitonin** Hormone produced by the thyroid gland; lowers blood calcium and promotes bone formation. (Contrast with parathyroid hormone.)

**calorie** [L. *calor*: heat] The amount of heat required to raise the temperature of 1 gram of water by 1°C. Physiologists commonly use the kilocalorie (kcal) as a unit of measure (1 kcal = 1,000 calories). Nutritionists also use the kilocalorie, but refer to it as the *Calorie* (capital C).

**Calvin cycle** The stage of photosynthesis in which CO<sub>2</sub> reacts with RubP to form 3PG, 3PG is reduced to a sugar, and RuBP is regenerated, while other products are released to the rest of the plant. Also known as the Calvin-Benson cycle.

**calyx** (kay' licks) [Gk. *kalyx*: cup] All of the sepals of a flower, collectively.

**CAM** See crassulacean acid metabolism.

**Cambrian explosion** The rapid diversification of multicellular life that took place during the Cambrian period.

**cAMP (cyclic AMP)** A compound formed from ATP that acts as a second messenger.

**cancellous bone** A type of bone with numerous internal cavities that make it appear spongy, although it is rigid. (Contrast with compact bone.)

**canopy** The leaf-bearing part of a tree. Collectively, the aggregate of the leaves and branches of the larger woody plants of an ecological community.

**capillaries** [L. *capillaris*: hair] Very small tubes, especially the smallest blood-carrying vessels of animals between the termination of the arteries and the beginnings of the veins. Capillaries are the site of exchange of materials between the blood and the interstitial fluid.

**capsid** The outer shell of a virus that encloses its nucleic acid.

**carbohydrates** Organic compounds containing carbon, hydrogen, and oxygen in the ratio 1:2:1 (i.e., with the general formula C<sub>n</sub>H<sub>2n</sub>O<sub>n</sub>). Common examples are sugars, starch, and cellulose.

**carbon skeleton** The chains or rings of carbon atoms that form the structural basis of organic molecules. Other atoms or functional groups are attached to the carbon atoms.

**carboxylase** An enzyme that catalyzes the addition of carboxyl groups to a substrate.

**cardiac** (kar' dee ak) [Gk. *kardia*: heart] Pertaining to the heart and its functions.

**cardiac cycle** Contraction of the two atria of the heart, followed by contraction of the two ventricles and then relaxation.

**cardiac muscle** A type of muscle tissue that makes up, and is responsible for the beating of, the heart. Characterized by branching cells with single nuclei and a striated (striped) appearance. (Contrast with smooth muscle, skeletal muscle.)

**cardiovascular system** [Gk. *kardia*: heart + L. *vasculum*: small vessel] The heart, blood, and vessels are of a circulatory system.

**carnivore** [L. *carn*: flesh + *vovare*: to devour] An organism that eats animal tissues. (Contrast with detritivore, herbivore, omnivore.)

**carotenoid** (ka rah' tuh noid) A yellow, orange, or red lipid pigment commonly found as an ac-

cessory pigment in photosynthesis; also found in fungi.

**carotid body** A chemosensor in the carotid artery that senses a decrease in blood supply or a dramatic decrease in partial pressure of oxygen in the blood.

**carpel** (kar' pel) [Gk. *karpos*: fruit] The organ of the flower that contains one or more ovules.

**carrier** (1) In facilitated diffusion, a membrane protein that binds a specific molecule and transports it through the membrane. (2) In respiratory and photosynthetic electron transport, a participating substance such as NAD that exists in both oxidized and reduced forms. (3) In genetics, a person heterozygous for a recessive trait.

**carrying capacity (*K*)** The number of individuals in a population that the resources of its environment can support.

**cartilage** In vertebrates, a tough connective tissue found in joints, the outer ear, and elsewhere. Forms the entire skeleton in some animal groups.

**cartilage bone** A type of bone that begins its development as a cartilaginous structure resembling the future mature bone, then gradually hardens into mature bone. (Contrast with membranous bone.)

**Caspian strip** A band of cell wall containing suberin and lignin, found in the endodermis. Restricts the movement of water across the endodermis.

**caspase** One of a group of proteases that catalyze cleavage of target proteins and are active in apoptosis.

**catabolic reaction** (kat uh bah' lik) [Gk. *kata*: to break down + *ballein*: to throw] A synthetic reaction in which complex molecules are broken down into simpler ones and energy is released. (Contrast with anabolic reaction.)

**catabolite repression** In the presence of abundant glucose, the diminished synthesis of catabolic enzymes for other energy sources.

**catalyst** (kat' a list) [Gk. *kata*: to break down] A chemical substance that accelerates a reaction without itself being consumed in the overall course of the reaction. Catalysts lower the activation energy of a reaction. Enzymes are biological catalysts.

**cation** (cat' eye on) An ion with one or more positive charges. (Contrast with anion.)

**caudal** [L. *cauda*: tail] Pertaining to the tail, or to the posterior part of the body.

**cDNA** See complementary DNA.

**cDNA library** A collection of complementary DNAs derived from mRNAs of a particular tissue at a particular time in the life cycle of an organism.

**cecum** (see' cum) [L. *blind*] A blind branch off the large intestine. In many nonruminant mammals, the cecum contains a colony of microorganisms that contribute to the digestion of food.

**cell** The simplest structural unit of a living organism. In multicellular organisms, the building blocks of tissues and organs.

**cell adhesion molecules** Molecules on animal cell surfaces that affect the selective association of cells into tissues during development of the embryo.

**cell cycle** The stages through which a cell passes between one division and the next. Includes all stages of interphase and mitosis.

**cell division** The reproduction of a cell to produce two new cells. In eukaryotes, this process

involves nuclear division (mitosis) and cytoplasmic division (cytokinesis).

**cell fate** The type of cell that an undifferentiated cell in an embryo will become in the adult.

**cell junctions** Specialized structures associated with the plasma membranes of epithelial cells. Some contribute to cell adhesion, others to intercellular communication.

**cell recognition** Binding of cells to one another mediated by membrane proteins or carbohydrates.

**cell theory** States that cells are the basic structural and physiological units of all living organisms, and that all cells come from preexisting cells.

**cell wall** A relatively rigid structure that encloses cells of plants, fungi, many protists, and most prokaryotes, and which gives these cells their shape and limits their expansion in hypotonic media.

**cellular immune response** Immune system response mediated by T cells and directed against parasites, fungi, intracellular viruses, and foreign tissues (grafts). (Contrast with humoral immune response.)

**cellular respiration** The catabolic pathways by which electrons are removed from various molecules and passed through intermediate electron carriers to O<sub>2</sub>, generating H<sub>2</sub>O and releasing energy.

**cellulose** (sell' you lowss) A straight-chain polymer of glucose molecules, used by plants as a structural supporting material.

**central dogma** The premise that information flows from DNA to RNA to polypeptide.

**central nervous system (CNS)** That portion of the nervous system that is the site of most information processing, storage, and retrieval; in vertebrates, the brain and spinal cord. (Contrast with peripheral nervous system.)

**central vacuole** In plant cells, a large organelle that stores the waste products of metabolism and maintains turgor.

**centrifuge** [L. *centrum*: center + *fugere*: to flee] A laboratory device in which a sample is spun around a central axis at high speed. Used to separate suspended materials of different densities.

**centriole** (sen' tree ole) A paired organelle that helps organize the microtubules in animal and protist cells during nuclear division.

**centromere** (sen' tro meer) [Gk. *centron*: center + *meros*: part] The region where sister chromatids join.

**centrosome** (sen' tro soam) The major microtubule organizing center of an animal cell.

**cephalization** (sef ah luh zay' shun) [Gk. *kephale*: head] The evolutionary trend toward increasing concentration of brain and sensory organs at the anterior end of the animal.

**cerebellum** (sair uh bell' um) [L. diminutive of *cerebrum*, brain] The brain region that controls muscular coordination; located at the anterior end of the hindbrain.

**cerebral cortex** The thin layer of gray matter (neuronal cell bodies) that overlies the cerebrum.

**cerebrum** (su ree' brum) [L. brain] The dorsal anterior portion of the forebrain, making up the largest part of the brain of mammals; the chief coordination center of the nervous system; consists of two *cerebral hemispheres*.

**cervix** (sir' vix) [L. neck] The opening of the uterus into the vagina.

**cGMP (cyclic guanosine monophosphate)** An intracellular messenger that is part of signal transmission pathways involving G proteins. (See G protein.)

**channel protein** An integral membrane protein that forms an aqueous passageway across the membrane in which it is inserted through which specific solutes may pass.

**chaperone** A protein that guards other proteins by counteracting molecular interactions that threaten their three-dimensional structure.

**character** In genetics, an observable feature, such as eye color. (Contrast with trait.)

**character displacement** An evolutionary phenomenon in which species that compete for the same resources within the same territory tend to diverge in morphology and/or behavior.

**chemical bond** An attractive force stably linking two atoms.

**chemical evolution** The theory that life originated through the chemical transformation of inanimate substances.

**chemical reaction** The change in the composition or distribution of atoms of a substance with consequent alterations in properties.

**chemical synapse** Neural junction at which neurotransmitter molecules released from a presynaptic cell induce changes in a postsynaptic cell. (Contrast with electrical synapse.)

**chemically gated channel** A type of gated channel that opens or closes depending on the presence or absence of a specific molecule, which binds to the channel protein or to a separate receptor that in turn alters the three-dimensional shape of channel protein.

**chemiosmosis** Formation of ATP in mitochondria and chloroplasts, resulting from a pumping of protons across a membrane (against a gradient of electrical charge and of pH), followed by the return of the protons through a protein channel with ATP synthase activity.

**chemoautotroph** See chemolithotroph.

**chemoheterotroph** An organism that must obtain both carbon and energy from organic substances. (Contrast with chemolithotroph, photoautotroph, photoheterotroph.)

**chemolithotroph** [Gk. *lithos*: stone, rock] An organism that uses carbon dioxide as a carbon source and obtains energy by oxidizing inorganic substances from its environment; also called chemoautotroph. (Contrast with chemoheterotroph, photoautotroph, photoheterotroph.)

**chemoreceptor** A sensory receptor cell that senses specific molecules (such as odorant molecules or pheromones) in the environment.

**chiasma** (kie az' muh) (plural: chiasmata) [Gk. cross] An X-shaped connection between paired homologous chromosomes in prophase I of meiosis. A chiasma is the visible manifestation of crossing over between homologous chromosomes.

**chitin** (kye' tin) [Gk. *kiton*: tunic] The characteristic tough but flexible organic component of the exoskeleton of arthropods, consisting of a complex, nitrogen-containing polysaccharide. Also found in cell walls of fungi.

**chlorophyll** (klor' o fill) [Gk. *kloros*: green + *phyllon*: leaf] Any of several green pigments associated with chloroplasts or with certain bacterial membranes; responsible for trapping light energy for photosynthesis.

**chloroplast** [Gk. *kloros*: green + *plast*: a particle] An organelle bounded by a double membrane containing the enzymes and pigments that perform photosynthesis. Chloroplasts occur only in eukaryotes.

**choanocyte** (ko' an uh site) The collared, flagellated feeding cells of sponges.

**cholecystokinin** (ko' luh sis tuh kai' nin) A hormone produced and released by the lining of the duodenum when it is stimulated by undigested fats and proteins. It stimulates the gallbladder to release bile and slows stomach activity.

**chorion** (kor' ee on) [Gk. *khorion*: afterbirth] The outermost of the membranes protecting mammal, bird, and reptile embryos; in mammals it forms part of the placenta.

**chromatid** (kro' ma tid) A newly replicated chromosome, from the time molecular duplication occurs until the time the centromeres separate (during anaphase of mitosis or of meiosis II).

**chromatin** The nucleic acid–protein complex that makes up eukaryotic chromosomes.

**chromosomal mutation** Loss of or changes in position/direction of a DNA segment on a chromosome.

**chromosome** (krome' o sowm) [Gk. *kroma*: color + *soma*: body] In bacteria and viruses, the DNA molecule that contains most or all of the genetic information of the cell or virus. In eukaryotes, a structure composed of DNA and proteins that bears part of the genetic information of the cell.

**chylomicron** (ky low my' cron) Particles of lipid coated with protein, produced in the gut from dietary fats and secreted into the extracellular fluids.

**chyme** (kime) [Gk. *kymus*: juice] Created in the stomach; a mixture of ingested food with the digestive juices secreted by the salivary glands and the stomach lining.

**cilium** (sil' ee um) (plural: cilia) [L. eyelash] Hairlike organelle used for locomotion by many unicellular organisms and for moving water and mucus by many multicellular organisms. Generally shorter than a flagellum.

**circadian rhythm** (sir kade' ee an) [L. *circa*: approximately + *dies*: day] A rhythm of growth or activity that recurs about every 24 hours.

**circannual rhythm** [L. *circa*: + *annus*: year] A rhythm of growth or activity that recurs on a yearly basis.

**circulatory system** A system consisting of a muscular pump (heart), a fluid (blood or hemolymph), and a series of conduits (blood vessels) that transports materials around the body.

**citric acid cycle** In cellular respiration, a set of chemical reactions whereby acetyl CoA is oxidized to carbon dioxide and hydrogen atoms are stored as NADH and FADH<sub>2</sub>. Also called the Krebs cycle.

**clade** [Gk. *klados*: branch] A monophyletic group made up of an ancestor and all of its descendants.

**class I MHC molecules** Cell surface proteins that participate in the cellular immune response directed against virus-infected cells.

**class II MHC molecules** Cell surface proteins that participate in the cell-cell interactions (of T-helper cells, macrophages, and B cells) of the humoral immune response.

**cleavage** The first few cell divisions of an animal zygote. See also complete cleavage, incomplete cleavage.

**climate** The long-term average atmospheric conditions (temperature, precipitation, humidity, wind direction and velocity) found in a region.

**climax community** The final stage of succession; a community that is capable of perpetuating itself under local climatic and soil conditions and persists for a relatively long time.

**clinal variation** [Gk. *klinein*: to lean] Gradual change in the phenotype of a species over a geographic gradient.

**clonal deletion** Inactivation or destruction of lymphocyte clones that would produce immune reactions against the animal's own body.

**clonal selection** Mechanism by which exposure to antigen results in the activation of selected T- or B-cell clones, resulting in an immune response.

**clone** [Gk. *klon*: twig, shoot] (1) Genetically identical cells or organisms produced from a common ancestor by asexual means. (2) To produce many identical copies of a DNA sequence by its introduction into, and subsequent asexual reproduction of, a cell or organism.

**closed circulatory system** Circulatory system in which the circulating fluid is contained within a continuous system of vessels. (Contrast with open circulatory system.)

**coastal zone** The marine life zone that extends from the shoreline to the edge of the continental shelf. Characterized by relatively shallow, well-oxygenated water and relatively stable temperatures and salinities.

**coccus** (kock' us) (plural: cocci) [Gk. *kokkos*: berry, pit] Any of various spherical or spheroidal bacteria.

**cochlea** (cock' lee uh) [Gk. *kokhlos*: snail] A spiral tube in the inner ear of vertebrates; it contains the sensory cells involved in hearing.

**codominance** A condition in which two alleles at a locus produce different phenotypic effects and both effects appear in heterozygotes.

**codon** Three nucleotides in messenger RNA that direct the placement of a particular amino acid into a polypeptide chain. (Contrast with anticodon.)

**coelom** (see' loam) [Gk. *koiroma*: cavity] An animal body cavity, enclosed by muscular mesoderm and lined with a mesodermal layer called peritoneum that also surrounds the internal organs.

**coenocytic** (seen' a sit ik) [Gk. *koinos*: common + *kytos*: container] Referring to the condition, found in some fungal hyphae, of "cells" containing many nuclei but enclosed by a single plasma membrane. Results from nuclear division without cytokinesis.

**coenzyme** A nonprotein organic molecule that plays a role in catalysis by an enzyme.

**coevolution** Evolutionary processes in which an adaptation in one species leads to the evolution of an adaptation in a species with which it interacts; also known as reciprocal adaptation.

**cofactor** An inorganic ion that is weakly bound to an enzyme and required for its activity.

**cohesin** A protein involved in binding chromatids together.

**cohesion** The tendency of molecules (or any substances) to stick together.

**cohort** (co' hort) [L. *cohors*: company of soldiers] A group of similar-aged organisms.

**coleoptile** A sheath that surrounds and protects the shoot apical meristem and young primary

leaves of a grass seedling as they move through the soil.

**collagen** [Gk. *kolla*: glue] A fibrous protein found extensively in bone and connective tissue.

**collecting duct** In vertebrates, a tubule that receives urine produced in the nephrons of the kidney and delivers that fluid to the ureter for excretion.

**collenchyma** (cull eng' kyma) [Gk. *kolla*: glue + *enchyma*: infusion] A type of plant cell, living at functional maturity, which lends flexible support by virtue of primary cell walls thickened at the corners. (Contrast with parenchyma, sclerenchyma.)

**colon** [Gk. *kolon*] The large intestine.

**commensalism** [L. *com*: together + *mensa*: table] A type of interaction between species in which one participant benefits while the other is unaffected.

**communication** A signal from one organism (or cell) that alters the functioning or behavior of another organism (or cell).

**community** Any ecologically integrated group of species of microorganisms, plants, and animals inhabiting a given area.

**compact bone** A type of bone with a solid, hard structure. (Contrast with cancellous bone.)

**companion cell** In angiosperms, a specialized cell found adjacent to a sieve tube element.

**comparative experiment** Experimental design in which data from various unmanipulated samples or populations are compared, but in which variables are not controlled or even necessarily identified. (Contrast with controlled experiment.)

**comparative genomics** Computer-aided comparison of DNA sequences between different organisms to reveal genes with related functions.

**competition** In ecology, use of the same resource by two or more species when the resource is present in insufficient supply for the combined needs of the species.

**competitive exclusion** A result of competition between species for a limiting resource in which one species completely eliminates the other.

**competitive inhibitor** A nonsubstrate that binds to the active site of an enzyme and thereby inhibits binding of its substrate. (Contrast with noncompetitive inhibitor.)

**complement system** A group of eleven proteins that play a role in some reactions of the immune system. The complement proteins are not immunoglobulins.

**complementary base pairing** The AT (or AU), TA (or UA), CG, and GC pairing of bases in double-stranded DNA, in transcription, and between tRNA and mRNA.

**complementary DNA (cDNA)** DNA formed by reverse transcriptase acting with an RNA template; essential intermediate in the reproduction of retroviruses; used as a tool in recombinant DNA technology; lacks introns.

**complete cleavage** Pattern of cleavage that occurs in eggs that have little yolk. Early cleavage furrows divide the egg completely and the blastomeres are of similar size. (Contrast with incomplete cleavage.)

**complete metamorphosis** A change of state during the life cycle of an organism in which the body is almost completely rebuilt to produce an individual with a very different body form. Characteristic of insects such as butterflies, moths, beetles, ants, wasps, and flies.

**compound** (1) A substance made up of atoms of more than one element. (2) Made up of many units, as in the *compound eyes* of arthropods.

**concerted evolution** The common evolution of a family of repeated genes, such that changes in one copy of the gene family are replicated in other copies of the gene family.

**condensation reaction** A chemical reaction in which two molecules become connected by a covalent bond and a molecule of water is released ( $AH + BOH \rightarrow AB + H_2O$ ). (Contrast with hydrolysis reaction.)

**conditional mutation** A mutation that results in a characteristic phenotype only under certain environmental conditions.

**conduction** The transfer of heat from one object to another through direct contact.

**cone** (1) In conifers, a reproductive structure consisting of spore-bearing scales extending from a central axis. (Contrast with strobilus.) (2) In the vertebrate retina, a type of photoreceptor cell responsible for color vision.

**conidium** (ko' nid' ee um) (plural: conidia) [Gk. *konis*: dust] A type of haploid fungal spore borne at the tips of hyphae, not enclosed in sporangia.

**conjugation** (kon ju gay' shun) [L. *conjugare*: yoke together] (1) A process by which DNA is passed from one cell to another through a *conjugation tube*, as in bacteria. (2) A nonreproductive sexual process by which *Paramecium* and other ciliates exchange genetic material.

**connective tissue** A type of tissue that connects or surrounds other tissues; its cells are embedded in a collagen-containing matrix. One of the four major tissue types in multicellular animals.

**connexon** In a gap junction, a protein channel linking adjacent animal cells.

**consensus sequences** Short stretches of DNA that appear, with little variation, in many different genes.

**conservation biology** An applied science that carries out investigations with the aim of maintaining the diversity of life on Earth.

**conserved** Pertaining to a gene or trait that has evolved very slowly and is similar or even identical in individuals of highly divergent groups.

**conspecifics** Individuals of the same species.

**constant region** The portion of an immunoglobulin molecule whose amino acid composition determines its class and does not vary among immunoglobulins in that class. (Contrast with variable region.)

**constitutive** Always present; produced continually at a constant rate. (Contrast with inducible.)

**consumer** An organism that eats the tissues of some other organism.

**continental drift** The gradual movements of the world's continents that have occurred over billions of years.

**contractile vacuole** (kon trak' tul) A specialized vacuole that collects excess water taken in by osmosis, then contracts to expel the water from the cell.

**controlled experiment** An experiment in which a sample is divided into groups whereby experimental groups are exposed to manipulations of an independent variable while one group serves as an untreated control. The data from the various groups are then compared to see if there are changes in a dependent variable as a result of the

experimental manipulation. (Contrast with comparative experiment.)

**convection** The transfer of heat to or from a surface via a moving stream of air or fluid.

**convergent evolution** Independent evolution of similar features from different ancestral traits.

**copulation** Reproductive behavior that results in a male depositing sperm in the reproductive tract of a female.

**cork cambium** [L. *cambiare*: to exchange] In plants, a lateral meristem that produces secondary growth, mainly in the form of waxy-walled protective cells, including some of the cells that become bark.

**cornea** The clear, transparent tissue that covers the eye and allows light to pass through to the retina.

**corolla** (ko' role' lah) [L. *corolla*: a small crown] All of the petals of a flower, collectively.

**coronary artery** (kor' oh nair ee) An artery that supplies blood to the heart muscle.

**coronary thrombosis** A fibrous clot that blocks a coronary artery.

**corpus luteum** (kor' pus loo' tee um) (plural: *corpora lutea*) [L. yellow body] A structure formed from a follicle after ovulation; produces hormones important to the maintenance of pregnancy.

**corridor** A connection between habitat patches through which organisms can disperse; plays a critical role in maintaining subpopulations.

**cortex** [L. *cortex*: covering, rind] (1) In plants, the tissue between the epidermis and the vascular tissue of a stem or root. (2) In animals, the outer tissue of certain organs, such as the adrenal gland (adrenal cortex) and the brain (cerebral cortex).

**corticosteroids** Steroid hormones produced and released by the cortex of the adrenal gland.

**corticotropin** A tropic hormone produced by the anterior pituitary hormone that stimulates cortisol release from the adrenal cortex. Also called adrenocorticotrophic hormone (ACTH).

**corticotropin-releasing hormone** A releasing hormone produced by the hypothalamus that controls the release of cortisol from the anterior pituitary.

**cortisol** A corticosteroid that mediates stress responses.

**cost-benefit analysis** An approach to evolutionary studies that assumes an animal has a limited amount of time and energy to devote to each of its activities, and that each activity has fitness costs as well as benefits. (See also trade-off.)

**cotyledon** (kot' ul lee' dun) [Gk. *kotyledon*: hollow space] A "seed leaf." An embryonic organ that stores and digests reserve materials; may expand when seed germinates.

**countercurrent flow** An arrangement that promotes the maximum exchange of heat, or of a diffusible substance, between two fluids by having the fluids flow in opposite directions through parallel vessels close together.

**countercurrent multiplier** The mechanism that increases the concentration of the interstitial fluid in the mammalian kidney through countercurrent flow in the loops of Henle and selective permeability and active transport of ions by segments of the loops of Henle.

**covalent bond** Chemical bond based on the sharing of electrons between two atoms.

**CpG islands** DNA regions rich in C residues adjacent to G residues. Especially abundant in promoters, these regions are where methylation of cytosine usually occurs.

**crassulacean acid metabolism (CAM)** A metabolic pathway enabling the plants that possess it to store carbon dioxide at night and then perform photosynthesis during the day with stomata closed.

**critical night length** In the photoperiodic flowering response of short-day plants, the length of night above which flowering occurs and below which the plant remains vegetative. (The reverse applies in the case of long-day plants.)

**critical period** See sensitive period.

**cross section** A section taken perpendicular to the longest axis of a structure. Also called a transverse section.

**crossing over** The mechanism by which linked genes undergo recombination. In general, the term refers to the reciprocal exchange of corresponding segments between two homologous chromatids.

**crypsis** [Gk. *kryptos*: hidden] The resemblance of an organism to some part of its environment, which helps it to escape detection by enemies.

**cryptochromes** [Gk. *kryptos*: hidden + *kroma*: color] Photoreceptors mediating some blue-light effects in plants and animals.

**ctene** (teen) [Gk. *cteis*: comb] In ctenophores, a comblike row of cilia-bearing plates. Ctenophores move by beating the cilia on their eight ctene.

**culture** (1) A laboratory association of organisms under controlled conditions. (2) The collection of knowledge, tools, values, and rules that characterize a human society.

**cuticle** (1) In plants, a waxy layer on the outer body surface that retards water loss. (2) In ecdysozoans, an outer body covering that provides protection and support and is periodically molted.

**cyclic AMP** See cAMP.

**cyclic electron transport** In photosynthetic light reactions, the flow of electrons that produces ATP but no NADPH or  $O_2$ .

**cyclin** A protein that activates a cyclin-dependent kinase, bringing about transitions in the cell cycle.

**cyclin-dependent kinase (Cdk)** A protein kinase whose target proteins are involved in transitions in the cell cycle and which is active only when complexed with additional protein subunits, called cyclins.

**cytokine** A regulatory protein made by immune system cells that affects other target cells in the immune system.

**cytokinesis** (sy' toe kine ee' sis) [Gk. *kytos*: container + *kinein*: to move] The division of the cytoplasm of a dividing cell. (Contrast with mitosis.)

**cytokinin** (sy' toe kine' in) A member of a class of plant growth substances that plays roles in senescence, cell division, and other phenomena.

**cytoplasm** The contents of the cell, excluding the nucleus.

**cytoplasmic determinants** In animal development, gene products whose spatial distribution may determine such things as embryonic axes.

**cytoplasmic segregation** The asymmetrical distribution of cytoplasmic determinants in a developing animal embryo.

**cytosine (C)** (site' oh seen) A nitrogen-containing base found in DNA and RNA.

**cytoskeleton** The network of microtubules and microfilaments that gives a eukaryotic cell its shape and its capacity to arrange its organelles and to move.

**cytosol** The fluid portion of the cytoplasm, excluding organelles and other solids.

**cytotoxic T cells (T<sub>c</sub>)** Cells of the cellular immune system that recognize and directly eliminate virus-infected cells. (Contrast with T-helper cells.)

## - D -

**DAG** See diacylglycerol.

**daughter chromosomes** During mitosis, the separated chromatids from the beginning of anaphase onward.

**dead space** The lung volume that fails to be ventilated with fresh air (because the lungs are never completely emptied during exhalation).

**deciduous** [L. *deciduus*: falling off] Pertaining to a woody plant that sheds its leaves but does not die.

**declarative memory** Memory of people, places, events, and things that can be consciously recalled and described. (Contrast with procedural memory.)

**decomposer** An organism that metabolizes organic compounds in debris and dead organisms, releasing inorganic material; found among the bacteria, protists, and fungi. *See also* detritivore, saprobe.

**defensin** A type of protein made by phagocytes that kills bacteria and enveloped viruses by insertion into their plasma membranes.

**degeneracy** The situation in which a single amino acid may be represented by any of two or more different codons in messenger RNA. Most of the amino acids can be represented by more than one codon.

**deletion** A mutation resulting from the loss of a continuous segment of a gene or chromosome. Such mutations almost never revert to wild type. (Contrast with duplication, point mutation.)

**demethylase** An enzyme that catalyzes the removal of the methyl group from cytosine, reversing DNA methylation.

**demography** The study of population structure and of the processes by which it changes.

**denaturation** Loss of activity of an enzyme or nucleic acid molecule as a result of structural changes induced by heat or other means.

**dendrite** [Gk. *dendron*: tree] A fiber of a neuron which often cannot carry action potentials. Usually much branched and relatively short compared with the axon, and commonly carries information to the cell body of the neuron.

**denitrification** Metabolic activity by which nitrate and nitrite ions are reduced to form nitrogen gas, carried by certain soil bacteria.

**denitrifiers** Bacteria that release nitrogen to the atmosphere as nitrogen gas (N<sub>2</sub>).

**density-dependent** Pertaining to a factor with an effect on population size that increases in proportion to population density.

**density-independent** Pertaining to a factor with an effect on population size that acts independently of population density.

**deoxyribonucleic acid** *See* DNA.

**deoxyribose** A five-carbon sugar found in nucleotides and DNA.

**depolarization** A change in the resting potential across a membrane so that the inside of the cell becomes less negative, or even positive, compared with the outside of the cell. (Contrast with hyperpolarization.)

**derived trait** A trait that differs from the ancestral trait. (Contrast with shared derived trait.)

**dermal tissue system** The outer covering of a plant, consisting of epidermis in the young plant and periderm in a plant with extensive secondary growth. (Contrast with ground tissue system and vascular tissue system.)

**desmosome** (dez' mo sōmə) [Gk. *desmos*: bond + *soma*: body] An adhering junction between animal cells.

**desmotubule** A membrane extension connecting the endoplasmic reticulum of two plant cells that traverses the plasmodesma.

**determination** In development, the process whereby the fate of an embryonic cell or group of cells (e.g., to become epidermal cells or neurons) is set.

**determinate growth** A growth pattern in which the growth of an organism or organ ceases when an adult state is reached; characteristic of most animals and some plant organs. (Contrast with indeterminate growth.)

**detritivore** (di trit' i vore) [L. *detritus*: worn away + *vorare*: to devour] An organism that obtains its energy from the dead bodies or waste products of other organisms.

**developmental module** A functional entity in the embryo encompassing genes and signaling pathways that determine a physical structure independently of other such modules.

**developmental plasticity** The capacity of an organism to alter its pattern of development in response to environmental conditions.

**diacylglycerol (DAG)** In hormone action, the second messenger produced by hydrolytic removal of the head group of certain phospholipids.

**diapause** A period of developmental or reproductive arrest, entered in response to day length, that enables an organism to better survive.

**diaphragm** (dye' uh fram) [Gk. *diaphrassein*: barricade] (1) A sheet of muscle that separates the thoracic and abdominal cavities in mammals; responsible for breathing. (2) A method of birth control in which a sheet of rubber is fitted over the woman's cervix, blocking the entry of sperm.

**diastole** (dye ass' tol ee) [Gk. dilation] The portion of the cardiac cycle when the heart muscle relaxes. (Contrast with systole.)

**diencephalon** The portion of the vertebrate forebrain that develops into the thalamus and hypothalamus.

**differential gene expression** The hypothesis that, given that all cells contain all genes, what makes one cell type different from another is the difference in transcription and translation of those genes.

**differentiation** The process whereby originally similar cells follow different developmental pathways; the actual expression of determination.

**diffuse coevolution** The evolution of similar traits in suites of species experiencing similar selection pressures imposed by other suites of species with which they interact.

**diffusion** Random movement of molecules or other particles, resulting in even distribution of the particles when no barriers are present.

**dihybrid cross** A mating in which the parents differ with respect to the alleles of two loci of interest.

**dikaryon** (di kär' ee ahn) [Gk. *di*: two + *karyon*: kernel] A cell or organism carrying two genetically distinguishable nuclei. Common in fungi.

**dioecious** (die eesh' us) [Gk. *di*: two + *oikos*: house] Pertaining to organisms in which the two sexes are "housed" in two different individuals, so that eggs and sperm are not produced in the same individuals. Examples: humans, fruit flies, date palms. (Contrast with monoecious.)

**diploblastic** Having two cell layers. (Contrast with triploblastic.)

**diploid** (dip'loid) [Gk. *diplos*: double] Having a chromosome complement consisting of two copies (homologs) of each chromosome. Designated *2n*.

**diplontic** A type of life cycle in which gametes are the only haploid cells and mitosis occurs only in diploid cells. (Contrast with haplontic.)

**direct transduction** A cell signaling mechanism in which the receptor acts as the effector in the cellular response. (Contrast with indirect transduction.)

**directional selection** Selection in which phenotypes at one extreme of the population distribution are favored. (Contrast with disruptive selection, stabilizing selection.)

**disaccharide** A carbohydrate made up of two monosaccharides (simple sugars).

**dispersal** Movement of organisms away from a parent organism or from an existing population.

**dispersion** The distribution of individuals in space within a population.

**disruptive selection** Selection in which phenotypes at both extremes of the population distribution are favored. (Contrast with directional selection; stabilizing selection.)

**distal** Away from the point of attachment or other reference point. (Contrast with proximal.)

**distal convoluted tubule** The portion of a renal tubule from where it reaches the renal cortex, just past the loop of Henle to where it joins a collecting duct. (Compare with proximal convoluted tubule.)

**disturbance** A short-term event that disrupts populations, communities, or ecosystems by changing the environment.

**disulfide bridge** The covalent bond between two sulfur atoms (—S—S—) linking two molecules or remote parts of the same molecule.

**DNA (deoxyribonucleic acid)** The fundamental hereditary material of all living organisms. In eukaryotes, stored primarily in the cell nucleus. A nucleic acid using deoxyribose rather than ribose.

**DNA fingerprint** An individual's unique pattern of allele sequences, commonly short tandem repeats and single nucleotide polymorphisms.

**DNA helicase** An enzyme that functions to unwind the double helix.

**DNA ligase** Enzyme that unites broken DNA strands during replication and recombination.

**DNA methylation** The addition of methyl groups to bases in DNA, usually cytosine or guanine.

**DNA methyltransferase** An enzyme that catalyzes the methylation of DNA.

**DNA microarray** A small glass or plastic square onto which thousands of single-stranded DNA sequences are fixed so that hybridization of cell-derived RNA or DNA to the target sequences can be performed.

**DNA polymerase** Any of a group of enzymes that catalyze the formation of DNA strands from a DNA template.

**DNA topoisomerase** An enzyme that unwinds and winds coils of DNA that form during replication and transcription.

**docking protein** A receptor protein that binds (docks) a ribosome to the membrane of the endoplasmic reticulum by binding the signal sequence attached to a new protein being made at the ribosome.

**domain** (1) An independent structural element within a protein. Encoded by recognizable nucleotide sequences, a domain often folds separately from the rest of the protein. Similar domains can appear in a variety of different proteins across phylogenetic groups (e.g., “homeobox domain”, “calcium-binding domain”). (2) In phylogenetics, the three monophyletic branches of life (Bacteria, Archaea, and Eukarya).

**dominance** In genetics, the ability of one allelic form of a gene to determine the phenotype of a heterozygous individual in which the homologous chromosomes carry both it and a different (recessive) allele. (Contrast with recessive.)

**dormancy** A condition in which normal activity is suspended, as in some spores, seeds, and buds.

**dorsal** [L. *dorsum*: back] Toward or pertaining to the back or upper surface. (Contrast with ventral.)

**dorsal lip** In amphibian embryos, the dorsal segment of the blastopore. Also called the “organizer,” this region directs the development of nearby embryonic regions.

**double fertilization** In angiosperms, a process in which the nuclei of two sperm fertilize one egg. One sperm’s nucleus combines with the egg nucleus to produce a zygote, while the other combines with the same egg’s two polar nuclei to produce the first cell of the triploid endosperm (the tissue that will nourish the growing plant embryo).

**double helix** Refers to DNA and the (usually right-handed) coil configuration of two complementary, antiparallel strands.

**downregulation** A negative feedback process in which continuous high concentrations of a hormone can decrease the number of its receptors. (Contrast with upregulation.)

**duodenum** (do’ uh dee’ num) The beginning portion of the vertebrate small intestine. (Contrast with ileum, jejunum.)

**duplication** A mutation in which a segment of a chromosome is duplicated, often by the attachment of a segment lost from its homolog. (Contrast with deletion.)

## - E -

**ecdysone** (eck die’ sone) [Gk. *ek*: out of + *dyo*: to clothe] In insects, a hormone that induces molting.

**ecological efficiency** The overall transfer of energy from one trophic level to the next, expressed as the ratio of consumer production to producer production.

**ecology** [Gk. *oikos*: house] The scientific study of the interaction of organisms with their living (biotic) and nonliving (abiotic) environments.

**ecosystem** (eek’ oh sis tum) The organisms of a particular habitat, such as a pond or forest, together with the physical environment in which they live.

**ecosystem engineer** An organism that builds structures that alter existing habitats or create new habitats.

**ecosystem services** Processes by which ecosystems maintain resources that benefit human society.

**ectoderm** [Gk. *ektos*: outside + *derma*: skin] The outermost of the three embryonic germ layers first delineated during gastrulation. Gives rise to the skin, sense organs, and nervous system.

**ectotherm** [Gk. *ektos*: outside + *thermos*: heat] An animal that is dependent on external heat sources for regulating its body temperature (Contrast with endotherm.)

**edema** (i dee’ mah) [Gk. *oidema*: swelling] Tissue swelling caused by the accumulation of fluid.

**edge effect** The changes in ecological processes in a community caused by physical and biological factors originating in an adjacent community.

**effector protein** In cell signaling, a protein responsible for the cellular response to a signal transduction pathway.

**afferent** (ef’ ur unt) [L. *ex*: out + *ferre*: to bear] Carrying outward or away from, as in a neuron that carries impulses outward from the central nervous system (afferent neuron), or a blood vessel that carries blood away from a structure. (Contrast with efferent.)

**egg** In all sexually reproducing organisms, the female gamete; in birds, reptiles, and some other vertebrates, a structure within which early embryonic development occurs. *See also* amniote egg, ovum.

**electrical synapse** A type of synapse at which action potentials spread directly from presynaptic cell to postsynaptic cell. (Contrast with chemical synapse.)

**electrocardiogram (ECG or EKG)** A graphic recording of electrical potentials from the heart.

**electrochemical gradient** The concentration gradient of an ion across a membrane plus the voltage difference across that membrane.

**electroencephalogram (EEG)** A graphic recording of electrical potentials from the brain.

**electromagnetic radiation** A self-propagating wave that travels through space and has both electrical and magnetic properties.

**electron** A subatomic particle outside the nucleus carrying a negative charge and very little mass.

**electron shell** The region surrounding the atomic nucleus at a fixed energy level in which electrons orbit.

**electron transport** The passage of electrons through a series of proteins with a release of energy which may be captured in a concentration gradient or chemical form such as NADH or ATP.

**electronegativity** The tendency of an atom to attract electrons when it occurs as part of a compound.

**electrophoresis** *See* gel electrophoresis.

**element** A substance that cannot be converted to simpler substances by ordinary chemical means.

**elongation** (1) In molecular biology, the addition of monomers to make a longer RNA or protein during transcription or translation. (2) Growth of a plant axis or cell primarily in the longitudinal direction.

**embolus** (em’ buh lus) [Gk. *embolos*: stopper] A circulating blood clot. Blockage of a blood vessel by an embolus or by a bubble of gas is referred to as an *embolism*. (Contrast with thrombus.)

**embryo** [Gk. *en*: within + *bryein*: to grow] A young animal, or young plant sporophyte, while it is still contained within a protective structure such as a seed, egg, or uterus.

**embryonic stem cell (ESC)** A pluripotent cell in the blastocyst.

**embryo sac** In angiosperms, the female gametophyte. Found within the ovule, it consists of eight or fewer cells, membrane bounded, but without cellulose walls between them.

**emergent property** A property of a complex system that is not exhibited by its individual component parts.

**emigration** The deliberate and usually oriented departure of an organism from the habitat in which it has been living.

**3' end** (3 prime) The end of a DNA or RNA strand that has a free hydroxyl group at the 3' carbon of the sugar (deoxyribose or ribose).

**5' end** (5 prime) The end of a DNA or RNA strand that has a free phosphate group at the 5' carbon of the sugar (deoxyribose or ribose).

**endemic** (en dem’ ik) [Gk. *endemos*: native] Confined to a particular region, thus often having a comparatively restricted distribution.

**endergonic** A chemical reaction in which the products have higher free energy than the reactants, thereby requiring free energy input to occur. (Contrast with exergonic.)

**endocrine gland** (en’ doh krin) [Gk. *endo*: within + *krinein*: to separate] An aggregation of secretory cells that secretes hormones into the blood. The *endocrine system* consists of all *endocrine cells* and endocrine glands in the body that produce and release hormones. (Contrast with exocrine gland.)

**endocytosis** A process by which liquids or solid particles are taken up by a cell through invagination of the plasma membrane. (Contrast with exocytosis.)

**endoderm** [Gk. *endo*: within + *derma*: skin] The innermost of the three embryonic germ layers delineated during gastrulation. Gives rise to the digestive and respiratory tracts and structures associated with them.

**endodermis** In plants, a specialized cell layer marking the inside of the cortex in roots and some stems. Frequently a barrier to free diffusion of solutes.

**endomembrane system** A system of intracellular membranes that exchange material with one another, consisting of the Golgi apparatus, endoplasmic reticulum, and lysosomes when present.

**endometrium** The epithelial lining of the uterus.

**endoplasmic reticulum (ER)** [Gk. *endo*: within + L. *reticulum*: net] A system of membranous tubes and flattened sacs found in the cytoplasm of eukaryotes. Exists in two forms: rough ER,

studded with ribosomes; and smooth ER, lacking ribosomes.

**endorphins** Molecules in the mammalian brain act as neurotransmitters in pathways that control pain.

**endoskeleton** [Gk. *endo*: within + *skleros*: hard] An internal skeleton covered by other, soft body tissues. (Contrast with exoskeleton.)

**endosperm** [Gk. *endo*: within + *sperma*: seed] A specialized triploid seed tissue found only in angiosperms; contains stored nutrients for the developing embryo.

**endospore** [Gk. *endo*: within + *spora*: to sow] In some bacteria, a resting structure that can survive harsh environmental conditions.

**endosymbiosis theory** [Gk. *endo*: within + *sym*: together + *bios*: life] The theory that the eukaryotic cell evolved via the engulfing of one prokaryotic cell by another.

**endothelium** The single layer of epithelial cells lining the interior of a blood vessel.

**endotherm** [Gk. *endo*: within + *thermos*: heat] An animal that can control its body temperature by the expenditure of its own metabolic energy. (Contrast with ectotherm.)

**endotoxin** A lipopolysaccharide that forms part of the outer membrane of certain Gram-negative bacteria that is released when the bacteria grow or lyse. (Contrast with exotoxin.)

**energetic cost** The difference between the energy an animal expends in performing a behavior and the energy it would have expended had it rested.

**energy** The capacity to do work or move matter against an opposing force. The capacity to accomplish change in physical and chemical systems.

**energy budget** A quantitative description of all paths of energy exchange between an animal and its environment.

**enkephalins** Molecules in the mammalian brain act as neurotransmitters in pathways that control pain.

**enthalpy (H)** The total energy of a system.

**entropy (S)** [en' tro pee] [Gk. *tropein*: to change] A measure of the degree of disorder in any system. Spontaneous reactions in a closed system are always accompanied by an increase in entropy.

**enveloped virus** A virus enclosed within a phospholipid membrane derived from its host cell.

**environment** Whatever surrounds and interacts with or otherwise affects a population, organism, or cell. May be external or internal.

**environmentalism** The use of ecological knowledge, along with economics, ethics, and many other considerations, to inform both personal decisions and public policy relating to stewardship of natural resources and ecosystems.

**enzyme** (en' zime) [Gk. *zyme*: to leaven (as in yeast bread)] A catalytic protein that speeds up a biochemical reaction.

**epi-** [Gk. upon, over] A prefix used to designate a structure located on top of another; for example, epidermis, epiphyte.

**epiblast** The upper or overlying portion of the avian blastula which is joined to the hypoblast at the margins of the blastodisc.

**epiboly** The movement of cells over the surface of the blastula toward the forming blastopore.

**epitope** See antigenic determinant.

**epidermis** [Gk. *epi*: over + *derma*: skin] In plants and animals, the outermost cell layers. (Only one cell layer thick in plants.)

**epididymis** (epuh did' uh mus) [Gk. *epi*: over + *didymos*: testicle] Coiled tubules in the testes that store sperm and conduct sperm from the seminiferous tubules to the vas deferens.

**epigenetics** The scientific study of changes in the expression of a gene or set of genes that occur without change in the DNA sequence.

**epinephrine** (ep i nef' rin) [Gk. *epi*: over + *nephros*: kidney] The “fight or flight” hormone produced by the medulla of the adrenal gland; it also functions as a neurotransmitter. (Also known as adrenaline.)

**epistasis** Interaction between genes in which the presence of a particular allele of one gene determines whether another gene will be expressed.

**epithelium** A type of animal tissue made up of sheets of cells that lines or covers organs, makes up tubules, and covers the surface of the body; one of the four major tissue types in multicellular animals.

**equilibrium** Any state of balanced opposing forces and no net change.

**ER** See endoplasmic reticulum.

**error signal** In regulatory systems, any difference between the set point of the system and its current condition.

**erythrocyte** (ur rith' row site) [Gk. *erythros*: red + *kytos*: container] A red blood cell.

**erythropoietin** A hormone produced by the kidney in response to lack of oxygen that stimulates the production of red blood cells.

**esophagus** (i soff' i gus) [Gk. *oisophagos*: gullet] That part of the gut between the pharynx and the stomach.

**essential acids** Amino acids or fatty acids that an animal cannot synthesize for itself and must obtain from its food.

**essential element** A mineral nutrient required for normal growth and reproduction in plants and animals.

**ester linkage** A condensation (water-releasing) reaction in which the carboxyl group of a fatty acid reacts with the hydroxyl group of an alcohol. Lipids are formed in this way.

**estivation** (ess tuh vay' shun) [L. *aestivalis*: summer] A state of dormancy and hypometabolism that occurs during the summer; usually a means of surviving drought and/or intense heat. (Contrast with hibernation.)

**estrogen** Any of several steroid sex hormones; produced chiefly by the ovaries in mammals.

**estrus** (es' trus) [L. *oestrus*: frenzy] The period of heat, or maximum sexual receptivity, in some female mammals. Ordinarily, the estrus is also the time of release of eggs in the female.

**ethology** [Gk. *ethos*: character + *logos*: study] An approach to the study of animal behavior that focuses on studying many species in natural environments and addresses questions about the evolution of behavior.

**ethylene** One of the plant growth hormones, the gas  $\text{H}_2\text{C}=\text{CH}_2$ . Involved in fruit ripening and other growth and developmental responses.

**eukaryotes** (yew car' ree oats) [Gk. *eu*: true + *karyon*: kernel or nucleus] Organisms whose cells contain their genetic material inside a nu-

cleus. Includes all life other than the viruses, archaea, and bacteria.

**eusocial** Pertaining to a social group that includes nonreproductive individuals, as in honey bees.

**eutrophication** (yoo trof' ik ay' shun) [Gk. *eu*: truly + *trephein*: to flourish] The addition of nutrient materials to a body of water, resulting in changes in ecological processes and species composition therein.

**evaporation** The transition of water from the liquid to the gaseous phase.

**evolution** Any gradual change. Most often refers to organic or Darwinian evolution, which is the genetic and resulting phenotypic change in populations of organisms from generation to generation. (See macroevolution, microevolution; contrast with speciation.)

**evolutionary radiation** The proliferation of many species within a single evolutionary lineage.

**evolutionary reversal** The reappearance of an ancestral trait in a group that had previously acquired a derived trait.

**excision repair** A mechanism that removes damaged DNA and replaces it with the appropriate nucleotide.

**excited state** The state of an atom or molecule when, after absorbing energy, it has more energy than in its normal, ground state. (Contrast with ground state.)

**excretion** Release of metabolic wastes by an organism.

**exergonic** A chemical reaction in which the products of the reaction have lower free energy than the reactants, resulting in a release of free energy. (Contrast with endergonic.)

**exocrine gland** (eks' oh krin) [Gk. *exo*: outside + *krinein*: to separate] Any gland, such as a salivary gland, that secretes to the outside of the body or into the gut. (Contrast with endocrine gland.)

**exocytosis** A process by which a vesicle within a cell fuses with the plasma membrane and releases its contents to the outside. (Contrast with endocytosis.)

**exon** A portion of a DNA molecule, in eukaryotes, that codes for part of a polypeptide. (Contrast with intron.)

**exoskeleton** (eks' oh skel' e ton) [Gk. *exos*: outside + *skleros*: hard] A hard covering on the outside of the body to which muscles are attached. (Contrast with endoskeleton.)

**exotoxin** A highly toxic, usually soluble protein released by living, multiplying bacteria. (Contrast with endotoxin.)

**expanding triplet repeat** A three-base-pair sequence in a human gene that is unstable and can be repeated a few to hundreds of times. Often, the more the repeats, the less the activity of the gene involved. Expanding triplet repeats occur in some human diseases such as Huntington's disease and fragile-X syndrome.

**experiment** A testing process to support or disprove hypotheses and to answer questions. The basis of the scientific method. See comparative experiment, controlled experiment.

**expiratory reserve volume** The amount of air that can be forcefully exhaled beyond the normal tidal expiration. (Contrast with inspiratory reserve volume, tidal volume, vital capacity.)

**exploitation competition** Competition in which individuals reduce the quantities of their shared resources. (Contrast with interference competition.)

**exponential growth** Growth, especially in the number of organisms in a population, which is a geometric function of the size of the growing entity: the larger the entity, the faster it grows. (Contrast with logistic growth.)

**expression vector** A DNA vector, such as a plasmid, that carries a DNA sequence that includes the adjacent sequences for its expression into mRNA and protein in a host cell.

**expressivity** The degree to which a genotype is expressed in the phenotype; may be affected by the environment.

**extensor** A muscle that extends an appendage.

**external fertilization** The release of gametes into the environment; typical of aquatic animals. Also called spawning. (Contrast with internal fertilization.)

**external gills** Highly branched and folded extensions of the body surface that provide a large surface area for gas exchange with water; typical of larval amphibians and many larval insects.

**extinction** The termination of a lineage of organisms.

**extracellular matrix** A material of heterogeneous composition surrounding cells and performing many functions including adhesion of cells.

**extraembryonic membranes** Four membranes that support but are not part of the developing embryos of reptiles, birds, and mammals, defining these groups phylogenetically as amniotes. (See amnion, allantois, chorion, and yolk sac.)

## - F -

**F<sub>1</sub>** The first filial generation; the immediate progeny of a parental (P) mating.

**F<sub>2</sub>** The second filial generation; the immediate progeny of a mating between members of the F<sub>1</sub> generation.

**facilitated diffusion** Passive movement through a membrane involving a specific carrier protein; does not proceed against a concentration gradient. (Contrast with active transport, diffusion.)

**facilitation** In succession, modification of the environment by a colonizing species in a way that allows colonization by other species. (Contrast with inhibition.)

**facultative anaerobe** A prokaryote that can shift its metabolism between anaerobic and aerobic operations modes on the presence or absence of O<sub>2</sub>. (Alternatively, facultative aerobe.)

**fast-twitch fibers** Skeletal muscle fibers that can generate high tension rapidly, but fatigue rapidly ("sprinter" fibers). Characterized by an abundance of enzymes of glycolysis.

**fat** A triglyceride that is solid at room temperature. (Contrast with oil.)

**fate map** A diagram of the blastula showing which cells (blastomeres) are "fated" to contribute to specific tissues and organs in the mature body.

**fatty acid** A molecule made up of a long non-polar hydrocarbon chain and a polar carboxyl group. Found in many lipids.

**fauna** (faw' nah) All the animals found in a given area. (Contrast with flora.)

**feces** [L. *faeces*: dregs] Waste excreted from the digestive system.

**fecundity (*m<sub>x</sub>*)** The average number of offspring produced by each female.

**feedback information** In regulatory systems, information about the relationship between the set point of the system and its current state.

**feedforward information** In regulatory systems, information that changes the set point of the system.

**fermentation** (fur men tay' shun) [L. *fermentum*: yeast] The anaerobic degradation of a substance such as glucose to smaller molecules such as lactic acid or alcohol with the extraction of energy.

**fertilization** Union of gametes. Also known as syngamy.

**fetus** Medical and legal term for the stages of a developing human embryo from about the eighth week of pregnancy (the point at which all major organ systems have formed) to the moment of birth.

**fiber** In angiosperms, an elongated, tapering sclerenchyma cell, usually with a thick cell wall, that serves as a support function in xylem. (See also muscle fiber.)

**fibrin** A protein that polymerizes to form long threads that provide structure to a blood clot.

**fibrinogen** A circulating protein that can be stimulated to fall out of solution and provide the structure for a blood clot.

**fibrous root system** A root system typical of monocots composed of numerous thin adventitious roots that are all roughly equal in diameter. (Contrast with taproot system.)

**Fick's law of diffusion** An equation that describes the factors that determine the rate of diffusion of a molecule from an area of higher concentration to an area of lower concentration.

**fight-or-flight response** A rapid physiological response to a sudden threat mediated by the hormone epinephrine.

**filter feeder** An organism that feeds on organisms much smaller than itself that are suspended in water or air by means of a straining device.

**first law of thermodynamics** The principle that energy can be neither created nor destroyed.

**fission** See binary fission.

**fitness** The contribution of a genotype or phenotype to the genetic composition of subsequent generations, relative to the contribution of other genotypes or phenotypes. (See also inclusive fitness.)

**flagellum** (fla jell' um) (plural: flagella) [L. *flagellum*: whip] Long, whiplike appendage that propels cells. Prokaryotic flagella differ sharply from those found in eukaryotes.

**fixed action pattern** In ethology, a genetically determined behavior that is performed without learning, stereotypic (performed the same way each time), and not modifiable by learning.

**flexor** A muscle that flexes an appendage.

**flora** (flo're ah) All of the plants found in a given area. (Contrast with fauna.)

**floral meristem** In angiosperms, a meristem that forms the floral organs (sepals, petals, stamens, and carpels).

**floral organ identity genes** In angiosperms, genes that determine the fates of floral meristem cells; their expression is triggered by the products of meristem identity genes.

**florigen** A plant hormone involved in the conversion of a vegetative shoot apex to a flower.

**flower** The sexual structure of an angiosperm.

**fluid feeder** An animal that feeds on fluids it extracts from the bodies of other organisms; examples include nectar-feeding birds and blood-sucking insects.

**fluid mosaic model** A molecular model for the structure of biological membranes consisting of a fluid phospholipid bilayer in which suspended proteins are free to move in the plane of the bilayer.

**follicle** [L. *folliculus*: little bag] In female mammals, an immature egg surrounded by nutritive cells.

**follicle-stimulating hormone (FSH)** A gonadotropin produced by the anterior pituitary.

**food chain** A portion of a food web, most commonly a simple sequence of prey species and the predators that consume them.

**food vacuole** Membrane enclosed structure formed by phagocytosis in which engulfed food particles are digested by the action of lysosomal enzymes.

**food web** The complete set of food links between species in a community; a diagram indicating which ones are the eaters and which are eaten.

**forebrain** The region of the vertebrate brain that comprises the cerebrum, thalamus, and hypothalamus.

**fossil** Any recognizable structure originating from an organism, or any impression from such a structure, that has been preserved over geological time.

**fossil fuels** Fuels, including oil, natural gas, coal, and peat, formed over geologic time from organic material buried in anaerobic sediments.

**founder effect** Random changes in allele frequencies resulting from establishment of a population by a very small number of individuals.

**fovea** [L. *fovea*: a small pit] In the vertebrate retina, the area of most distinct vision.

**frame-shift mutation** The addition or deletion of a single or two adjacent nucleotides in a gene's sequence. Results in the misreading of mRNA during translation and the production of a non-functional protein. (Contrast with missense mutation, nonsense mutation, silent mutation.)

**Frank-Starling law** The stroke volume of the heart increases with increased return of blood to the heart.

**free energy (G)** Energy that is available for doing useful work, after allowance has been made for the increase or decrease of disorder.

**freeze-fracturing** Method of tissue preparation for transmission and scanning electron microscopy in which a tissue is frozen and a knife is then used to crack open the tissue; the fracture often occurs in the path of least resistance, within a membrane.

**frequency-dependent selection** Selection that changes in intensity with the proportion of individuals in a population having the trait.

**fruit** In angiosperms, a ripened and mature ovary (or group of ovaries) containing the seeds. Sometimes applied to reproductive structures of other groups of plants.

**functional genomics** The assignment of functional roles to the proteins encoded by genes identified by sequencing entire genomes.

**functional group** A characteristic combination of atoms that contribute specific properties when attached to larger molecules.

**fundamental niche** A species' niche as defined by its physiological capabilities. (Contrast with realized niche.)

- G -

**G cap** A chemically modified GTP added to the 5' end of mRNA; facilitates binding of mRNA to ribosome and prevents mRNA breakdown.

**G1** In the cell cycle, the gap between the end of mitosis and the onset of the S phase.

**G2** In the cell cycle, the gap between the S (synthesis) phase and the onset of mitosis.

**G protein** A membrane protein involved in signal transduction; characterized by binding GDP or GTP.

**gain of function mutation** A mutation that results in a protein with a new function. (Contrast with loss of function mutation.)

**gallbladder** In the human digestive system, an organ in which bile is stored.

**gametangium** (gam uh tan' gee um) (plural: gametangia) [Gk. *gamos*: marriage + *angeion*: vessel] Any plant or fungal structure within which a gamete is formed.

**gamete** (gam' eet) [Gk. *gamete/gametes*: wife, husband] The mature sexual reproductive cell: the egg or the sperm.

**gametogenesis** (ga meet' oh jen' e sis) The specialized series of cellular divisions that leads to the production of gametes. (*See also* oogenesis, spermatogenesis.)

**gametophyte** (ga meet' oh fyte) In plants and photosynthetic protists with alternation of generations, the multicellular haploid phase that produces the gametes. (Contrast with sporophyte.)

**gamma diversity** The regional diversity found over a range of communities or habitats in a geographic region. (Contrast with alpha diversity, beta diversity.)

**ganglion** (gang' glee un) (plural: ganglia) [Gk. tumor] A cluster of neurons that have similar characteristics or function.

**ganglion cells** Cells at the front of the human retina that transmit information from the bipolar cells to the brain.

**gap junction** A 2.7-nanometer gap between plasma membranes of two animal cells, spanned by protein channels. Gap junctions allow chemical substances or electrical signals to pass from cell to cell.

**gastric pits** Deep infoldings in the walls of the stomach lined with secretory cells.

**gastrin** A hormone secreted by cells in the lower region of the stomach that stimulates the secretion of digestive juices as well as movements of the stomach.

**gastrovascular cavity** Serving for both digestion (gastro) and circulation (vascular); in particular, the central cavity of the body of jellyfish and other cnidarians.

**gastrulation** Development of a blastula into a gastrula. In embryonic development, the process by which a blastula is transformed by massive movements of cells into a *gastrula*, an embryo with three germ layers and distinct body axes.

**gated channel** A membrane protein that changes its three-dimensional shape, and therefore its ion conductance, in response to a stimulus. When open, it allows specific ions to move across the membrane.

**gel electrophoresis** (e lek' tro fo ree' sis) [L. *electrum*: amber + Gk. *phorein*: to bear] A technique

for separating molecules (such as DNA fragments) from one another on the basis of their electric charges and molecular weights by applying an electric field to a gel.

**gene** [Gk. *genes*: to produce] A unit of heredity. Used here as the unit of genetic function which carries the information for a single polypeptide or RNA.

**gene family** A set of similar genes derived from a single parent gene; need not be on the same chromosomes. The vertebrate globin genes constitute a classic example of a gene family.

**gene flow** Exchange of genes between populations through migration of individuals or movements of gametes.

**gene-for-gene resistance** In plants, a mechanism of resistance to pathogens in which resistance is triggered by the specific interaction of the products of a pathogen's *Avr* genes and a plant's *R* genes.

**gene pool** All of the different alleles of all of the genes existing in all individuals of a population.

**gene therapy** Treatment of a genetic disease by providing patients with cells containing functioning alleles of the genes that are nonfunctional in their bodies.

**gene tree** A graphic representation of the evolutionary relationships of a single gene in different species or of the members of a gene family.

**genetic code** The set of instructions, in the form of nucleotide triplets, that translate a linear sequence of nucleotides in mRNA into a linear sequence of amino acids in a protein.

**genetic drift** Changes in gene frequencies from generation to generation as a result of random (chance) processes.

**genetic map** The positions of genes along a chromosome as revealed by recombination frequencies.

**genetic marker** (1) In gene cloning, a gene of identifiable phenotype that indicates the presence of another gene, DNA segment, or chromosome fragment. (2) In general, a DNA sequence such as a single nucleotide polymorphism whose presence is correlated with the presence of other linked genes on that chromosome.

**genetic structure** The frequencies of different alleles at each locus and the frequencies of different genotypes in a Mendelian population.

**genetic switches** Mechanisms that control how the genetic toolkit is used, such as promoters and the transcription factors that bind them. The signal cascades that converge on and operate these switches determine when and where genes will be turned on and off.

**genetic toolkit** In evolutionary developmental biology, DNA sequences controlling developmental mechanisms that have been conserved over evolutionary time.

**genetics** The scientific study of the structure, functioning, and inheritance of genes, the units of hereditary information.

**genome** (jee' nome) The complete DNA sequence for a particular organism or individual.

**genomic equivalence** The principle that no information is lost from the nuclei of cells as they pass through the early stages of embryonic development.

**genomic imprinting** The form of a gene's expression is determined by parental source (i.e.,

whether the gene is inherited from the male or female parent).

**genomic library** All of the cloned DNA fragments generated by the action of a restriction endonuclease on a genome.

**genomics** The scientific study of entire sets of genes and their interactions.

**genotype** (jean' oh type) [Gk. *gen*: to produce + *typos*: impression] An exact description of the genetic constitution of an individual, either with respect to a single trait or with respect to a larger set of traits. (Contrast with phenotype.)

**genus** (jean' us) (plural: genera) [Gk. *genos*: stock, kind] A group of related, similar species recognized by taxonomists with a distinct name used in binomial nomenclature.

**germ cell** [L. *germen*: to beget] A reproductive cell or gamete of a multicellular organism. (Contrast with somatic cell.)

**germ layers** The three embryonic layers formed during gastrulation (ectoderm, mesoderm, and endoderm). Also called cell layers or tissue layers.

**germ line mutation** Mutation in a cell that produces gametes (i.e., a germ line cell). (Contrast with somatic mutation.)

**germination** Sprouting of a seed or spore.

**gestation** (jes tay' shun) [L. *gestare*: to bear] The period during which the embryo of a mammal develops within the uterus. Also known as pregnancy.

**ghrelin** A hormone produced and secreted by cells in the stomach that stimulates appetite.

**gibberellin** (jib er el' lin) A class of plant growth hormones playing roles in stem elongation, seed germination, flowering of certain plants, etc.

**gill** An organ specialized for gas exchange with water.

**gizzard** (giz' erd) [L. *gigeria*: cooked chicken parts] A muscular part of the stomach of birds that grinds up food, sometimes with the aid of fragments of stone.

**glia** (glee' uh) [Gk. *glia*: glue] Cells of the nervous system that do not conduct action potentials.

**glomerular filtration rate (GFR)** The rate at which the blood is filtered in the glomeruli of the kidney.

**glomerulus** (glo mare' yew lus) [L. *glomus*: ball] Sites in the kidney where blood filtration takes place. Each glomerulus consists of a knot of capillaries served by afferent and efferent arterioles.

**glucagon** Hormone produced by alpha cells of the pancreatic islets of Langerhans. Glucagon stimulates the liver to break down glycogen and release glucose into the circulation.

**gluconeogenesis** The biochemical synthesis of glucose from other substances, such as amino acids, lactate, and glycerol.

**glucose** [Gk. *gleukos*: sugar, sweet] The most common monosaccharide; the monomer of the polysaccharides starch, glycogen, and cellulose.

**glycerol** (gliiss' er ole) A three-carbon alcohol with three hydroxyl groups; a component of phospholipids and triglycerides.

**glycogen** (gly' ko jen) An energy storage polysaccharide found in animals and fungi; a branched-chain polymer of glucose, similar to starch.

**glycolipid** A lipid to which sugars are attached.

**glycolysis** (gly kol' li sis) [Gk. *gleukos*: sugar + *lysis*: break apart] The enzymatic breakdown of glucose to pyruvic acid.

**glycoprotein** A protein to which sugars are attached.

**glycosidic linkage** Bond between carbohydrate (sugar) molecules through an intervening oxygen atom ( $-O-$ ).

**glycosylation** The addition of carbohydrates to another type of molecule, such as a protein.

**glyoxysome** (gly ox' ee soam) An organelle found in plants, in which stored lipids are converted to carbohydrates.

**Golgi apparatus** (goal' jee) A system of concentrically folded membranes found in the cytoplasm of eukaryotic cells; functions in secretion from cell by exocytosis.

**gonad** (go' nad) [Gk. *gone*: seed] An organ that produces gametes in animals: either an ovary (female gonad) or testis (male gonad).

**gonadotropin** A type of trophic hormone that stimulates the gonads.

**gonadotropin-releasing hormone (GnRH)**

Hormone produced by the hypothalamus that stimulates the anterior pituitary to secrete ("release") gonadotropins.

**Gondwana** The large southern land mass that existed from the Cambrian (540 mya) to the Jurassic (138 mya). Present-day remnants are South America, Africa, India, Australia, and Antarctica.

**grafting** Artificial transplantation of tissue from one organism to another. In horticulture, the transfer of a bud or stem segment from one plant onto the root of another as a form of asexual reproduction.

**Gram stain** A differential purple stain useful in characterizing bacteria. The peptidoglycan-rich cell walls of Gram-positive bacteria stain purple; cell walls of Gram-negative bacteria generally stain orange.

**gravitropism** [Gk. *tropos*: to turn] A directed plant growth response to gravity.

**gray matter** In the nervous system, tissue that is rich in neuronal cell bodies. (Contrast with white matter.)

**greenhouse gases** Gases in the atmosphere, such as carbon dioxide and methane, that are transparent to sunlight, but trap heat radiating from Earth's surface, causing heat to build up at Earth's surface.

**gross primary production** The amount of energy captured by the primary producers in a community.

**gross primary productivity (GPP)** The rate at which the primary producers in a community turn solar energy into stored chemical energy via photosynthesis.

**ground meristem** That part of an apical meristem that gives rise to the ground tissue system of the primary plant body.

**ground tissue system** Those parts of the plant body not included in the dermal or vascular tissue systems. Ground tissues function in storage, photosynthesis, and support.

**growth** An increase in the size of the body and its organs by cell division and cell expansion.

**growth factor** A chemical signal that stimulates cells to divide.

**growth hormone** A peptide hormone released by the anterior pituitary that stimulates many anabolic processes.

**guanine (G)** (gwan' een) A nitrogen-containing base found in DNA, RNA, and GTP.

**guard cells** In plants, specialized, paired epidermal cells that surround and control the opening of a stoma (pore). See stoma.

**guild** In ecology, a group of species that exploit the same resource, but in slightly different ways.

**gustation** The sense of taste.

**gut** An animal's digestive tract.

## - H -

**habitat** The particular environment in which an organism lives. A *habitat patch* is an area of a particular habitat surrounded by other habitat types that may be less suitable for that organism.

**hair cell** A type of mechanoreceptor in animals. Detects sound waves and other forms of motion in air or water.

**half-life** The time required for half of a sample of a radioactive isotope to decay to its stable, nonradioactive form, or for a drug or other substance to reach half its initial dosage.

**halophyte** (hal' oh fyte) [Gk. *halos*: salt + *phyton*: plant] A plant that grows in a saline (salty) environment.

**Hamilton's rule** The principle that, for an apparent altruistic behavior to be adaptive, the fitness benefit of that act to the recipient times the degree of relatedness of the performer and the recipient must be greater than the cost to the performer.

**haplodiploidy** A sex determination mechanism in which diploid individuals (which develop from fertilized eggs) are female and haploid individuals (which develop from unfertilized eggs) are male; typical of hymenopterans.

**haploid** (hap' loid) [Gk. *haploides*: single] Having a chromosome complement consisting of just one copy of each chromosome; designated *1n* or *n*. (Contrast with diploid.)

**haplontic** A type of life cycle in which the zygote is the only diploid cell and mitosis occurs only in haploid cells. (Contrast with diplontic.)

**haplotype** Linked nucleotide sequences that are usually inherited as a unit (as a "sentence" rather than as individual "words").

**Hardy-Weinberg equilibrium** In a sexually reproducing population, the allele frequency at a given locus that is not being acted on by agents of evolution; the conditions that would result in no evolution in a population.

**haustorium** (haw stor' ee um) (plural: haustoria) [L. *haustus*: draw up] A specialized hypha or other structure by which fungi and some parasitic plants draw nutrients from a host plant.

**Haversian systems** Units of organization in compact bone that reflect the action of intercommunicating osteoblasts.

**heart** In circulatory systems, a muscular pump that moves extracellular fluid around the body.

**heat of vaporization** The energy that must be supplied to convert a molecule from a liquid to a gas at its boiling point.

**heat shock proteins** Chaperone proteins expressed in cells exposed to high or low temperatures or other forms of environmental stress.

**helical** Shaped like a screw or spring; this shape occurs in DNA and proteins.

**helper T cells** See T-helper cells.

**hemiparasite** A parasitic plant that can photosynthesize, but derives water and mineral nutrients from the living body of another plant. (Contrast with holoparasite.)

**hemizygous** (hem' ee zie' gus) [Gk. *hemi*: half + *zygotos*: joined] In a diploid organism, having only one allele for a given trait, typically the case for X-linked genes in male mammals and Z-linked genes in female birds. (Contrast with homozygous, heterozygous.)

**hemoglobin** (hee' mo glow bin) [Gk. *heama*: blood + L. *globus*: globe] Oxygen-transporting protein found in the red blood cells of vertebrates (and found in some invertebrates).

**Hensen's node** In avian embryos, a structure at the anterior end of the primitive groove; determines the fates of cells passing over it during gastrulation.

**hepatic** (heh pat' ik) [Gk. *hepar*: liver] Pertaining to the liver.

**herbivore** (ur' bi vore) [L. *herba*: plant + *vorare*: to devour] An animal that eats plant tissues. (Contrast with carnivore, detritivore, omnivore.)

**heritable trait** A trait that is at least partly determined by genes.

**hermaphroditism** (her maf' row dite ism) The coexistence of both female and male sex organs in the same organism.

**hetero-** [Gk.: *heteros*: other, different] A prefix indicating two or more different conditions, structures, or processes. (Contrast with homo-.)

**heterochrony** Alteration in the timing of developmental events, leading to different results in the adult organism.

**heterocyst** A large, thick-walled cell type in the filaments of certain cyanobacteria that performs nitrogen fixation.

**heteromorphic** (het' er oh more' fizik) [Gk. *heteros*: different + *morphe*: form] Having a different form or appearance, as two heteromorphic life stages of a plant. (Contrast with isomorphic.)

**heterosporous** (het' er os' por us) Producing two types of spores, one of which gives rise to a female megasporangium and the other to a male microsporangium. (Contrast with homosporous.)

**heterosis** The superior fitness of heterozygous offspring as compared with that of their dissimilar homozygous parents. Also called hybrid vigor.

**heterotherm** An animal that regulates its body temperature at a constant level at some times but not others, such as a hibernator.

**heterotroph** (het' er oh trof) [Gk. *heteros*: different + *trophe*: feed] An organism that requires pre-formed organic molecules as food. (Contrast with autotroph.)

**heterotrophic succession** Succession in detritus-based communities, which differs from other types of succession in taking place without the participation of plants.

**heterotypic** Pertaining to adhesion of cells of different types. (Contrast with homotypic.)

**heterozygous** (het' er oh zie' gus) [Gk. *heteros*: different + *zygotos*: joined] In diploid organisms, having different alleles of a given gene on the pair of homologs carrying that gene. (Contrast with homozygous.)

**hexose** [Gk. *hex*: six] A sugar containing six carbon atoms.

**hibernation** [L. *hibernum*: winter] The state of inactivity of some animals during winter; marked by a drop in body temperature and metabolic rate.

**hierarchical sequencing** An approach to DNA sequencing in which genetic markers are mapped and DNA sequences are aligned by matching overlapping sites of known sequence. (Contrast with shotgun sequencing.)

**high-density lipoproteins (HDLs)** Lipoproteins that remove cholesterol from tissues and carry it to the liver; HDLs are the “good” lipoproteins associated with good cardiovascular health.

**high-throughput sequencing** Rapid DNA sequencing on a micro scale in which many fragments of DNA are sequenced in parallel.

**highly repetitive sequences** Short (less than 100 bp), nontranscribed DNA sequences, repeated thousands of times in tandem arrangements.

**hindbrain** The region of the developing vertebrate brain that gives rise to the medulla, pons, and cerebellum.

**hippocampus** [Gr. sea horse] A part of the forebrain that takes part in long-term memory formation.

**histamine** (hiss’ tah meen) A substance released by damaged tissue, or by mast cells in response to allergens. Histamine increases vascular permeability, leading to edema (swelling).

**histone** Any one of a group of proteins forming the core of a nucleosome, the structural unit of a eukaryotic chromosome.

**HIV** Human immunodeficiency virus, the retrovirus that causes acquired immune deficiency syndrome (AIDS).

**holoparasite** A fully parasitic plant (i.e., one that does not perform photosynthesis).

**homeobox** 180-base-pair segment of DNA found in certain homeotic genes; regulates the expression of other genes and thus controls large-scale developmental processes.

**homeostasis** (home’ ee o sta’ sis) [Gk. *homos*: same + *stasis*: position] The maintenance of a steady state, such as a constant temperature or a stable social structure, by means of physiological or behavioral feedback responses.

**homeotic genes** Genes that act during development to determine the formation of an organ from a region of the embryo.

**homeotic mutation** Mutation in a homeotic gene that results in the formation of a different organ than that normally made by a region of the embryo.

**homo-** [Gk. *homos*: same] A prefix indicating two or more similar conditions, structures, or processes. (Contrast with hetero-.)

**homolog** (1) In cytogenetics, one of a pair (or larger set) of chromosomes having the same overall genetic composition and sequence. In diploid organisms, each chromosome inherited from one parent is matched by an identical (except for mutational changes) chromosome—its homolog—from the other parent. (2) In evolutionary biology, one of two or more features in different species that are similar by reason of descent from a common ancestor.

**homology** (ho mol’ o jee) [Gk. *homologia*: of one mind; agreement] A similarity between two or more features that is due to inheritance from a common ancestor. The structures are said to be *homologous*, and each is a *homolog* of the others. (Contrast with analogy.)

**homoplasy** (home’ uh play zee) [Gk. *homos*: same + *plastikos*: shape, mold] The presence in multiple groups of a trait that is not inherited from the common ancestor of those groups. Can result from convergent evolution, evolutionary reversal, or parallel evolution.

**homosporous** Producing a single type of spore that gives rise to a single type of gametophyte, bearing both female and male reproductive organs. (Contrast with heterosporous.)

**homotypic** Pertaining to adhesion of cells of the same type. (Contrast with heterotypic.)

**homozygous** (home’ oh zie’ gus) [Gk. *homos*: same + *zygotos*: joined] In diploid organisms, having identical alleles of a given gene on both homologous chromosomes. An individual may be a homozygote with respect to one gene and a heterozygote with respect to another. (Contrast with heterozygous.)

**horizons** The horizontal layers of a soil profile, including the topsoil (A horizon), subsoil (B horizon) and parent rock or bedrock (C horizon)

**hormone** (hore’ mone) [Gk. *hormon*: to excite, stimulate] A chemical signal produced in minute amounts at one site in a multicellular organism and transported to another site where it acts on target cells.

**host** An organism that harbors a parasite or symbiont and provides it with nourishment.

**Hox genes** Conserved homeotic genes found in vertebrates, *Drosophila*, and other animal groups. Hox genes contain the homeobox domain and specify pattern and axis formation in these animals.

**human chorionic gonadotropin (hCG)** A hormone secreted by the placenta which sustains the corpus luteum and helps maintain pregnancy.

**humoral immune response** The response of the immune system mediated by B cells that produces circulating antibodies active against extracellular bacterial and viral infections. (Contrast with cellular immune response.)

**humus** (hew’ mus) The partly decomposed remains of plants and animals on the surface of a soil.

**hybrid** (high’ brid) [L. *hybrida*: mongrel] (1) The offspring of genetically dissimilar parents. (2) In molecular biology, a double helix formed of nucleic acids from different sources.

**hybridize** (1) In genetics, to combine the genetic material of two distinct species or of two distinguishable populations within a species. (2) In molecular biology, to form a double-stranded nucleic acid in which the two strands originate from different sources.

**hybrid vigor** See heterosis.

**hybridoma** A cell produced by the fusion of an antibody-producing cell with a myeloma (tumor) cell; it produces monoclonal antibodies.

**hydrocarbon** A compound containing only carbon and hydrogen atoms.

**hydrogen bond** A weak electrostatic bond which arises from the attraction between the slight positive charge on a hydrogen atom and a slight negative charge on a nearby oxygen or nitrogen atom.

**hydrologic cycle** The movement of water from the oceans to the atmosphere, to the soil, and back to the oceans.

**hydrolysis reaction** (high drol’ uh sis) [Gk. *hydro*: water + *lysis*: break apart] A chemical reaction that breaks a bond by inserting the components

of water ( $\text{AB} + \text{H}_2\text{O} \rightarrow \text{AH} + \text{BOH}$ ). (Contrast with condensation reaction.)

**hydrophilic** (high dro fill’ ik) [Gk. *hydro*: water + *philia*: love] Having an affinity for water. (Contrast with hydrophobic.)

**hydrophobic** (high dro foe’ bik) [Gk. *hydro*: water + *phobia*: fear] Having no affinity for water. Uncharged and nonpolar groups of atoms are hydrophobic. (Contrast with hydrophilic.)

**hydroponic** Pertaining to a method of growing plants with their roots suspended in nutrient solutions instead of soil.

**hydrostatic pressure** Pressure generated by compression of liquid in a confined space. Generated in plants, fungi, and some protists with cell walls by the osmotic uptake of water. Generated in animals with closed circulatory systems by the beating of a heart.

**hydrostatic skeleton** A fluid-filled body cavity that transfers forces from one part of the body to another when acted on by surrounding muscles.

**hydroxyl group** The —OH group found on alcohols and sugars.

**hyper-** [Gk. *hyper*: above, over] Prefix indicating above, higher, more. (Contrast with hypo-.)

**hyperpolarization** A change in the resting potential across a membrane so that the inside of a cell becomes more negative compared with the outside of the cell. (Contrast with depolarization.)

**hypersensitive response** A defensive response of plants to microbial infection in which phytoalexins and pathogenesis-related proteins are produced and the infected tissue undergoes apoptosis to isolate the pathogen from the rest of the plant.

**hypertonic** Having a greater solute concentration. Said of one solution compared with another. (Contrast with hypotonic, isotonic.)

**hypha** (high’ fuh) (plural: hyphae) [Gk. *hyphē*: web] In the fungi and oomycetes, any single filament.

**hypo-** [Gk. *hypo*: beneath, under] Prefix indicating underneath, below, less. (Contrast with hyper-.)

**hypoblast** The lower tissue portion of the avian blastula which is joined to the epiblast at the margins of the blastodisc.

**hypothalamus** The part of the brain lying below the thalamus; it coordinates water balance, reproduction, temperature regulation, and metabolism.

**hypothermia** Below-normal body temperature.

**hypothesis** A tentative answer to a question, from which testable predictions can be generated. (Contrast with theory.)

**hypotonic** Having a lesser solute concentration. Said of one solution in comparing it to another. (Contrast with hypertonic, isotonic.)

**hypoxia** A deficiency of oxygen.

- - -

**ileum** The final segment of the small intestine.

**imbibition** Water uptake by a seed; first step in germination.

**immediate hypersensitivity** A rapid, extensive overreaction of the immune system against an allergen, resulting in the release of large amounts of histamine. (Contrast with delayed hypersensitivity.)

**immediate memory** A form of memory for events happening in the present that is almost

perfectly photographic, but lasts only seconds. (Contrast with short-term memory, long-term memory.)

**immune system** [L. *immunis*: exempt from] A system in an animal that recognizes and attempts to eliminate or neutralize foreign substances such as bacteria, viruses, and pollutants.

**immunoassay** The use of antibodies to measure the concentration of an antigen in a sample.

**immunoglobulins** A class of proteins containing a tetramer consisting of four polypeptide chains—two identical light chains and two identical heavy chains—held together by disulfide bonds; active as receptors and effectors in the immune system.

**immunological memory** The capacity to more rapidly and massively respond to a second exposure to an antigen than occurred on first exposure.

**imperfect flower** A flower lacking either functional stamens or functional carpels. (Contrast with perfect flower.)

**implantation** The process by which the early mammalian embryo becomes attached to and embedded in the lining of the uterus.

**imprinting** In animal behavior, a rapid form of learning in which an animal learns, during a brief critical period, to make a particular response, which is maintained for life, to some object or other organism. *See also* genomic imprinting.

**in vitro** [L. in glass] A biological process occurring outside of the organism, in the laboratory. (Contrast with *in vivo*.)

**in vivo** [L. alive] A biological process occurring within a living organism or cell. (Contrast with *in vitro*.)

**inbreeding** Breeding among close relatives.

**inclusive fitness** The sum of an individual's genetic contribution to subsequent generations both via production of its own offspring and via its influence on the survival of relatives who are not direct descendants.

**incomplete cleavage** A pattern of cleavage that occurs in many eggs that have a lot of yolk, in which the cleavage furrows do not penetrate all of it. (*See also* discoidal cleavage, superficial cleavage; contrast with complete cleavage.)

**incomplete dominance** Condition in which the heterozygous phenotype is intermediate between the two homozygous phenotypes.

**incomplete metamorphosis** Insect development in which changes between instars are gradual.

**independent assortment** During meiosis, the random separation of genes carried on nonhomologous chromosomes into gametes so that inheritance of these genes is random. This principle was articulated by Mendel as his second law.

**indeterminate growth** A open-ended growth pattern in which an organism or organ continues to grow as long as it lives; characteristic of some animals and of plant shoots and roots. (Contrast with determinate growth.)

**indirect transduction** Cell signaling mechanism in which a second messenger mediates the interaction between receptor binding and cellular response. (Contrast with direct transduction.)

**individual fitness** That component of inclusive fitness resulting from an organism producing its own offspring. (Contrast with kin selection.)

**induced fit** A change in the shape of an enzyme caused by binding to its substrate that exposes the active site of the enzyme.

**induced mutation** A mutation resulting from exposure to a mutagen from outside the cell. (Contrast with spontaneous mutation.)

**induced pluripotent stem cells (iPS cells)** Multipotent or pluripotent animal stem cells produced from differentiated cells *in vitro* by the addition of several genes that are expressed.

**inducer** (1) A compound that stimulates the synthesis of a protein. (2) In embryonic development, a substance that causes a group of target cells to differentiate in a particular way.

**inducible** Produced only in the presence of a particular compound or under particular circumstances. (Contrast with constitutive.)

**induction** In embryonic development, the process by which a factor produced and secreted by certain cells determines the fates of other cells.

**inflammation** A nonspecific defense against pathogens; characterized by redness, swelling, pain, and increased temperature.

**inflorescence** A structure composed of several to many flowers.

**inflorescence meristem** A meristem that produces floral meristems as well as other small leafy structures (bracts).

**ingroup** In a phylogenetic study, the group of organisms of primary interest. (Contrast with outgroup.)

**inhibitor** A substance that blocks a biological process.

**initials** Cells that perpetuate plant meristems, comparable to animal stem cells. When an initial divides, one daughter cell develops into another initial, while the other differentiates into a more specialized cell.

**initiation** In molecular biology, the beginning of transcription or translation.

**initiation complex** In protein translation, a combination of a small ribosomal subunit, an mRNA molecule, and the tRNA charged with the first amino acid coded for by the mRNA; formed at the onset of translation.

**initiation site** The part of a promoter where transcription begins.

**inner cell mass** Derived from the mammalian blastula (bastocyst), the inner cell mass will give rise to the yolk sac (via hypoblast) and embryo (via epiblast).

**inositol trisphosphate (IP<sub>3</sub>)** An intracellular second messenger derived from membrane phospholipids.

**inspiratory reserve volume** The amount of air that can be inhaled above the normal tidal inspiration. (Contrast with expiratory reserve volume, tidal volume, vital capacity.)

**instar** (in' star) An immature stage of an insect between molts.

**insulin** (in' su lin) [L. *insula*: island] A hormone synthesized in islet cells of the pancreas that promotes the conversion of glucose into the storage material, glycogen.

**integrin** In animals, a transmembrane protein that mediates the attachment of epithelial cells to the extracellular matrix.

**integument** [L. *integumentum*: covering] A protective surface structure. In gymnosperms and angiosperms, a layer of tissue around the ovule which will become the seed coat.

**intercostal muscles** Muscles between the ribs that can augment breathing movements by elevating and suppressing the rib cage.

**interference competition** Competition in which individuals actively interfere with one another's access to resources. (Contrast with exploitation competition.)

**interference RNA (RNAi)** See RNA interference.

**interferon** A glycoprotein produced by virus-infected animal cells; increases the resistance of neighboring cells to the virus.

**intermediate filaments** Components of the cytoskeleton whose diameters fall between those of the larger microtubules and those of the smaller microfilaments.

**internal environment** In multicellular organisms, the extracellular fluid surrounding the cells.

**internal fertilization** The release of sperm into the female reproductive tract; typical of most terrestrial animals. (Contrast with external fertilization.)

**internal gills** Gills enclosed in protective body cavities; typical of mollusks, arthropods, and fishes.

**interneuron** A neuron that communicates information between two other neurons.

**internode** The region between two nodes of a plant stem.

**interphase** In the cell cycle, the period between successive nuclear divisions during which the chromosomes are diffuse and the nuclear envelope is intact. During interphase the cell is most active in transcribing and translating genetic information.

**interspecific competition** Competition between members of two or more species. (Contrast with intraspecific competition.)

**interstitial fluid** Extracellular fluid that is not contained in the vessels of a circulatory system.

**intestine** The portion of the gut following the stomach, in which most digestion and absorption occurs.

**intraspecific competition** Competition among members of the same species. (Contrast with interspecific competition.)

**intrinsic rate of increase (r)** The rate at which a population can grow when its density is low and environmental conditions are highly favorable.

**intron** Portion of a gene within the coding region that is transcribed into pre-mRNA but is spliced out prior to translation. (Contrast with exon.)

**invasive species** An exotic species that reproduces rapidly, spreads widely, and has negative effects on the native species of the region to which it has been introduced.

**invasiveness** The ability of a pathogen to multiply in a host's body. (Contrast with toxicity.)

**inversion** A rare 180° reversal of the order of genes within a segment of a chromosome.

**ion** (eye' on) [Gk. *ion*: wanderer] An electrically charged particle that forms when an atom gains or loses one or more electrons.

**ion channel** An integral membrane protein that allows ions to diffuse across the membrane in which it is embedded.

**ionic bond** An electrostatic attraction between positively and negatively charged ions.

**ionotropic receptors** A receptor that directly alters membrane permeability to a type of ion when it combines with its ligand.

**iris** (eye' ris) [Gk. *iris*: rainbow] The round, pigmented membrane that surrounds the pupil of the eye and adjusts its aperture to regulate the amount of light entering the eye.

**island biogeography** A theory proposing that the number of species on an island (or in another geographically defined and isolated area) represents a balance, or equilibrium, between the rate at which species immigrate to the island and the rate at which resident species go extinct.

**islets of Langerhans** Clusters of hormone-producing cells in the pancreas.

**iso-** [Gk. *iso*: equal] Prefix used for two separate entities that share some element of identity.

**isogamous** Having male and female gametes that are morphologically identical. (Contrast with anisogamous.)

**isomers** Molecules consisting of the same numbers and kinds of atoms, but differing in the bonding patterns by which the atoms are held together.

**isomorphic** (eye so more' fik) [Gk. *isos*: equal + *morphe*: form] Having the same form or appearance, as when the haploid and diploid life stages of an organism appear identical. (Contrast with heteromorphic.)

**isotonic** Having the same solute concentration; said of two solutions. (Contrast with hypertonic, hypotonic.)

**isotope** (eye' so tope) [Gk. *isos*: equal + *topos*: place] Isotopes of a given chemical element have the same number of protons in their nuclei (and thus are in the same position on the periodic table), but differ in the number of neutrons.

**isozymes** Enzymes of an organism that have somewhat different amino acid sequences but catalyze the same reaction.

**iteroparous** [L. *itero*, to repeat + *pario*, to beget] Reproducing multiple times in a lifetime. (Contrast with semelparous.)

### - J -

**jejunum** (jih jew' num) The middle division of the small intestine, where most absorption of nutrients occurs. (See duodenum, ileum.)

**jelly coat** The outer protective layer of a sea urchin egg, which triggers an acrosomal reaction in sperm.

**joint** In skeletal systems, a junction between two or more bones.

**juvenile hormone** In insects, a hormone maintaining larval growth and preventing maturation or pupation.

### - K -

**K-strategist** A species whose life history strategy allows it to persist at or near the carrying capacity (*K*) of its environment. (Contrast with *r*-strategist.)

**karyogamy** The fusion of nuclei of two cells. (Contrast with plasmogamy.)

**karyotype** The number, forms, and types of chromosomes in a cell.

**keystone species** Species that have a dominant influence on the composition of a community.

**kidneys** A pair of excretory organs in vertebrates.

**kin selection** That component of inclusive fitness resulting from helping the survival of rela-

tives containing the same alleles by descent from a common ancestor. (Contrast with individual fitness.)

**kinase** See protein kinase.

**kinetic energy** (kuh-net' ik) [Gk. *kinetos*: moving] The energy associated with movement. (Contrast with potential energy.)

**kinetochore** (kuh net' oh core) Specialized structure on a centromere to which microtubules attach.

**knockout** A molecular genetic method in which a single gene of an organism is permanently inactivated.

**Koch's postulates** A set of rules for establishing that a particular microorganism causes a particular disease.

**Krebs cycle** See citric acid cycle.

### - L -

**lagging strand** In DNA replication, the daughter strand that is synthesized in discontinuous stretches. (See Okazaki fragments.)

**larva** (plural: larvae) [L. *lares*: guiding spirits] An immature stage of any animal that differs dramatically in appearance from the adult.

**lateral** [L. *latus*: side] Pertaining to the side.

**lateral gene transfer** The transfer of genes from one species to another, common among bacteria and archaea.

**lateral line** A sensory system in fishes consisting of a canal filled with water and hair cells running down each side under the surface of the skin, which senses disturbances in the surrounding water.

**lateral meristem** Either of the two meristems, the vascular cambium and the cork cambium, that give rise to a plant's secondary growth.

**lateral root** A root extending outward from the taproot in a taproot system; typical of eudicots.

**laticifers** (luh tiss' uh furs) In some plants, elongated cells containing secondary plant products such as latex.

**Laurasia** The northernmost of the two large continents produced by the breakup of Pangaea.

**laws of thermodynamics** [Gk. *thermos*: heat + *dynamis*: power] Laws derived from studies of the physical properties of energy and the ways energy interacts with matter. (See also first law of thermodynamics, second law of thermodynamics.)

**leaching** In soils, a process by which mineral nutrients in upper soil horizons are dissolved in water and carried to deeper horizons, where they are unavailable to plant roots.

**leading strand** In DNA replication, the daughter strand that is synthesized continuously. (Contrast with lagging strand.)

**leaf** (plural: leaves) In plants, the chief organ of photosynthesis.

**leaf primordium** (plural: primordia) An outgrowth on the side of the shoot apical meristem that will eventually develop into a leaf.

**leghemoglobin** In nitrogen-fixing plants, an oxygen-carrying protein in the cytoplasm of nodule cells that transports enough oxygen to the nitrogen-fixing bacteria to support their respiration, while keeping free oxygen concentrations low enough to protect nitrogenase.

**lek** A display ground within which male animals compete for and defend small display areas as a means of demonstrating their territorial prowess and winning opportunities to mate.

**lens** In the vertebrate eye, a crystalline protein structure that makes fine adjustments in the focus of images falling on the retina.

**lenticel** (len' ti sill) In plants, a spongy region in the periderm that allows gas exchange.

**leptin** A hormone produced by fat cells that is believed to provide feedback information to the brain about the status of the body's fat reserves.

**leukocyte** See white blood cell.

**lichen** (lie' kun) An organism resulting from the symbiotic association of a fungus and either a cyanobacterium or a unicellular alga.

**life cycle** The entire span of the life of an organism from the moment of fertilization (or asexual generation) to the time it reproduces in turn.

**life history strategy** The way in which an organism partitions its time and energy among growth, maintenance, and reproduction.

**ligament** A band of connective tissue linking two bones in a joint.

**ligand** (lig' and) Any molecule that binds to a receptor site of another (usually larger) molecule.

**light reactions** The initial phase of photosynthesis, in which light energy is converted into chemical energy.

**light-independent reactions** The phase of photosynthesis in which chemical energy captured in the light reactions is used to drive the reduction of CO<sub>2</sub> to form carbohydrates.

**lignin** A complex, hydrophobic polyphenolic polymer in plant cell walls that crosslinks other wall polymers, strengthening the walls, especially in wood.

**limbic system** A group of evolutionarily primitive structures in the vertebrate telencephalon that are involved in emotions, drives, instinctive behaviors, learning, and memory.

**liming** Application of compounds such as calcium carbonate, calcium hydroxide, or magnesium carbonate—commonly known as lime—to soil to reverse its acidification and increase the availability of calcium to plants.

**limiting resource** The required resource whose supply most strongly influences the size of a population.

**lineage species concept** The definition of a species as a branch on the tree of life, which has a history that starts at a speciation event and ends either at extinction or at another speciation event. (Contrast with biological species concept; morphological species concept.)

**linkage** Association between genes on the same chromosome such that they do not show random assortment and seldom recombine; the closer the genes, the lower the frequency of recombination.

**lipase** (lip' ase; lye' pase) An enzyme that digests fats.

**lipid** (lip' id) [Gk. *lipos*: fat] Nonpolar, hydrophobic molecules that include fats, oils, waxes, steroids, and the phospholipids that make up biological membranes.

**lipid bilayer** See phospholipid bilayer.

**liver** A large digestive gland. In vertebrates, it secretes bile and is involved in the formation of blood.

**loam** A type of soil consisting of a mixture of sand, silt, clay, and organic matter. One of the best soil types for agriculture.

**locus** (low' kus) (plural: loci, low' sigh) In genetics, a specific location on a chromosome. May be considered synonymous with *gene*.

**logistic growth** Growth, especially in the size of an organism or in the number of organisms in a population, that slows steadily as the entity approaches its maximum size. (Contrast with exponential growth.)

**long-day plant (LDP)** A plant that requires long days (actually, short nights) in order to flower.

**long-term depression (LTD)** A long-lasting decrease in the responsiveness resulting from continuous, repetitive, low-level stimulation. (Contrast with long-term potentiation.)

**long-term potentiation (LTP)** A long-lasting increase in the responsiveness of a neuron resulting from a period of intense stimulation. (Contrast with long-term depression.)

**loop of Henle** (her' lee) Long, hairpin loop of the mammalian renal tubule that runs from the cortex down into the medulla and back to the cortex; creates a concentration gradient in the interstitial fluids in the medulla.

**lophophore** A U-shaped fold of the body wall with hollow, ciliated tentacles that encircles the mouth of animals in several different groups. Used for filtering prey from the surrounding water.

**loss of function mutation** A mutation that results in the loss of a functional protein. (Contrast with gain of function mutation.)

**low-density lipoproteins (LDLs)** Lipoproteins that transport cholesterol around the body for use in biosynthesis and for storage; LDLs are the "bad" lipoproteins associated with a high risk of cardiovascular disease.

**lumen** (loo' men) [L. *lumen*: light] The open cavity inside any tubular organ or structure, such as the gut or a renal tubule.

**lung** An internal organ specialized for respiratory gas exchange with air.

**luteinizing hormone (LH)** A gonadotropin produced by the anterior pituitary that stimulates the gonads to produce sex hormones.

**lymph** [L. *lymphe*: liquid] A fluid derived from blood and other tissues that accumulates in intercellular spaces throughout the body and is returned to the blood by the lymphatic system.

**lymph node** A specialized structure in the vessels of the lymphatic system. Lymph nodes contain lymphocytes, which encounter and respond to foreign cells and molecules in the lymph as it passes through the vessels.

**lymphatic system** A system of vessels that returns interstitial fluid to the blood.

**lymphocyte** One of the two major classes of white blood cells; includes T cells, B cells, and other cell types important in the immune system.

**lymphoid tissues** Tissues of the immune system that are dispersed throughout the body, consisting of the thymus, spleen, bone marrow, and lymph nodes.

**lysis** (lie' sis) [Gk. *lysis*: break apart] Bursting of a cell.

**lysogeny** A form of viral replication in which the virus becomes incorporated into the host chromosome and remains inactive. Also called a lysogenic cycle. (Contrast with lytic cycle.)

**lysosome** (lie' so soam) [Gk. *lysis*: break away + *soma*: body] A membrane-enclosed organelle originating from the Golgi apparatus and containing hydrolytic enzymes. (Contrast with secondary lysosome.)

**lysozyme** (lie' so zyme) An enzyme in saliva, tears, and nasal secretions that hydrolyzes bacterial cell walls.

**lytic cycle** A viral reproductive cycle in which the virus takes over a host cell's synthetic machinery to replicate itself, then bursts (lyses) the host cell, releasing the new viruses. (Contrast with lysogeny.)

## - M -

**M phase** The portion of the cell cycle in which mitosis takes place.

**macroevolution** [Gk. *makros*: large] Evolutionary changes occurring over long time spans and usually involving changes in many traits. (Contrast with microevolution.)

**macromolecule** A giant (molecular weight > 1,000) polymeric molecule. The macromolecules are the proteins, polysaccharides, and nucleic acids.

**macronutrient** In plants, a mineral element required in concentrations of at least 1 milligram per gram of plant dry matter; in animals, a mineral element required in large amounts. (Contrast with micronutrient.)

**macrophage** (mac' roh faj) Phagocyte that engulfs pathogens by endocytosis.

**MADS box** DNA-binding domain in many plant transcription factors that is active in development.

**maintenance methylase** An enzyme that catalyzes the methylation of the new DNA strand when DNA is replicated.

**major histocompatibility complex (MHC)** A complex of linked genes, with multiple alleles, that control a number of cell surface antigens that identify self and can lead to graft rejection.

**malignant** Pertaining to a tumor that can grow indefinitely and/or spread from the original site of growth to other locations in the body. (Contrast with benign.)

**Malpighian tubule** (mal pee' gy un) A type of protonephridium found in insects.

**map unit** The distance between two genes as calculated from genetic crosses; a recombination frequency.

**marine** [L. *mare*: sea, ocean] Pertaining to or living in the ocean. (Contrast with aquatic, terrestrial.)

**mark-recapture method** A method of estimating population sizes of mobile organisms by capturing, marking, and releasing a sample of individuals, then capturing another sample at a later time.

**mass extinction** A period of evolutionary history during which rates of extinction are much higher than during intervening times.

**mass number** The sum of the number of protons and neutrons in an atom's nucleus.

**mast cells** Cells, typically found in connective tissue, that release histamine in response to tissue damage.

**maternal effect genes** Genes coding for morphogens that determine the polarity of the egg and larva in fruit flies.

**mating type** A particular strain of a species that is incapable of sexual reproduction with another member of the same strain but capable of sexual reproduction with members of other strains of the same species.

**maximum likelihood** A statistical method of determining which of two or more hypotheses

(such as phylogenetic trees) best fit the observed data, given an explicit model of how the data were generated.

**mechanically gated channel** A molecular channel that opens or closes in response to mechanical force applied to the plasma membrane in which it is inserted.

**mechanoreceptor** A cell that is sensitive to physical movement and generates action potentials in response.

**medulla** (meh dull' luuh) (1) The inner, core region of an organ, as in the adrenal medulla (adrenal gland) or the renal medulla (kidneys). (2) The portion of the brainstem that connects to the spinal cord.

**medusa** (plural: medusae) In cnidarians, a free-swimming, sexual life cycle stage shaped like a bell or an umbrella.

**megaphyll** The generally large leaf of a fern, horsetail, or seed plant, with several to many veins. (Contrast with microphyll.)

**megaspore** [Gk. *megas*: large + *spora*: to sow] In plants, a haploid spore that produces a female gametophyte.

**megastrobilus** In conifers, the female (seed-bearing) cone. (Contrast with microstrobilus.)

**meiosis** (my oh' sis) [Gk. *meiosis*: diminution] Division of a diploid nucleus to produce four haploid daughter cells. The process consists of two successive nuclear divisions with only one cycle of chromosome replication. In *meiosis I*, homologous chromosomes separate but retain their chromatids. The second division *meiosis II*, is similar to mitosis, in which chromatids separate.

**melatonin** A hormone released by the pineal gland. Involved in photoperiodicity and circadian rhythms.

**membrane potential** The difference in electrical charge between the inside and the outside of a cell, caused by a difference in the distribution of ions.

**membranous bone** A type of bone that develops by forming on a scaffold of connective tissue. (Contrast with cartilage bone.)

**memory cells** Long-lived lymphocytes produced by exposure to antigen. They persist in the body and are able to mount a rapid response to subsequent exposures to the antigen.

**Mendel's laws** See independent assortment; segregation.

**meristem** [Gk. *meristos*: divided] Plant tissue made up of undifferentiated actively dividing cells.

**meristem identity genes** In angiosperms, a group of genes whose expression initiates flower formation, probably by switching meristem cells from a vegetative to a reproductive fate.

**mesenchyme** (mez' en kyme) [Gk. *mesos*: middle + *enchyma*: infusion] Embryonic or unspecialized cells derived from the mesoderm.

**mesoderm** [Gk. *mesos*: middle + *derma*: skin] The middle of the three embryonic germ layers first delineated during gastrulation. Gives rise to the skeleton, circulatory system, muscles, excretory system, and most of the reproductive system.

**mesoglea** (mez' uh glee uh) [Gk. *mesos*: middle + *gloia*, glue] A thick, gelatinous noncellular layer that separates the two cellular tissue layers of ctenophores, cnidarians, and scyphozoans.

**mesophyll** (mez' uh fill) [Gk. *mesos*: middle + *phyllon*: leaf] Chloroplast-containing, photosynthetic cells in the interior of leaves.

**messenger RNA (mRNA)** Transcript of a region of one of the strands of DNA; carries information (as a sequence of codons) for the synthesis of one or more proteins.

**meta-** [Gk.: between, along with, beyond] Prefix denoting a change or a shift to a new form or level; for example, as used in metamorphosis.

**metabolic pathway** A series of enzyme-catalyzed reactions so arranged that the product of one reaction is the substrate of the next.

**metabolism** (meh tab' a lizm) [Gk. *metabolē*: change] The sum total of the chemical reactions that occur in an organism, or some subset of that total (as in respiratory metabolism).

**metabolome** The quantitative description of all the small molecules in a cell or organism.

**metabotropic receptor** A receptor that indirectly alters membrane permeability to a type of ion when it combines with its ligand.

**metagenomics** The practice of analyzing DNA from environmental samples without isolating intact organisms.

**metamorphosis** (met' a mor' fo sis) [Gk. *meta*: between + *morphe*: form, shape] A change occurring between one developmental stage and another, as for example from a tadpole to a frog. (See complete metamorphosis, incomplete metamorphosis.)

**metanephridia** The paired excretory organs of annelids.

**metaphase** (met' a phase) The stage in nuclear division at which the centromeres of the highly supercoiled chromosomes are all lying on a plane (the metaphase plane or plate) perpendicular to a line connecting the division poles.

**metapopulation** A population divided into subpopulations, among which there are occasional exchanges of individuals.

**metastasis** (meh tass' tuh sis) The spread of cancer cells from their original site to other parts of the body.

**methylation** The addition of a methyl group ( $-CH_3$ ) to a molecule.

**MHC** See major histocompatibility complex.

**micelle** A particle of lipid covered with bile salts that is produced in the duodenum and facilitates digestion and absorption of lipids.

**microclimate** A subset of climatic conditions in a small specific area, which generally differ from those in the environment at large, as in an animal's underground burrow.

**microevolution** Evolutionary changes below the species level, affecting allele frequencies. (Contrast with macroevolution.)

**microfibril** Crosslinked cellulose polymers, forming strong aggregates in the plant cell wall.

**microfilament** In eukaryotic cells, a fibrous structure made up of actin monomers. Microfilaments play roles in the cytoskeleton, in cell movement, and in muscle contraction.

**microglia** Glial cells that act as macrophages and mediators of inflammatory responses in the central nervous system.

**micronutrient** In plants, a mineral element required in concentrations of less than 100 micrograms per gram of plant dry matter; in animals, a mineral element required in concentrations of

less than 100 micrograms per day. (Contrast with macronutrient.)

**microphyll** A small leaf with a single vein, found in club mosses and their relatives. (Contrast with megaphyll.)

**micropyle** (mike' roh pile) [Gk. *mikros*: small + *pylon*: gate] Opening in the integument(s) of a seed plant ovule through which pollen grows to reach the female gametophyte within.

**microRNA** A small, noncoding RNA molecule, typically about 21 bases long, that binds to mRNA to inhibit its translation.

**microspore** [Gk. *mikros*: small + *spora*: to sow] In plants, a haploid spore that produces a male gametophyte.

**microstrobilus** In conifers, male pollen-bearing cone. (Contrast with megastrobilus.)

**microtubules** Tubular structures found in centrioles, spindle apparatus, cilia, flagella, and cytoskeleton of eukaryotic cells. These tubules play roles in the motion and maintenance of shape of eukaryotic cells.

**microvilli** (sing.: microvillus) Projections of epithelial cells, such as the cells lining the small intestine, that increase their surface area.

**midbrain** One of the three regions of the vertebrate brain. Part of the brainstem, it serves as a relay station for sensory signals sent to the cerebral hemispheres.

**middle lamella** (la mell' ah) [L. *lamina*: thin sheet] A layer of polysaccharides that separates plant cells; a shared middle lamella lies outside the primary walls of the two cells.

**mineral nutrients** Inorganic ions required by organisms for normal growth and reproduction.

**mismatch repair** A mechanism that scans DNA after it has been replicated and corrects any base-pairing mismatches.

**missense mutation** A change in a gene's sequence that results in a change in the sequence of the amino acid specified by the corresponding codon. (Contrast with frame-shift mutation, nonsense mutation, silent mutation.)

**mitochondrial matrix** The fluid interior of the mitochondrion, enclosed by the inner mitochondrial membrane.

**mitochondrion** (my' toe kon' dree un) (plural: mitochondria) [Gk. *mitos*: thread + *chondros*: grain] An organelle in eukaryotic cells that contains the enzymes of the citric acid cycle, the respiratory chain, and oxidative phosphorylation.

**mitosis** (my' toe' sis) [Gk. *mitos*: thread] Nuclear division in eukaryotes leading to the formation of two daughter nuclei, each with a chromosome complement identical to that of the original nucleus.

**model systems** Also known as model organisms, these include the small group of species that are the subject of extensive research. They are organisms that adapt well to laboratory situations and findings from experiments on them can apply across a broad range of species. Classic examples include white rats and the fruit fly *Drosophila*.

**moderately repetitive sequences** DNA sequences repeated 10–1,000 times in the eukaryotic genome. They include the genes that code for rRNAs and tRNAs, as well as the DNA in telomeres.

**Modern Synthesis** An understanding of evolutionary biology that emerged in the early twentieth century as the principles of evolution were

integrated with the principles of modern genetics.

**modularity** In evolutionary developmental biology, the principle that the molecular pathways that determine different developmental processes operate independently from one another. *See also developmental module.*

**mole** A quantity of a compound whose weight in grams is numerically equal to its molecular weight expressed in atomic mass units. Avogadro's number of molecules:  $6.023 \times 10^{23}$  molecules.

**molecular clock** The approximately constant rate of divergence of macromolecules from one another over evolutionary time; used to date past events in evolutionary history.

**molecular evolution** The scientific study of the mechanisms and consequences of the evolution of macromolecules.

**molecular tool kit** A set of developmental genes and proteins that is common to most animals and is hypothesized to be responsible for the evolution of their differing developmental pathways.

**molecular weight** The sum of the atomic weights of the atoms in a molecule.

**molecule** A chemical substance made up of two or more atoms joined by covalent bonds or ionic attractions.

**molting** The process of shedding part or all of an outer covering, as the shedding of feathers by birds or of the entire exoskeleton by arthropods.

**monoclonal antibody** Antibody produced in the laboratory from a clone of hybridoma cells, each of which produces the same specific antibody.

**monoculture** In agriculture, a large-scale planting of a single species of domesticated crop plant.

**monoecious** (mo nee' shus) [Gk. *mono*: one + *oikos*: house] Pertaining to organisms in which both sexes are "housed" in a single individual that produces both eggs and sperm. (In some plants, these are found in different flowers within the same plant.) Examples include corn, peas, earthworms, hydras. (Contrast with dioecious.)

**monohybrid cross** A mating in which the parents differ with respect to the alleles of only one locus of interest.

**monomer** [Gk. *mono*: one + *meros*: unit] A small molecule, two or more of which can be combined to form oligomers (consisting of a few monomers) or polymers (consisting of many monomers).

**monophyletic** (mon' oh fih leh' ik) [Gk. *mono*: one + *phylon*: tribe] Pertaining to a group that consists of an ancestor and all of its descendants. (Contrast with paraphyletic, polyphyletic.)

**monosaccharide** A simple sugar. Oligosaccharides and polysaccharides are made up of monosaccharides.

**monosomic** Pertaining to an organism with one less than the normal diploid number of chromosomes.

**monosynaptic reflex** A neural reflex that begins in a sensory neuron and makes a single synapse before activating a motor neuron.

**morphogen** A diffusible substance whose concentration gradient determines a developmental pattern in animals and plants.

**morphogenesis** (môr'fə jen'ē sis) [Gk. *morphe*: form + *genesis*: origin] The development of form; the overall consequence of determination, differentiation, and growth.

**morphological species concept** The definition of a species as a group of individuals that look alike. (Contrast with biological species concept; lineage species concept.)

**morphology** (môr'fə lōjē) [Gk. *morphe*: form + *logos*: study, discourse] The scientific study of organic form, including both its development and function.

**mosaic development** Pattern of animal embryonic development in which each blastomere contributes a specific part of the adult body. (Contrast with regulative development.)

**motif** See structural motif.

**motile** (mō' təl) Able to move from one place to another. (Contrast with sessile.)

**motor cortex** The region of the cerebral cortex that contains motor neurons that directly stimulate specific muscle fibers to contract.

**motor neuron** A neuron carrying information from the central nervous system to a cell that produces movement.

**motor proteins** Specialized proteins that use energy to change shape and move cells or structures within cells. See dynein, kinesin.

**motor unit** A motor neuron and the muscle fibers it controls.

**mouth** An opening through which food is taken in, located at the anterior end of a tubular gut.

**mRNA** See messenger RNA.

**mucosal epithelium** An epithelial cell layer containing cells that secrete mucus; found in the digestive and respiratory tracts. Also called mucosa.

**Müllerian mimicry** Convergence in appearance of two or more unpalatable species.

**multipotent** Having the ability to differentiate into a limited number of cell types. (Contrast with pluripotent, totipotent.)

**muscle fiber** A single muscle cell. In the case of skeletal muscle, a syncytial, multinucleate cell.

**muscle tissue** Excitable tissue that can contract through the interactions of actin and myosin; one of the four major tissue types in multicellular animals. There are three types of muscle tissue: skeletal, smooth, and cardiac.

**mutagen** (müt'əgən) [L. *mutare*: change + Gk. *genesis*: source] Any agent (e.g., chemicals, radiation) that increases the mutation rate.

**mutation** A change in the genetic material not caused by recombination.

**mutualism** A type of interaction between species that benefits both species.

**mycelium** (my'sēlē'ē yūm) [Gk. *mykes*: fungus] In the fungi, a mass of hyphae.

**mycorrhiza** (mī'kō rē'zā) (plural: mycorrhizae) [Gk. *mykes*: fungus + *rhiza*: root] An association of the root of a plant with the mycelium of a fungus.

**myelin** (mī'ēlin) Concentric layers of plasma membrane that form a sheath around some axons; myelin provides the axon with electrical insulation and increases the rate of transmission of action potentials.

**myocardial infarction** Blockage of an artery that carries blood to the heart muscle.

**myofibril** (mī'ō fī'bril) [Gk. *mys*: muscle + L. *fibrilla*: small fiber] A polymeric unit of actin or myosin in a muscle.

**myoglobin** (mī'ō glo'bēn) [Gk. *mys*: muscle + L. *globus*: sphere] An oxygen-binding molecule found in muscle. Consists of a heme unit and a single globin chain; carries less oxygen than hemoglobin.

**myosin** One of the two contractile proteins of muscle.

## - N -

**natural killer cell** A type of lymphocyte that attacks virus-infected cells and some tumor cells as well as antibody-labeled target cells.

**natural selection** The differential contribution of offspring to the next generation by various genetic types belonging to the same population. The mechanism of evolution proposed by Charles Darwin.

**nauplius** (naw' plee us) [Gk. *nauplios*: shellfish] A bilaterally symmetrical larval form typical of crustaceans.

**necrosis** (nēk'roh' sis) [Gk. *nekros*: death] Premature cell death caused by external agents such as toxins.

**negative feedback** In regulatory systems, information that decreases a regulatory response, returning the system to the set point. (Contrast with positive feedback.)

**negative regulation** A type of gene regulation in which a gene is normally transcribed, and the binding of a repressor protein to the promoter prevents transcription. (Contrast with positive regulation.)

**nematocyst** (nē mat'ō sist) [Gk. *nema*: thread + *kystis*: cell] An elaborate, threadlike structure produced by cells of jellyfishes and other cnidarians, used chiefly to paralyze and capture prey.

**nephron** (nēf'ron) [Gk. *nephros*: kidney] The functional unit of the kidney, consisting of a structure for receiving a filtrate of blood and a tubule that reabsorbs selected parts of the filtrate.

**Nernst equation** A mathematical statement that calculates the potential across a membrane permeable to a single type of ion that differs in concentration on the two sides of the membrane.

**nerve** A structure consisting of many neuronal axons and connective tissue.

**nervous tissue** Tissue specialized for processing and communicating information; one of the four major tissue types in multicellular animals.

**net primary productivity (NPP)** The rate at which energy captured by photosynthesis is incorporated into the bodies of primary producers bodies through growth and reproduction.

**net primary production** The amount of primary producer biomass made available for consumption by heterotrophs.

**neural network** An organized group of neurons that contains three functional categories of neurons—afferent neurons, interneurons, and efferent neurons—and is capable of processing information.

**neural tube** An early stage in the development of the vertebrate nervous system consisting of a hollow tube created by two opposing folds of the dorsal ectoderm along the anterior-posterior body axis.

**neurohormone** A chemical signal produced and released by neurons that subsequently acts as a hormone.

**neuromuscular junction** Synapse (point of contact) where a motor neuron axon stimulates a muscle fiber cell.

**neuron** (noor'ōn) [Gk. *neuron*: nerve] A nervous system cell that can generate and conduct action potentials along an axon to a synapse with another cell.

**neurotransmitter** A substance produced in and released by a neuron (the presynaptic cell) that diffuses across a synapse and excites or inhibits another cell (the postsynaptic cell).

**neurulation** Stage in vertebrate development during which the nervous system begins to form.

**neutral allele** An allele that does not alter the functioning of the proteins for which it codes.

**neutral theory** A view of molecular evolution that postulates that most mutations do not affect the amino acid being coded for, and that such mutations accumulate in a population at rates driven by genetic drift and mutation rates.

**neutron** (new' trōn) One of the three fundamental particles of matter (along with protons and electrons), with mass approximately 1 amu and no electrical charge.

**niche** (nitch) [L. *nidus*: nest] The set of physical and biological conditions a species requires to survive, grow, and reproduce. (See also fundamental niche, realized niche.)

**nitrate reduction** The process by which nitrate ( $\text{NO}_3^-$ ) is reduced to ammonia ( $\text{NH}_3$ ).

**nitric oxide (NO)** An unstable molecule (a gas) that serves as a second messenger causing smooth muscle to relax. In the nervous system it operates as a neurotransmitter.

**nitrifiers** Chemolithotrophic bacteria that oxidize ammonia to nitrate in soil and in seawater.

**nitrogen fixation** Conversion of atmospheric nitrogen gas ( $\text{N}_2$ ) into a more reactive and biologically useful form (ammonia), which makes nitrogen available to living things. Carried out by nitrogen-fixing bacteria, some of them free-living and others living within plant roots.

**nitrogenase** An enzyme complex found in nitrogen-fixing bacteria that mediates the stepwise reduction of atmospheric  $\text{N}_2$  to ammonia and which is strongly inhibited by oxygen.

**node** [L. *nodus*: knob, knot] In plants, a (sometimes enlarged) point on a stem where a leaf is or was attached.

**node of Ranvier** A gap in the myelin sheath covering an axon; the point where the axonal membrane can fire action potentials.

**nodule** A specialized structure in the roots of nitrogen-fixing plants that houses nitrogen-fixing bacteria, in which oxygen is maintained at a low level by leghemoglobin.

**noncompetitive inhibitor** A nonsubstrate that inhibits the activity of an enzyme by binding to a site other than its active site. (Contrast with competitive inhibitor.)

**noncyclic electron transport** In photosynthesis, the flow of electrons that forms ATP, NADPH, and  $\text{O}_2$ .

**nondisjunction** Failure of sister chromatids to separate in meiosis II or mitosis, or failure of homologous chromosomes to separate in meiosis I. Results in aneuploidy.

**nonpolar** Having electric charges that are evenly balanced from one end to the other. (Contrast with polar.)

**nonrandom mating** Selection of mates on the basis of a particular trait or group of traits.

**nonsense mutation** Change in a gene's sequence that prematurely terminates translation by changing one of its codons to a stop codon.

**nonsynonymous substitution** A change in a gene from one nucleotide to another that changes the amino acid specified by the corresponding codon (i.e., AGC → AGA, or serine → arginine). (Contrast with synonymous substitution.)

**norepinephrine** A neurotransmitter found in the central nervous system and also at the post-ganglionic nerve endings of the sympathetic nervous system. Also called noradrenaline.

**normal flora** Microorganisms that normally live and reproduce on or in the body without causing disease, and which form a nonspecific defense against pathogens by competing with them for space and nutrients.

**notochord** (no' tow kord) [Gk. *notos*: back + *chorde*: string] A flexible rod of gelatinous material serving as a support in the embryos of all chordates and in the adults of tunicates and lancelets.

**nucleic acid** (new klā' ik) A polymer made up of nucleotides, specialized for the storage, transmission, and expression of genetic information. DNA and RNA are nucleic acids.

**nucleic acid hybridization** A technique in which a single-stranded nucleic acid probe is made that is complementary to, and binds to, a target sequence, either DNA or RNA. The resulting double-stranded molecule is a hybrid.

**nucleoid** (new' klee oid) The region that harbors the chromosomes of a prokaryotic cell. Unlike the eukaryotic nucleus, it is not bounded by a membrane.

**nucleolus** (new klee' oh lus) A small, generally spherical body found within the nucleus of eukaryotic cells. The site of synthesis of ribosomal RNA.

**nucleoside** A nucleotide without the phosphate group; a nitrogenous base attached to a sugar.

**nucleosome** A portion of a eukaryotic chromosome, consisting of part of the DNA molecule wrapped around a group of histone molecules, and held together by another type of histone molecule. The chromosome is made up of many nucleosomes.

**nucleotide** The basic chemical unit in nucleic acids, consisting of a pentose sugar, a phosphate group, and a nitrogen-containing base.

**nucleotide substitution** A change of one base pair to another in a DNA sequence.

**nucleus** (new' klee us) [L. *nux*: kernel or nut] (1) In cells, the centrally located compartment of eukaryotic cells that is bounded by a double membrane and contains the chromosomes. (2) In the brain, an identifiable group of neurons that share common characteristics or functions.

**nutrient** A food substance; or, in the case of mineral nutrients, an inorganic element required for completion of the life cycle of an organism.

## - O -

**obligate anaerobe** An anaerobic prokaryote that cannot survive exposure to O<sub>2</sub>.

**odorant** A molecule that can bind to an olfactory receptor.

**oil** A triglyceride that is liquid at room temperature. (Contrast with fat.)

**Okazaki fragments** Newly formed DNA making up the lagging strand in DNA replication. DNA ligase links Okazaki fragments together to give a continuous strand.

**olfactory** [L. *olfacere*: to smell] Pertaining to the sense of smell (*olfaction*).

**oligodendrocyte** A type of glial cell that myelinates axons in the central nervous system.

**oligosaccharide** A polymer containing a small number of monosaccharides.

**ommatidia** [Gk. *omma*: eye] The units that make up the compound eye of some arthropods.

**omnivore** [L. *omnis*: everything + *vorare*: to devour] An organism that eats both animal and plant material. (Contrast with carnivore, detritivore, herbivore.)

**oncogene** [Gk. *onkos*: mass, tumor + *genes*: born] A gene that codes for a protein product that stimulates cell proliferation. Mutations in oncogenes that result in excessive cell proliferation can give rise to cancer.

**oocyte** See primary oocyte, secondary oocyte.

**oogenesis** (oh' eh jen e sis) [Gk. *oon*: egg + *genesis*: source] Gametogenesis leading to production of an ovum.

**oogonium** (oh' eh go' nee um) (plural: oogonia) (1) In some algae and fungi, a cell in which an egg is produced. (2) In animals, the diploid progeny of a germ cell in females.

**operator** The region of an operon that acts as the binding site for the repressor.

**open circulatory system** Circulatory system in which extracellular fluid leaves the vessels of the circulatory system, percolates between cells and through tissues, and then flows back into the circulatory system to be pumped out again. (Contrast with closed circulatory system.)

**operon** A genetic unit of transcription, typically consisting of several structural genes that are transcribed together; the operon contains at least two control regions: the promoter and the operator.

**opportunity cost** The sum of the benefits an animal forfeits by not being able to perform some other behavior during the time when it is performing a given behavior.

**opsin** (op' sin) [Gk. *opsis*: sight] The protein portion of the visual pigment rhodopsin. (See rhodopsin.)

**optic chiasm** [Gk. *chiasma*: cross] Structure on the lower surface of the vertebrate brain where the two optic nerves come together.

**optical isomers** Two isomers that are mirror images of each other.

**optimal foraging theory** The application of a cost-benefit approach to feeding behavior to identify the fitness value of feeding choices.

**orbital** A region in space surrounding the atomic nucleus in which an electron is most likely to be found.

**organ** [Gk. *organon*: tool] A body part, such as the heart, liver, brain, root, or leaf. Organs are composed of different tissues integrated to perform a distinct function. Organs, in turn, are integrated into organ systems.

**organ identity genes** In angiosperms, genes that specify the different organs of the flower. (Compare with homeotic genes.)

**organ of Corti** Structure in the inner ear that transforms mechanical forces produced from pressure waves ("sound waves") into action potentials that are sensed as sound.

**organ system** An interrelated and integrated group of tissues and organs that work together in a physiological function.

**organelle** (or' gan el') Any of the membrane-enclosed structures within a eukaryotic cell. Examples include the nucleus, endoplasmic reticulum, and mitochondria.

**organic** (1) Pertaining to any chemical compound that contains carbon. (2) Pertaining to any aspect of living matter, e.g., to its evolution, structure, or chemistry.

**organism** Any living entity.

**organizer** Region of the early amphibian embryo that directs early embryonic development. Also known as the primary embryonic organizer.

**organogenesis** The formation of organs and organ systems during development.

**origin of replication (ori)** DNA sequence at which helicase unwinds the DNA double helix and DNA polymerase binds to initiate DNA replication.

**orthology** (or thol' o jee) Type of homology in which the divergence of homologous genes can be traced to speciation events. (Contrast with paralogy.)

**osmoconformer** An aquatic animal that equilibrates the osmolarity of its extracellular fluid that is the same as with that of the external environment.

**osmolarity** The concentration of osmotically active particles in a solution.

**osmoregulation** Regulation of the chemical composition of the body fluids of an organism.

**osmosis** (oz mo' sis) [Gk. *osmos*: to push] Movement of water across a differentially permeable membrane, from one region to another region where the water potential is more negative.

**ossicle** (oss' ick ul) [L. *os*: bone] The calcified construction unit of echinoderm skeletons.

**osteoblast** (oss' tee oh blast) [Gk. *osteon*: bone + *blastos*: sprout] A cell that lays down the protein matrix of bone.

**osteoclast** (oss' tee oh clast) [Gk. *osteon*: bone + *klastos*: broken] A cell that dissolves bone.

**osteocyte** An osteoblast that has become enclosed in lacunae within the bone it has built.

**outgroup** In phylogenetics, a group of organisms used as a point of reference for comparison with the groups of primary interest (the in-group).

**oval window** The flexible membrane that, when moved by the bones of the middle ear, produces pressure waves in the inner ear.

**ovarian cycle** In human females, the monthly cycle of events by which eggs and hormones are produced. (Contrast with uterine cycle.)

**ovary** (oh' var ee) [L. *ovum*: egg] Any female organ, in plants or animals, that produces an egg.

**overtopping** Plant growth pattern in which one branch differentiates from and grows beyond the others.

**oviduct** In mammals, the tube serving to transport eggs to the uterus or to outside of the body.

**oviparity** Reproduction in which eggs are released by the female and development is external to the mother's body. (Contrast with viviparity.)

**ovoviparity** Pertaining to reproduction in which fertilized eggs develop and hatch within the mother's body but are not attached to the mother by means of a placenta.

**ovulation** Release of an egg from an ovary.

**ovule** (oh' vule) In plants, a structure comprising the megasporangium and the integument, which develops into a seed after fertilization.

**ovum** (oh' vum) (plural: ova) [L. egg] The female gamete.

**oxidation** (ox i day' shun) Relative loss of electrons in a chemical reaction; either outright removal to form an ion, or the sharing of electrons with substances having a greater affinity for them, such as oxygen. Most oxidations, including biological ones, are associated with the liberation of energy. (Contrast with reduction.)

**oxidative phosphorylation** ATP formation in the mitochondrion, associated with flow of electrons through the respiratory chain.

**oxygenase** An enzyme that catalyzes the addition of oxygen to a substrate from  $O_2$ .

**oxytocin** A hormone released by the posterior pituitary that promotes social bonding.

### - P -

**pancreas** (pan' cree us) A gland located near the stomach of vertebrates that secretes digestive enzymes into the small intestine and releases insulin into the bloodstream.

**Pangaea** (pan jee' uh) [Gk. *pan*: all, every] The single land mass formed when all the continents came together in the Permian period.

**para-** [Gk. *para*: akin to, beside] Prefix indicating association in being along side or accessory to.

**parabronchi** Passages in the lungs of birds through which air flows.

**paracrine** [Gk. *para*: near] Pertaining to a chemical signal, such as a hormone, that acts locally, near the site of its secretion. (Contrast with autocrine.)

**paralogy** (par al' o jee) Type of homology in which the divergence of homologous genes can be traced to gene duplication events. (Contrast with orthology.)

**paraphyletic** (par' a fih leht' ik) [Gk. *para*: beside + *phylon*: tribe] Pertaining to a group that consists of an ancestor and some, but not all, of its descendants. (Contrast with monophyletic, polyphyletic.)

**parasite** An organism that consumes parts of an organism much larger than itself (known as its host). Parasites sometimes, but not always, kill their host.

**parasympathetic nervous system** The division of the autonomic nervous system that works in opposition to the sympathetic nervous system. (Contrast with sympathetic nervous system.)

**parathyroid glands** Four glands on the posterior surface of the thyroid gland that produce and release parathyroid hormone.

**parathyroid hormone (PTH)** A hormone secreted by the parathyroid glands that stimulates osteoclast activity and raises blood calcium levels. Also called parathormone.

**parenchyma** (pair eng' kyma) A plant tissue composed of relatively unspecialized cells without secondary walls.

**parent rock** The soil horizon consisting of the rock that is breaking down to form the soil. Also called bedrock, or the C horizon.

**parental (P) generation** The individuals that mate in a genetic cross. Their offspring are the first filial ( $F_1$ ) generation.

**parsimony** Preferring the simplest among a set of plausible explanations of any phenomenon.

**parthenocarpy** Formation of fruit from a flower without fertilization.

**parthenogenesis** [Gk. *parthenos*: virgin] Production of an organism from an unfertilized egg.

**particulate theory** In genetics, the theory that genes are physical entities that retain their identities after fertilization.

**passive transport** Diffusion across a membrane; may or may not require a channel or carrier protein. (Contrast with active transport.)

**patch clamping** A technique for isolating a tiny patch of membrane to allow the study of ion movement through a particular channel.

**pathogen** (path' o jen) [Gk. *pathos*: suffering + *genesis*: source] An organism that causes disease.

**pattern formation** In animal embryonic development, the organization of differentiated tissues into specific structures such as wings.

**pedigree** The pattern of transmission of a genetic trait within a family.

**pelagic zone** [Gk. *pelagos*: sea] The open ocean.

**penetrance** The proportion of individuals with a particular genotype that show the expected phenotype.

**penis** An accessory sex organ of male animals that enables the male to deposit sperm in the female's reproductive tract.

**pentose** [Gk. *penta*: five] A sugar containing five carbon atoms.

**PEP carboxylase** The enzyme that combines carbon dioxide with PEP to form a 4-carbon dicarboxylic acid at the start of  $C_4$  photosynthesis or of crassulacean acid metabolism (CAM).

**pepsin** [Gk. *pepsis*: digestion] An enzyme in gastric juice that digests protein.

**pepsinogen** Inactive secretory product that is converted into pepsin by low pH or by enzymatic action.

**peptide linkage** The bond between amino acids in a protein; formed between a carboxyl group and amino group ( $CO-NH^-$ ) with the loss of water molecules.

**peptidoglycan** The cell wall material of many bacteria, consisting of a single enormous molecule that surrounds the entire cell.

**perennial** (per ren' ee al) [L. *per*: throughout + *annus*: year] A plant that survives from year to year. (Contrast with annual, biennial.)

**perfect flower** A flower with both stamens and carpels; a hermaphroditic flower. (Contrast with imperfect flower.)

**pericycle** [Gk. *peri*: around + *kyklos*: ring or circle] In plant roots, tissue just within the endodermis, but outside of the root vascular tissue. Meristematic activity of pericycle cells produces lateral root primordia.

**periderm** The outer tissue of the secondary plant body, consisting primarily of cork.

**period** (1) A category in the geological time scale. (2) The duration of a single cycle in a cyclical event, such as a circadian rhythm.

**peripheral nervous system (PNS)** The portion of the nervous system that transmits information to and from the central nervous system, consisting of neurons that extend or reside outside the brain or spinal cord and their supporting cells. (Contrast with central nervous system.)

**peristalsis** (pair' i stall' sis) Wavelike muscular contractions proceeding along a tubular organ, propelling the contents along the tube.

**peritoneum** The mesodermal lining of the body cavity in coelomate animals.

**peroxisome** An organelle that houses reactions in which toxic peroxides are formed and then converted to water.

**petal** [Gk. *petalon*: spread out] In an angiosperm flower, a sterile modified leaf, nonphotosynthetic, frequently brightly colored, and often serving to attract pollinating insects.

**petiole** (pet' ee ole) [L. *petiolus*: small foot] The stalk of a leaf.

**pH** The negative logarithm of the hydrogen ion concentration; a measure of the acidity of a solution. A solution with  $pH = 7$  is said to be neutral;  $pH$  values higher than 7 characterize basic solutions, while acidic solutions have  $pH$  values less than 7.

**phage** (fayj) See bacteriophage.

**phagocyte** [Gk. *phagein*: to eat + *kystos*: sac] One of two major classes of white blood cells; one of the nonspecific defenses of animals; ingests invading microorganisms by phagocytosis.

**phagocytosis** Endocytosis by a cell of another cell or large particle.

**pharming** The use of genetically modified animals to produce medically useful products in their milk.

**pharynx** [Gk. throat] The part of the gut between the mouth and the esophagus.

**phenotype** (fee' no type) [Gk. *phanein*: to show] The observable properties of an individual resulting from both genetic and environmental factors. (Contrast with genotype.)

**phenotypic plasticity** See developmental plasticity.

**pheromone** (feer' o mone) [Gk. *pheros*: carry + *hormon*: excite, arouse] A chemical substance used in communication between organisms of the same species.

**phloem** (flo' um) [Gk. *phloos*: bark] In vascular plants, the vascular tissue that transports sugars and other solutes from sources to sinks.

**phosphate group** The functional group  $-OPO_3H_2$ .

**phosphodiester linkage** The connection in a nucleic acid strand, formed by linking two nucleotides.

**phospholipid** A lipid containing a phosphate group; an important constituent of cellular membranes. (See lipid.)

**phospholipid bilayer** The basic structural unit of biological membranes; a sheet of phospholipids two molecules thick in which the phospholipids are lined up with their hydrophobic "tails" packed tightly together and their hydrophilic, phosphate-containing "heads" facing outward. Also called lipid bilayer.

**phosphorylation** Addition of a phosphate group.

**photoautotroph** An organism that obtains energy from light and carbon from carbon dioxide. (Contrast with chemolithotroph, chemoheterotroph, photoheterotroph.)

**photoheterotroph** An organism that obtains energy from light but must obtain its carbon from organic compounds. (Contrast with chemolithotroph, chemoheterotroph, photoautotroph.)

**photon** (foe' ton) [Gk. *photos*: light] A quantum of visible radiation; a "packet" of light energy.

**photoperiodicity** Control of an organism's physiological or behavioral responses by the length of the day or night.

**photoreceptor** (1) In plants, a pigment that triggers a physiological response when it absorbs a photon. (2) In animals, a sensory receptor cell that senses and responds to light energy.

**photorespiration** Light-driven uptake of oxygen and release of carbon dioxide, the carbon being derived from the early reactions of photosynthesis.

**photosynthesis** (foe tow sin' the sis) [literally, "synthesis from light"] Metabolic processes, carried out by green plants, by which visible light is trapped and the energy used to synthesize compounds such as ATP and glucose.

**photosystem** [Gk. *phos*: light + *systema*: assembly] A light-harvesting complex in the chloroplast thylakoid composed of pigments and proteins.

**photosystem I** In photosynthesis, the reactions that absorb light at 700 nm, passing electrons to ferrodoxin and thence to NADPH. Rich in chlorophyll *a*.

**photosystem II** In photosynthesis, the reactions that absorb light at 660 nm, passing electrons to the electron transport chain in the chloroplast. Rich in chlorophyll *b*.

**phototropins** A class of blue light receptors that mediate phototropism and other plant responses.

**phototropism** [Gk. *photos*: light + *tropē*: turning] A directed plant growth response to light.

**phycobilin** Photosynthetic pigment that absorbs red, yellow, orange, and green light and is found in cyanobacteria and some red algae.

**phylogenetic tree** A graphic representation of lines of descent among organisms or their genes.

**phylogeny** (fy loj' e nee) [Gk. *phylon*: tribe, race + *genesis*: source] The evolutionary history of a particular group of organisms or their genes.

**physiology** (fiz' ee ol' o jee) [Gk. *physis*: natural form] The scientific study of the functions of living organisms and the individual organs, tissues, and cells of which they are composed.

**phytoalexins** Substances toxic to pathogens, produced by plants in response to fungal or bacterial infection.

**phytochrome** (fy' tow krome) [Gk. *phyton*: plant + *chroma*: color] A plant pigment regulating a large number of developmental and other phenomena in plants.

**phytomers** In plants, the repeating modules that compose a shoot, each consisting of one or more leaves, attached to the stem at a node; an internode; and one or more axillary buds.

**phytoplankton** Photosynthetic plankton.

**phytoremediation** A form of bioremediation that uses plants to clean up environmental pollution.

**pigment** A substance that absorbs visible light.

**pineal gland** Gland located between the cerebral hemispheres that secretes melatonin.

**pinocytosis** Endocytosis by a cell of liquid containing dissolved substances.

**pistil** [L. *pistillum*: pestle] The structure of an angiosperm flower within which the ovules are borne. May consist of a single carpel, or of several carpels fused into a single structure. Usually differentiated into ovary, style, and stigma.

**pith** In plants, relatively unspecialized tissue found within a cylinder of vascular tissue.

**pituitary gland** A small gland attached to the base of the brain in vertebrates. Its hormones control the activities of other glands. Also known as the hypophysis.

**placenta** (pla sen' ta) The organ in female mammals that provides for the nourishment of the fetus and elimination of the fetal waste products.

**plankton** Free-floating small aquatic organisms. Photosynthetic members of the plankton are referred to as phytoplankton.

**planula** (plan' yew la) [L. *planum*: flat] A free-swimming, ciliated larval form typical of the cnidarians.

**plaque** (plack) [Fr.: a metal plate or coin]

- (1) A circular clearing in a layer (lawn) of bacteria growing on the surface of a nutrient agar gel.
- (2) An accumulation of prokaryotic organisms on tooth enamel. Acids produced by these microorganisms cause tooth decay.
- (3) A region of arterial wall invaded by fibroblasts and fatty deposits. (See atherosclerosis.)

**plasma** (plaz' muh) The liquid portion of blood, in which blood cells and other particulates are suspended.

**plasma cell** An antibody-secreting cell that develops from a B cell; the effector cell of the humoral immune system.

**plasma membrane** The membrane that surrounds the cell, regulating the entry and exit of molecules and ions. Every cell has a plasma membrane.

**plasmid** A DNA molecule distinct from the chromosome(s); that is, an extrachromosomal element; found in many bacteria. May replicate independently of the chromosome.

**plasmodesma** (plural: plasmodesmata) [Gk. *plassein*: to mold + *desmos*: band] A cytoplasmic strand connecting two adjacent plant cells.

**plasmogamy** The fusion of the cytoplasm of two cells. (Contrast with karyogamy.)

**plastid** Any of the plant cell organelles that house biochemical pathways for photosynthesis.

**plate tectonics** [Gk. *tekton*: builder] The scientific study of the structure and movements of Earth's lithospheric plates, which are the cause of continental drift.

**platelet** A membrane-bounded body without a nucleus, arising as a fragment of a cell in the bone marrow of mammals. Important to blood-clotting action.

**pleiotropy** (plee' a tro pee) [Gk. *pleion*: more] The determination of more than one character by a single gene.

**pleural membrane** [Gk. *pleuras*: rib, side] The membrane lining the outside of the lungs and the walls of the thoracic cavity. Inflammation of these membranes is a condition known as pleurisy.

**pluripotent** [L. *pluri*: many + *potens*: powerful] Having the ability to form all of the cells in the body. (Contrast with multipotent, totipotent.)

**podocytes** Cells of Bowman's capsule of the nephron that cover the capillaries of the glomerulus, forming filtration slits.

**point mutation** A mutation that results from the gain, loss, or substitution of a single nucleotide.

**polar** Having separate and opposite electric charges at two ends, or poles. (Contrast with nonpolar.)

**polar body** A nonfunctional nucleus produced by meiosis during oogenesis.

**polar nuclei** In angiosperms, the two nuclei in the central cell of the megagametophyte; following fertilization they give rise to the endosperm.

**polarity** (1) In chemistry, the property of unequal electron sharing in a covalent bond that defines a polar molecule. (2) In development, the difference between one end of an organism or structure and the other.

**pollen** [L. *pollin*: fine flour] In seed plants, microscopic grains that contain the male gametophyte (microgametophyte) and gamete (microspore).

**pollen tube** A structure that develops from a pollen grain through which sperm are released into the megagametophyte.

**pollination** The process of transferring pollen from an anther to the stigma of a pistil in an angiosperm or from a strobilus to an ovule in a gymnosperm.

**poly-** [Gk. *poly*: many] A prefix denoting multiple entities.

**poly A tail** A long sequence of adenine nucleotides (50–250) added after transcription to the 3' end of most eukaryotic mRNAs.

**polyandry** Mating system in which one female mates with multiple males.

**polygyny** Mating system in which one male mates with multiple females.

**polymer** [Gk. *poly*: many + *meros*: unit] A large molecule made up of similar or identical subunits called monomers. (Contrast with monomer, oligomer.)

**polymerase chain reaction (PCR)** An enzymatic technique for the rapid production of millions of copies of a particular stretch of DNA where only a small amount of the parent molecule is available.

**polymorphic** (pol' lee mor' fik) [Gk. *poly*: many + *morphe*: form, shape] Coexistence in a population of two or more distinct traits.

**polyp** (pah' lip) [Gk. *poly*: many + *pous*: foot] In cnidarians, a sessile, asexual life cycle stage.

**polypeptide** A large molecule made up of many amino acids joined by peptide linkages. Large polypeptides are called proteins.

**polyphyletic** (pol' lee fih leht' ik) [Gk. *poly*: many + *phylon*: tribe] Pertaining to a group that consists of multiple distantly related organisms, and does not include the common ancestor of the group. (Contrast with monophyletic, paraphyletic.)

**polyploidy** (pol' lee ploid ee) The possession of more than two entire sets of chromosomes.

**polyribosome (polysome)** A complex consisting of a threadlike molecule of messenger RNA and several (or many) ribosomes. The ribosomes move along the mRNA, synthesizing polypeptide chains as they proceed.

**polysaccharide** A macromolecule composed of many monosaccharides (simple sugars). Common examples are cellulose and starch.

**pons** [L. *pons*: bridge] Region of the brainstem anterior to the medulla.

**population** Any group of organisms coexisting at the same time and in the same place and capable of interbreeding with one another.

**population bottleneck** A period during which only a few individuals of a normally large population survive.

**population density** The number of individuals of a population per unit of area or volume.

**population dynamics** The patterns and processes of change in populations.

**population genetics** The study of genetic variation and its causes within populations.

**portal blood vessels** Blood vessels that begin and end in capillary beds.

**positive cooperativity** Occurs when a molecule can bind several ligands and each one that binds alters the conformation of the molecule so that it can bind the next ligand more easily. The binding of four molecules of O<sub>2</sub> by hemoglobin is an example of positive cooperativity.

**positive feedback** In regulatory systems, information that amplifies a regulatory response, increasing the deviation of the system from the set point. (Contrast with negative feedback.)

**positive regulation** A form of gene regulation in which a regulatory macromolecule is needed to turn on the transcription of a structural gene; in its absence, transcription will not occur. (Contrast with negative regulation.)

**post-** [L. *postere*: behind, following after] Prefix denoting something that comes after.

**postabsorptive state** State in which no food remains in the gut and thus no nutrients are being absorbed. (Contrast with absorptive state.)

**posterior** Toward or pertaining to the rear. (Contrast with anterior.)

**postsynaptic cell** The cell that receives information from a neuron at a synapse. (Contrast with presynaptic neuron.)

**postzygotic reproductive barriers** Barriers to the reproductive process that occur after the union of the nuclei of two gametes. (Contrast with prezygotic reproductive barriers.)

**potential energy** Energy not doing work, such as the energy stored in chemical bonds. (Contrast with kinetic energy.)

**precapillary sphincter** A cuff of smooth muscle that can shut off the blood flow to a capillary bed.

**pre-mRNA (precursor mRNA)** Initial gene transcript before it is modified to produce functional mRNA. Also known as the primary transcript.

**predator** An organism that kills and eats other organisms.

**prereplication complex** In eukaryotes, a complex of proteins that binds to DNA at the initiation of DNA replication.

**pressure flow model** An effective model for phloem transport in angiosperms. It holds that sieve element transport is driven by an osmotically driven pressure gradient between source and sink.

**pressure potential** The hydrostatic pressure of an enclosed solution in excess of the surrounding atmospheric pressure. (Contrast with solute potential, water potential.)

**presynaptic neuron** The neuron that transmits information to another cell at a synapse. (Contrast with postsynaptic cell.)

**prey** [L. *praeda*: booty] An organism consumed by a predator as an energy source.

**prezygotic reproductive barriers** Barriers to the reproductive process that occur before the union of the nuclei of two gametes. (Contrast with postzygotic reproductive barriers.)

**primary active transport** Active transport in which ATP is hydrolyzed, yielding the energy required to transport an ion or molecule against its

concentration gradient. (Contrast with secondary active transport.)

**primary cell wall** In plant cells, a structure that forms at the middle lamella after cytokinesis, made up of cellulose microfibrils, hemicelluloses, and pectins. (Contrast with secondary cell wall.)

**primary consumer** An organism (herbivore) that eats plant tissues.

**primary growth** In plants, growth that is characterized by the lengthening of roots and shoots and by the proliferation of new roots and shoots through branching. (Contrast with secondary growth.)

**primary immune response** The first response of the immune system to an antigen, involving recognition by lymphocytes and the production of effector cells and memory cells. (Contrast with secondary immune response.)

**primary lysosome** See lysosome.

**primary meristem** Meristem that produces the tissues of the primary plant body.

**primary oocyte** (oh' eh site) [Gk. *oon*: egg + *kytos*: container] The diploid progeny of an oogonium. In many species, a primary oocyte enters prophase of the first meiotic division, then remains in developmental arrest for a long time before resuming meiosis to form a secondary oocyte and a polar body.

**primary plant body** That part of a plant produced by primary growth. Consists of all the *nonwoody* parts of a plant; many herbaceous plants consist entirely of a primary plant body. (Contrast with secondary plant body.)

**primary producer** A photosynthetic or chemosynthetic organism that synthesizes complex organic molecules from simple inorganic ones.

**primary sex determination** Genetic determination of gametic sex, male or female. (Contrast with secondary sex determination.)

**primary spermatocyte** The diploid progeny of a spermatogonium; undergoes the first meiotic division to form secondary spermatocytes.

**primary succession** Succession that begins in an area initially devoid of life, such as on recently exposed glacial till or lava flows. (Contrast with secondary succession.)

**primary structure** The specific sequence of amino acids in a protein.

**primase** An enzyme that catalyzes the synthesis of a primer for DNA replication.

**primer** Strand of nucleic acid, usually RNA, that is the necessary starting material for the synthesis of a new DNA strand, which is synthesized from the 3' end of the primer.

**primordium** (plural: primordia) [L. origin] The most rudimentary stage of an organ or other part.

**prion** An infectious protein that can proliferate by converting the inactive form of a particular protein into an active protein.

**pro-** [L.: first, before, favoring] A prefix often used in biology to denote a developmental stage that comes first or an evolutionary form that appeared earlier than another. For example, prokaryote, prophase.

**probe** A segment of single stranded nucleic acid used to identify DNA molecules containing the complementary sequence.

**procambium** Primary meristem that produces the vascular tissue.

**procedural memory** Memory of motor tasks. Cannot be consciously recalled and described. (Contrast with declarative memory.)

**processive** Pertaining to an enzyme that catalyzes many reactions each time it binds to a substrate, as DNA polymerase does during DNA replication.

**progesterone** [L. *pro*: favoring + *gestare*: to bear] A female sex hormone that maintains pregnancy.

**prolactin** A hormone released by the anterior pituitary, one of whose functions is the stimulation of milk production in female mammals.

**proliferating cell nuclear antigen (PCNA)** A protein complex that ensures processivity of DNA replication in eukaryotes.

**prometaphase** The phase of nuclear division that begins with the disintegration of the nuclear envelope.

**promoter** A DNA sequence to which RNA polymerase binds to initiate transcription.

**prophage** (pro' fay) The noninfectious units that are linked with the chromosomes of the host bacteria and multiply with them but do not cause dissolution of the cell. Prophage can later enter into the lytic phase to complete the virus life cycle.

**prophase** (pro' phase) The first stage of nuclear division, during which chromosomes condense from diffuse, threadlike material to discrete, compact bodies.

**prostaglandin** Any one of a group of specialized lipids with hormone-like functions. It is not clear that they act at any considerable distance from the site of their production.

**prostate gland** In male humans, surrounds the urethra at its junction with the vas deferens; supplies an acid-neutralizing fluid to the semen.

**prosthetic group** Any nonprotein portion of an enzyme.

**proteasome** In the eukaryotic cytoplasm, a huge protein structure that binds to and digests cellular proteins that have been tagged by ubiquitin.

**protein** (pro' teen) [Gk. *protos*: first] Long-chain polymer of amino acids with twenty different common side chains. Occurs with its polymer chain extended in fibrous proteins, or coiled into a compact macromolecule in enzymes and other globular proteins.

**protein kinase** (kye' nase) An enzyme that catalyzes the addition of a phosphate group from ATP to a target protein.

**protein kinase cascade** A series of reactions in response to a molecular signal, in which a series of protein kinases activates one another in sequence, amplifying the signal at each step.

**proteoglycan** A glycoprotein containing a protein core with attached long, linear carbohydrate chains.

**proteolysis** [protein + Gk. *lysis*: break apart] An enzymatic digestion of a protein or polypeptide.

**proteome** The set of proteins that can be made by an organism. Because of alternative splicing of pre-mRNA, the number of proteins that can be made is usually much larger than the number of protein-coding genes present in the organism's genome.

**protoderm** Primary meristem that gives rise to the plant epidermis.

**proton** (pro' ton) [Gk. *protos*: first, before] (1) A subatomic particle with a single positive charge.

**The number of protons in the nucleus of an atom determine its element.** (2) A hydrogen ion, H<sup>+</sup>.

**proton pump** An active transport system that uses ATP energy to move hydrogen ions across a membrane, generating an electric potential.

**proton-motive force** Force generated across a membrane having two components: a chemical potential (difference in proton concentration) plus an electrical potential due to the electrostatic charge on the proton.

**protonephridium** The excretory organ of flatworms, made up of a tubule and a flame cell.

**protoplasm** The living contents of a plant cell; the plasma membrane and everything contained within it.

**provirus** Double-stranded DNA made by a virus that is integrated into the host's chromosome and contains promoters that are recognized by the host cell's transcription apparatus.

**proximal** Near the point of attachment or other reference point. (Contrast with distal.)

**proximal convoluted tubule** The initial segment of a renal tubule, closest to the glomerulus. (Compare with distal convoluted tubule.)

**proximate cause** The immediate genetic, physiological, neurological, and developmental mechanisms responsible for a behavior or morphology. (Contrast with ultimate cause.)

**pseudocoelomate** (soo' do see' low mate) [Gk. *pseudes*: false + *koiroma*: cavity] Having a body cavity, called a pseudocoel, consisting of a fluid-filled space in which many of the internal organs are suspended, but which is enclosed by mesoderm only on its outside.

**pseudogene** [Gk. *pseudes*: false] A DNA segment that is homologous to a functional gene but is not expressed because of changes to its sequence or changes to its location in the genome.

**pseudopod** (soo' do pod) [Gk. *pseudes*: false + *podos*: foot] A temporary, soft extension of the cell body that is used in location, attachment to surfaces, or engulfing particles.

**pulmonary** [L. *pulmo*: lung] Pertaining to the lungs.

**pulmonary circuit** The portion of the circulatory system by which blood is pumped from the heart to the lungs or gills for oxygenation and back to the heart for distribution. (Contrast with systemic circuit.)

**pulmonary valve** A one-way valve between the right ventricle of the heart and the pulmonary artery that prevents backflow of blood into the ventricle when it relaxes.

**Punnett square** Method of predicting the results of a genetic cross by arranging the gametes of each parent at the edges of a square.

**pupa** (pew' pa) [L. *pupa*: doll, puppet] In certain insects (the Holometabola), the encased developmental stage between the larva and the adult.

**pupil** The opening in the vertebrate eye through which light passes.

**purine** (pure' een) One of the two types of nitrogenous bases in nucleic acids. Each of the purines—adenine and guanine—pairs with a specific pyrimidine.

**Purkinje fibers** Specialized heart muscle cells that conduct excitation throughout the ventricular muscle.

**pyrimidine** (per im' a deen) One of the two types of nitrogenous bases in nucleic acids. Each

of the pyrimidines—cytosine, thymine, and uracil—pairs with a specific purine.

**pyrogen** Molecule that produces a rise in body temperature (fever); may be produced by an invading pathogen or by cells of the immune system in response to infection.

**pyruvate** A three-carbon acid; the end product of glycolysis and the raw material for the citric acid cycle.

**pyruvate oxidation** Conversion of pyruvate to acetyl CoA and CO<sub>2</sub> that occurs in the mitochondrial matrix in the presence of O<sub>2</sub>.

## - Q -

**Q<sub>10</sub>** A value that compares the rate of a biochemical process or reaction over 10°C temperature ranges. A process that is not temperature-sensitive has a Q<sub>10</sub> of 1; values of 2 or 3 mean the reaction speeds up as temperature increases.

**quantitative trait loci** A set of genes that determines a complex character that exhibits quantitative variation.

**quaternary structure** The specific three-dimensional arrangement of protein subunits.

## - R -

**R group** The distinguishing group of atoms of a particular amino acid; also known as a side chain.

**r-strategist** A species whose life history strategy allows for a high intrinsic rate of population increase (*r*). (Contrast with K-strategist.)

**radial symmetry** The condition in which any two halves of a body are mirror images of each other, providing the cut passes through the center; a cylinder cut lengthwise down its center displays this form of symmetry.

**radiation** The transfer of heat from warmer objects to cooler ones via the exchange of infrared radiation. *See also* electromagnetic radiation; evolutionary radiation.

**radicle** An embryonic root.

**radioisotope** A radioactive isotope of an element. Examples are carbon-14 (C<sup>14</sup>) and hydrogen-3, or tritium (H<sup>3</sup>).

**reactant** A chemical substance that enters into a chemical reaction with another substance.

**reaction center** A group of electron transfer proteins that receive energy from light-absorbing pigments and convert it to chemical energy by redox reactions.

**realized niche** A species' niche as defined by its interactions with other species. (Contrast with fundamental niche.)

**receptive field** The area of visual space that activates a particular cell in the visual system.

**receptor** *See* receptor protein, sensory receptor cell.

**receptor-mediated endocytosis** Endocytosis initiated by macromolecular binding to a specific membrane receptor.

**receptor potential** The change in the resting potential of a sensory cell when it is stimulated.

**receptor protein** A protein that can bind to a specific molecule, or detect a specific stimulus, within the cell or in the cell's external environment.

**recessive** In genetics, an allele that does not determine phenotype in the presence of a dominant allele. (Contrast with dominance.)

**reciprocal adaptation** *See* coevolution.

**reciprocal crosses** A pair of matings in one of which a female of genotype A mates with a male of genotype B and in the other of which a female of genotype B mates with a male of genotype A.

**recognition sequence** *See* restriction site.

**recombinant** Pertaining to an individual, meiotic product, or chromosome in which genetic materials originally present in two individuals end up in the same haploid complement of genes.

**recombinant DNA** A DNA molecule made in the laboratory that is derived from two or more genetic sources.

**recombinant frequency** The proportion of offspring of a genetic cross that have phenotypes different from the parental phenotypes due to crossing over between linked genes during gamete formation.

**reconciliation ecology** The practice of making exploited lands more biodiversity-friendly.

**rectum** The terminal portion of the gut, ending at the anus.

**redox reaction** A chemical reaction in which one reactant becomes oxidized and the other becomes reduced.

**reduction** Gain of electrons by a chemical reactant; any reduction is accompanied by an oxidation. (Contrast with oxidation.)

**refractory period** The time interval after an action potential during which another action potential cannot be elicited from an excitable membrane.

**regeneration** The development of a complete individual from a fragment of an organism.

**regulative development** A pattern of animal embryonic development in which the fates of the first blastomeres are not absolutely fixed. (Contrast with mosaic development.)

**regulatory sequence** A DNA sequence to which the protein product of a regulatory gene binds.

**regulatory gene** A gene that codes for a protein (or RNA) that in turn controls the expression of another gene.

**regulatory system** A system that uses feedback information to maintain a physiological function or parameter at an optimal level. (Contrast with controlled system.)

**regulatory T cells (T<sub>reg</sub>)** Class of T cells that mediates tolerance to self antigens.

**reinforcement** The evolution of enhanced reproductive isolation between populations due to natural selection for greater isolation.

**releaser** Sensory stimulus that triggers performance of a stereotyped behavior pattern.

**REM (rapid-eye-movement) sleep** A sleep state characterized by vivid dreams, skeletal muscle relaxation, and rapid eye movements. (Contrast with slow-wave sleep.)

**renal** [L. *renes*: kidneys] Relating to the kidneys.

**renal tubule** A structural unit of the kidney that collects filtrate from the blood, reabsorbs specific ions, nutrients, and water and returns them to the blood, and concentrates excess ions and waste products such as urea for excretion from the body.

**replication** The duplication of genetic material.

**replication complex** The close association of several proteins operating in the replication of DNA.

**replication fork** A point at which a DNA molecule is replicating. The fork forms by the unwinding of the parent molecule.

**replicon** A region of DNA replicated from a single origin of replication.

**reporter gene** A genetic marker included in recombinant DNA to indicate the presence of the recombinant DNA in a host cell.

**repressor** A protein encoded by a regulatory gene that can bind to a specific operator and prevent transcription of the operon. (Contrast with activator.)

**reproductive isolation** Condition in which two divergent populations are no longer exchanging genes. Can lead to speciation.

**rescue effect** The process by which individuals moving between subpopulations of a metapopulation may prevent declining subpopulations from becoming extinct.

**resistance (R) genes** Plant genes that confer resistance to specific strains of pathogens.

**resource** Something in the environment required by an organism for its maintenance and growth that is consumed in the process of being used.

**resource partitioning** A situation in which selection pressures resulting from interspecific competition cause changes in the ways in which the competing species use the limiting resource, thereby allowing them to coexist.

**respiration** (res pi ra' shun) [L. *spirare*: to breathe] (1) Cellular respiration. (2) Breathing.

**respiratory chain** The terminal reactions of cellular respiration, in which electrons are passed from NAD or FAD, through a series of intermediate carriers, to molecular oxygen, with the concomitant production of ATP.

**respiratory gases** Oxygen ( $O_2$ ) and carbon dioxide ( $CO_2$ ); the gases that an animal must exchange between its internal body fluids and the outside medium (air or water).

**resting potential** The membrane potential of a living cell at rest. In cells at rest, the interior is negative to the exterior. (Contrast with action potential, electrotonic potential.)

**restoration ecology** The science and practice of restoring damaged or degraded ecosystems.

**restriction enzyme** Any of a type of enzyme that cleaves double-stranded DNA at specific sites; extensively used in recombinant DNA technology. Also called a restriction endonuclease.

**restriction fragment length polymorphism** See RFLP.

**restriction point (R)** The specific time during G1 of the cell cycle at which the cell becomes committed to undergo the rest of the cell cycle.

**restriction site** A specific DNA base sequence that is recognized and acted on by a restriction endonuclease.

**reticular system** A central region of the vertebrate brainstem that includes complex fiber tracts conveying neural signals between the forebrain and the spinal cord, with collateral fibers to a variety of nuclei that are involved in autonomic functions, including arousal from sleep.

**retina** (rett' in uh) [L. *rete*: net] The light-sensitive layer of cells in the vertebrate or cephalopod eye.

**retinoblastoma protein** A protein that inhibits an animal cell from passing through the restriction point; inactivation of this protein is necessary for the cell cycle to proceed.

**retrovirus** An RNA virus that contains reverse transcriptase. Its RNA serves as a template for cDNA production, and the cDNA is integrated into a chromosome of the host cell.

**reverse genetics** Method of genetic analysis in which a phenotype is first related to a DNA variation, then the protein involved is identified.

**reverse transcriptase** An enzyme that catalyzes the production of DNA (cDNA), using RNA as a template; essential to the reproduction of retroviruses.

**RFLP** Restriction fragment length polymorphism, the coexistence of two or more patterns of restriction fragments resulting from underlying differences in DNA sequence.

**rhizoids** (rye' zoids) [Gk. root] Hairlike extensions of cells in mosses, liverworts, and a few vascular plants that serve the same function as roots and root hairs in vascular plants. The term is also applied to branched, rootlike extensions of some fungi and algae.

**rhizome** (rye' zome) An underground stem (as opposed to a root) that runs horizontally beneath the ground.

**rhodopsin** A photopigment used in the visual process of transducing photons of light into changes in the membrane potential of photoreceptor cells.

**ribonucleic acid** See RNA.

**ribose** A five-carbon sugar in nucleotides and RNA.

**ribosomal RNA (rRNA)** Several species of RNA that are incorporated into the ribosome. Involved in peptide bond formation.

**ribosome** A small particle in the cell that is the site of protein synthesis.

**ribozyme** An RNA molecule with catalytic activity.

**risk cost** The increased chance of being injured or killed as a result of performing a behavior, compared to resting.

**RNA (ribonucleic acid)** An often single stranded nucleic acid whose nucleotides use ribose rather than deoxyribose and in which the base uracil replaces thymine found in DNA. Serves as genome from some viruses. (See rRNA, tRNA, mRNA, and ribozyme.)

**RNA interference (RNAi)** A mechanism for reducing mRNA translation whereby a double-stranded RNA, made by the cell or synthetically, is processed into a small, single-stranded RNA, whose binding to a target mRNA results in the latter's breakdown.

**RNA polymerase** An enzyme that catalyzes the formation of RNA from a DNA template.

**RNA splicing** The last stage of RNA processing in eukaryotes, in which the transcripts of introns are excised through the action of small nuclear ribonucleoprotein particles (snRNP).

**rod cells** Light-sensitive cell in the vertebrate retina; these sensory receptor cells are sensitive in extremely dim light and are responsible for dim light, black and white vision.

**root** The organ responsible for anchoring the plant in the soil, absorbing water and minerals, and producing certain hormones. Some roots are storage organs.

**root cap** A thimble-shaped mass of cells, produced by the root apical meristem, that protects the meristem; the organ that perceives the gravitational stimulus in root gravitropism.

**root hair** A long, thin process from a root epidermal cell that absorbs water and minerals from the soil solution.

**root system** The organ system that anchors a plant in place, absorbs water and dissolved minerals, and may store products of photosynthesis from the shoot system.

**rough endoplasmic reticulum (RER)** The portion of the endoplasmic reticulum whose outer surface has attached ribosomes. (Contrast with smooth endoplasmic reticulum.)

**rRNA** See ribosomal RNA.

**rubisco** Contraction of ribulose bisphosphate carboxylase/oxygenase, the enzyme that combines carbon dioxide or oxygen with ribulose bisphosphate to catalyze the first step of photosynthetic carbon fixation or photorespiration, respectively.

**ruminant** Herbivorous, cud-chewing mammals such as cows or sheep, characterized by a stomach that consists of four compartments: the rumen, reticulum, omasum, and abomasum.

## - S -

**S phase** In the cell cycle, the stage of interphase during which DNA is replicated. (Contrast with  $G_1$  phase,  $G_2$  phase, M phase.)

**saltatory conduction** [L. *saltare*: to jump] The rapid conduction of action potentials in myelinated axons; so called because action potentials appear to "jump" between nodes of Ranvier along the axon.

**saprobe** [Gk. *sapros*: rotten] An organism (usually a bacterium or fungus) that obtains its carbon and energy by absorbing nutrients from dead organic matter.

**sarcomere** (sark' o meer) [Gk. *sark*: flesh + *meros*: unit] The contractile unit of a skeletal muscle.

**sarcoplasm** The cytoplasm of a muscle cell.

**sarcoplasmic reticulum** The endoplasmic reticulum of a muscle cell.

**saturated fatty acid** A fatty acid in which all the bonds between carbon atoms in the hydrocarbon chain are single bonds—that is, all the bonds are saturated with hydrogen atoms. (Contrast with unsaturated fatty acid.)

**scientific method** A means of gaining knowledge about the natural world by making observations, posing hypotheses, and conducting experiments to test those hypotheses.

**Schwann cell** A type of glial cell that myelinates axons in the peripheral nervous system.

**scion** In horticulture, the bud or stem from one plant that is grafted to a root or root-bearing stem of another plant (the stock).

**sclerenchyma** (skler eng' kyma) [Gk. *skleros*: hard + *kymus*: juice] A plant tissue composed of cells with heavily thickened cell walls. The cells are dead at functional maturity. The principal types of sclerenchyma cells are fibers and sclereids.

**second law of thermodynamics** The principle that when energy is converted from one form to another, some of that energy becomes unavailable for doing work.

**second messenger** A compound, such as cAMP, that is released within a target cell after a hormone (the first messenger) has bound to a surface receptor on a cell; the second messenger triggers further reactions within the cell.

**secondary active transport** A form of active transport that does not use ATP as an energy source; rather, transport is coupled to ion diffu-

sion down a concentration gradient established by primary active transport.

**secondary cell wall** A thick, cellulosic structure internal to the primary cell wall formed in some plant cells after cell expansion stops (Contrast with primary cell wall.)

**secondary consumer** An organism that eat primary consumers.

**secondary growth** In plants, growth that contributes to an increase in girth. (Contrast with primary growth.)

**secondary immune response** A rapid and intense response to a second or subsequent exposure to an antigen, initiated by memory cells. (Contrast with primary immune response.)

**secondary lysosome** Membrane-enclosed organelle formed by the fusion of a primary lysosome with a phagosome, in which macromolecules taken up by phagocytosis are hydrolyzed into their monomers. (Contrast with lysosome.)

**secondary metabolite** A compound synthesized by a plant that is not needed for basic cellular metabolism. Typically has an antiherbivore or antiparasite function.

**secondary plant body** That part of a plant produced by secondary growth; consists of woody tissues. (Contrast with primary plant body.)

**secondary sex determination** Formation of secondary sexual characteristics (i.e., those other than gonads), such as external sex organs and body hair. (Contrast with primary sex determination.)

**secondary spermatocyte** One of the products of the first meiotic division of a primary spermatocyte.

**secondary structure** Of a protein, localized regularities of structure, such as the  $\alpha$  helix and the  $\beta$  pleated sheet.

**secondary succession** Succession after a disturbance that did not eliminate all the organisms originally living on the site. (Contrast with primary succession.)

**secretin** (si kreet' in) A peptide hormone secreted by the upper region of the small intestine when acidic chyme is present. Stimulates the pancreatic duct to secrete bicarbonate ions.

**sedimentary rock** Rock formed by the accumulation of sediment grains on the bottom of a body of water.

**seed** A fertilized, ripened ovule of a gymnosperm or angiosperm. Consists of the embryo, nutritive tissue, and a seed coat.

**segmentation** Division of an animal body into segments.

**segmentation genes** Genes that determine the number and polarity of body segments.

**segregation** In genetics, the separation of alleles, or of homologous chromosomes, from each other during meiosis so that each of the haploid daughter nuclei produced contains one or the other member of the pair found in the diploid parent cell, but never both. This principle was articulated by Mendel as his first law.

**selective permeability** Allowing certain substances to pass through while other substances are excluded; a characteristic of membranes.

**self-incompatibility** In plants, the possession of mechanisms that prevent self-fertilization.

**semelparous** [L. *semel*: once + *pario*: to beget] Reproducing only once in a lifetime. (Contrast with iteroparous.)

**semen** (see' men) [L. *semin*: seed] The thick, whitish liquid produced by the male reproductive system in mammals, containing the sperm.

**semiconservative replication** The way in which DNA is synthesized. Each of the two partner strands in a double helix acts as a template for a new partner strand. Hence, after replication, each double helix consists of one old and one new strand.

**seminiferous tubules** The tubules within the testes within which sperm production occurs.

**senescence** [L. *senescere*: to grow old] Aging; deteriorative changes with aging; the increased probability of dying with increasing age.

**sensitive period** The life stage during which some particular type of learning must take place, or during which it occurs much more easily than at other times. Typical of song learning among birds.

**sensor** See sensory receptor cell.

**sensory neuron** A specialized neuron that transduces a particular type of sensory stimulus into action potentials.

**sensory receptor cell** Cell that is responsive to a particular type of physical or chemical stimulation.

**sensory transduction** The transformation of environmental stimuli or information into neural signals.

**sepal** (see' pul) [L. *sepulum*: covering] One of the outermost structures of the flower, usually protective in function and enclosing the rest of the flower in the bud stage.

**septum** (plural: septa) [L. wall] (1) A partition or cross-wall appearing in the hyphae of some fungi. (2) The bony structure dividing the nasal passages.

**sequence alignment** A method of identifying homologous positions in DNA or amino acid sequences by pinpointing the locations of deletions and insertions that have occurred since two (or more) organisms diverged from a common ancestor.

**Sertoli cells** Cells in the seminiferous tubules that nurture the developing sperm.

**sessile** (sess' ul) [L. *sedere*: to sit] Permanently attached; not able to move from one place to another. (Contrast with motile.)

**set point** In a regulatory system, the threshold sensitivity to the feedback stimulus.

**sex chromosome** In organisms with a chromosomal mechanism of sex determination, one of the chromosomes involved in sex determination.

**sex linkage** The pattern of inheritance characteristic of genes located on the sex chromosomes of organisms having a chromosomal mechanism for sex determination.

**sexual reproduction** Reproduction involving the union of gametes.

**sexual selection** Selection by one sex of characteristics in individuals of the opposite sex. Also, the favoring of characteristics in one sex as a result of competition among individuals of that sex for mates.

**Shannon diversity index** A formula for quantifying diversity that takes both species richness and species evenness into account; based on a mathematical expression of the certainty with which the next item sampled in a series can be predicted.

**shared derived trait** See synapomorphy.

**shoot system** In plants, the organ system consisting of the leaves, stem(s), and flowers.

**short tandem repeat (STR)** A short (1–5 base pairs), moderately repetitive sequence of DNA. The number of copies of an STR at a particular location varies between individuals and is inherited.

**shotgun sequencing** A relatively rapid method of DNA sequencing in which a DNA molecule is broken up into overlapping fragments, each fragment is sequenced, and high-speed computers analyze and realign the fragments. (Contrast with hierarchical sequencing.)

**side chain** See R group.

**sieve tube element** The characteristic cell of the phloem in angiosperms, which contains cytoplasm but relatively few organelles, and whose end walls (*sieve plates*) contain pores that form connections with neighboring cells.

**signal sequence** The sequence of a protein that directs the protein protein to a particular organelle.

**signal transduction pathway** The series of biochemical steps whereby a stimulus to a cell (such as a hormone or neurotransmitter binding to a receptor) is translated into a response of the cell.

**silent mutation** A change in a gene's sequence that has no effect on the amino acid sequence of a protein because it occurs in noncoding DNA or because it does not change the amino acid specified by the corresponding codon. (Contrast with frame-shift mutation, missense mutation, nonsense mutation.)

**similarity matrix** A matrix used to compare the degree of divergence among pairs of objects. For molecular sequences, constructed by summing the number or percentage of nucleotides or amino acids that are identical in each pair of sequences.

**single nucleotide polymorphisms (SNPs)** Inherited variations in a single nucleotide base in DNA that differ between individuals.

**single-strand binding protein** In DNA replication, a protein that binds to single strands of DNA after they have been separated from each other, keeping the two strands separate for replication.

**sink** In plants, any organ that imports the products of photosynthesis, such as roots, developing fruits, and immature leaves. (Contrast with source.)

**sinoatrial node** (sigh' no ay' tree al) [L. *sinus*: curve + *atrium*: chamber] The pacemaker of the mammalian heart.

**siRNAs (small interfering RNAs)** Short, double-stranded RNA molecules used in RNA interference.

**sister chromatid** Each of a pair of newly replicated chromatids.

**sister groups** Two phylogenetic groups that are each other's closest relatives.

**skeletal muscle** A type of muscle tissue characterized by multinucleated cells containing highly ordered arrangements of actin and myosin microfilaments. Also called striated muscle. (Contrast with cardiac muscle, smooth muscle.)

**skeletal systems** Organ systems that provide rigid supports against which muscles can pull to create directed movements.

**sliding DNA clamp** Protein complex that keeps DNA polymerase bound to DNA during replication.

**sliding filament theory** Mechanism of muscle contraction based on the formation and breaking of crossbridges between actin and myosin filaments, causing the filaments to slide together.

**slow-wave sleep** A state of deep, restorative sleep characterized by high-amplitude slow waves in the EEG. (Contrast with REM sleep.)

**small intestine** The portion of the gut between the stomach and the colon; consists of the duodenum, the jejunum, and the ileum.

**small nuclear ribonucleoprotein particle (snRNP)** A complex of an enzyme and a small nuclear RNA molecule, functioning in RNA splicing.

**smooth endoplasmic reticulum (SER)** Portion of the endoplasmic reticulum that lacks ribosomes and has a tubular appearance. (Contrast with rough endoplasmic reticulum.)

**smooth muscle** Muscle tissue consisting of sheets of mononucleated cells innervated by the autonomic nervous system. (Contrast with cardiac muscle, skeletal muscle.)

**sodium-potassium ( $\text{Na}^+ \text{-K}^+$ ) pump** Antiporter responsible for primary active transport; it pumps sodium ions out of the cell and potassium ions into the cell, both against their concentration gradients. Also called a sodium-potassium ATPase.

**soil horizon** See horizon.

**solute** A substance that is dissolved in a liquid (solvent) to form a solution.

**solute potential** A property of any solution, resulting from its solute contents; it may be zero or have a negative value. The more negative the solute potential, the greater the tendency of the solution to take up water through a differentially permeable membrane. (Contrast with pressure potential, water potential.)

**solution** A liquid (the solvent) and its dissolved solutes.

**solvent** Liquid in which a substance (solute) is dissolved to form a solution.

**somatic cell** [Gk. *soma*: body] All the cells of the body that are not specialized for reproduction. (Contrast with germ cell.)

**somatic mutation** Permanent genetic change in a somatic cell. These mutations affect the individual only; they are not passed on to offspring. (Contrast with germ line mutation.)

**somatosensory cortex** The region of the cerebral cortex that receives input from mechanosensors distributed throughout the body.

**somatostatin** Peptide hormone made in the hypothalamus that inhibits the release of other hormones from the pituitary and intestine.

**somite** (so' mith') One of the segments into which an embryo becomes divided longitudinally, leading to the eventual segmentation of the animal as illustrated by the spinal column, ribs, and associated muscles.

**Sorenson's index** Mathematical formula that measures beta diversity.

**source** In plants, any organ that exports the products of photosynthesis in excess of its own needs, such as a mature leaf or storage organ. (Contrast with sink.)

**spatial summation** In the production or inhibition of action potentials in a postsynaptic cell, the interaction of depolarizations and hyperpolarizations produced at different sites on the postsynaptic cell. (Contrast with temporal summation.)

**spawning** See external fertilization.

**speciation** (spee' see ay' shun) The process of splitting one population into two populations that are reproductively isolated from one another.

**species** (spee' sees) [L. kind] The base unit of taxonomic classification, consisting of an ancestor-descendant group of populations of evolutionarily closely related, similar organisms. The more narrowly defined "biological species" consists of individuals capable of interbreeding with each other but not with members of other species.

**species-area relationship** The relationship between the size of an area and the numbers of species it supports.

**species richness** The total number of species living in a region.

**specific defenses** Defensive reactions of the vertebrate immune system that are based on the reaction of an antibody to a specific antigen. (Contrast with nonspecific defenses.)

**specific heat** The amount of energy that must be absorbed by a gram of a substance to raise its temperature by one degree centigrade. By convention, water is assigned a specific heat of one.

**sperm** [Gk. *sperma*: seed] The male gamete.

**spermatid** One of the products of the second meiotic division of a primary spermatocyte; four haploid spermatids, which remain connected by cytoplasmic bridges, are produced for each primary spermatocyte that enters meiosis.

**spermatogenesis** (spur mat' oh jen' e sis) [Gk. *sperma*: seed + *genesis*: source] Gametogenesis leading to the production of sperm.

**spermatogonia** In animals, the diploid progeny of a germ cell in males.

**spherical symmetry** The simplest form of symmetry, in which body parts radiate out from a central point such that an infinite number of planes passing through that central point can divide the organism into similar halves.

**spicule** [L. arrowhead] A hard, calcareous skeletal element typical of sponges.

**spinal reflex** The conversion of afferent to efferent information in the spinal cord without participation of the brain.

**sphincter** (sfink' ter) [Gk. *spinkter*: something that binds tightly] A ring of muscle that can close an orifice, for example, at the anus.

**spindle** Array of microtubules emanating from both poles of a dividing cell during mitosis and playing a role in the movement of chromosomes at nuclear division. Named for its shape.

**spleen** Organ that serves as a reservoir for venous blood and eliminates old, damaged red blood cells from the circulation.

**spliceosome** RNA-protein complex that splices out introns from eukaryotic pre-mRNAs.

**splicing** See RNA splicing.

**spontaneous mutation** A genetic change caused by internal cellular mechanisms, such as an error in DNA replication. (Contrast with induced mutation.)

**sporangiophore** A stalked reproductive structure produced by zygosporangium fungi that extends from a hypha and bears one or many sporangia.

**sporangium** (spor an' gee um) (plural: sporangia) [Gk. *spora*: seed + *angeion*: vessel or reservoir] In plants and fungi, any specialized structure within which one or more spores are formed.

**spore** [Gk. *spora*: seed] (1) Any asexual reproductive cell capable of developing into an adult organism without gametic fusion. In plants, haploid spores develop into gametophytes, diploid spores into sporophytes. (2) In prokaryotes, a resistant cell capable of surviving unfavorable periods.

**sporocyte** Specialized cells of the diploid sporophyte that will divide by meiosis to produce four haploid spores. Germination of these spores produces the haploid gametophyte.

**sporophyte** (spor' o fyte) [Gk. *spora*: seed + *phyton*: plant] In plants and protists with alternation of generations, the diploid phase that produces the spores. (Contrast with gametophyte.)

**stabilizing selection** Selection against the extreme phenotypes in a population, so that the intermediate types are favored. (Contrast with disruptive selection.)

**stamen** (stay' men) [L. *stamen*: thread] A male (pollen-producing) unit of a flower, usually composed of an anther, which bears the pollen, and a filament, which is a stalk supporting the anther.

**starch** [O.E. *stearc*: stiff] A polymer of glucose; used by plants to store energy.

**Starling's forces** The two opposing forces responsible for water movement across capillary walls: blood pressure, which squeezes water and small solutes out of the capillaries, and osmotic pressure, which pulls water back into the capillaries.

**start codon** The mRNA triplet (AUG) that acts as a signal for the beginning of translation at the ribosome. (Contrast with stop codon.)

**stele** (steel) [Gk. *stylos*: pillar] The central cylinder of vascular tissue in a plant stem.

**stem** In plants, the organ that holds leaves and/or flowers and transports and distributes materials among the other organs of the plant.

**stem cell** In animals, an undifferentiated cell that is capable of continuous proliferation. A stem cell generates more stem cells and a large clone of differentiated progeny cells. (See also embryonic stem cell.)

**steroid** Any of a family of lipids whose multiple rings share carbons. The steroid cholesterol is an important constituent of membranes; other steroids function as hormones.

**sticky ends** On a piece of two-stranded DNA, short, complementary, one-stranded regions produced by the action of a restriction endonuclease. Sticky ends facilitate the joining of segments of DNA from different sources.

**stigma** [L. *stigma*: mark, brand] The part of the pistil at the apex of the style that is receptive to pollen, and on which pollen germinates.

**stimulus** [L. *stimulare*: to goad] Something causing a response; something in the environment detected by a receptor.

**stock** In horticulture, the root or root-bearing stem to which a bud or piece of stem from another plant (the scion) is grafted.

**stoma** (plural: stomata) [Gk. *stoma*: mouth, opening] Small opening in the plant epidermis that permits gas exchange; bounded by a pair of guard cells whose osmotic status regulates the size of the opening.

**stomatal crypt** In plants, a sunken cavity below the leaf surface in which a stoma is sheltered from the drying effects of air currents.

**stop codon** Any of the three mRNA codons that signal the end of protein translation at the ribosome: UAG, UGA, UAA.

**stratosphere** The upper part of Earth's atmosphere, above the troposphere; extends from approximately 18 kilometers upward to approximately 50 kilometers above the surface.

**stratum** (plural strata) [L. *stratos*: layer] A layer of sedimentary rock laid down at a particular time in the past.

**stretch receptor** A modified muscle cell embedded in the connective tissue of a muscle that acts as a mechanoreceptor in response to stretching of that muscle.

**striated muscle** See skeletal muscle.

**strobilus** (plural: strobili) One of several cone-like structures in various groups of plants (including club mosses, horsetails, and conifers) associated with the production and dispersal of reproductive products.

**stroma** The fluid contents of an organelle such as a chloroplast or mitochondrion.

**structural gene** A gene that encodes the primary structure of a protein not involved in the regulation of gene expression.

**structural isomers** Molecules made up of the same kinds and numbers of atoms, in which the atoms are bonded differently.

**structural motif** A three-dimensional structural element that is part of a larger molecule. For example, there are four common motifs in DNA-binding proteins: helix-turn-helix, zinc finger, leucine zipper, and helix-loop-helix.

**style** [Gk. *stylos*: pillar or column] In the angiosperm flower, a column of tissue extending from the tip of the ovary, and bearing the stigma or receptive surface for pollen at its apex.

**sub-** [L. under] A prefix used to designate a structure that lies beneath another or is less than another. For example, subcutaneous (beneath the skin); subspecies.

**suberin** A waxlike lipid that is a barrier to water and solute movement across the Caspary strip of the endodermis.

**submucosa** (sub mew koe' sah) The tissue layer just under the epithelial lining of the lumen of the digestive tract.

**subsoil** The soil horizon lying below the topsoil and above the parent rock (bedrock); the zone of infiltration and accumulation of materials leached from the topsoil. Also called the B horizon.

**substrate** (sub' strayte) The molecule or molecules on which an enzyme exerts catalytic action.

**substratum** (plural: substrata) The base material on which a sessile organism lives.

**succession** The gradual, sequential series of changes in the species composition of a community following a disturbance.

**succulence** In plants, possession of fleshy, water-storing leaves or stems; an adaptation to dry environments.

**superficial cleavage** A variation of incomplete cleavage in which cycles of mitosis occur without cell division, producing a syncytium (a single cell with many nuclei).

**suprachiasmatic nuclei (SCN)** In mammals, two clusters of neurons just above the optic chiasm that act as the master circadian clock.

**surface area-to-volume ratio** For any cell, organism, or geometrical solid, the ratio of surface

area to volume; this is an important factor in setting an upper limit on the size a cell or organism can attain.

**surface tension** The attractive intermolecular forces at the surface of liquid; especially important in water.

**surfactant** A substance that decreases the surface tension of a liquid. Lung surfactant, secreted by cells of the alveoli, is mostly phospholipid and decreases the amount of work necessary to inflate the lungs.

**survivorship ( $L_x$ )** In life tables, the proportion of individuals in a cohort that are alive at age  $x$ . A graph of this data is a survivorship curve.

**suspensor** In the embryos of seed plants, the stalk of cells that pushes the embryo into the endosperm and is a source of nutrient transport to the embryo.

**sustainable** Pertaining to the use and management of ecosystems in such a way that humans benefit over the long term from specific ecosystem goods and services without compromising others.

**symbiosis** (sim' bee oh' sis) [Gk. *sym*: together + *bios*: living] The living together of two or more species in a prolonged and intimate relationship.

**symmetry** Pertaining to an attribute of an animal body in which at least one plane can divide the body into similar, mirror-image halves. (See bilateral symmetry, radial symmetry.)

**sympathetic nervous system** The division of the autonomic nervous system that works in opposition to the parasympathetic nervous system. (Contrast with parasympathetic nervous system.)

**sympatric speciation** (sim pat' rik) [Gk. *sym*: same + *patria*: homeland] Speciation due to reproductive isolation without any physical separation of the subpopulation. (Contrast with allopatric speciation.)

**symplast** The continuous meshwork of the interiors of living cells in the plant body, resulting from the presence of plasmodesmata. (Contrast with apoplast.)

**symporter** A membrane transport protein that carries two substances in the same direction. (Contrast with antiporter, uniporter.)

**synapomorphy** A trait that arose in the ancestor of a phylogenetic group and is present (sometimes in modified form) in all of its members, thus helping to delimit and identify that group. Also called a shared derived trait.

**synapse** (sin' aps) [Gk. *syn*: together + *haptein*: to fasten] A specialized type of junction where a neuron meets its target cell (which can be another neuron or some other type of cell) and information in the form of neurotransmitter molecules is exchanged across a synaptic cleft.

**synapsis** (sin ap' sis) The highly specific parallel alignment (pairing) of homologous chromosomes during the first division of meiosis.

**synergids** [Gk. *syn*: together + *ergos*: work] In angiosperms, the two cells accompanying the egg cell at one end of the megagametophyte.

**syngamy** See fertilization.

**synonymous (silent) substitution** A change of one nucleotide in a sequence to another when that change does not affect the amino acid specified (i.e., UUA → UUG, both specifying leucine). (Contrast with nonsynonymous substitution, missense substitution, nonsense substitution.)

**systematics** The scientific study of the diversity and relationships among organisms.

**systemic acquired resistance** A general resistance to many plant pathogens following infection by a single agent.

**systemic circuit** Portion of the circulatory system by which oxygenated blood from the lungs or gills is distributed throughout the rest of the body and returned to the heart. (Contrast with pulmonary circuit.)

**systems biology** The scientific study of an organism as an integrated and interacting system of genes, proteins, and biochemical reactions.

**systole** (sis' tuh lee) [Gk. *systole*: contraction] Contraction of a chamber of the heart, driving blood forward in the circulatory system. (Contrast with diastole.)

## - T -

**T cell** A type of lymphocyte involved in the cellular immune response. The final stages of its development occur in the thymus gland. (Contrast with B cell; see also cytotoxic T cell, T-helper cell.)

**T cell receptor** A protein on the surface of a T cell that recognizes the antigenic determinant for which the cell is specific.

**T-helper cell (T<sub>H</sub>)** Type of T cell that stimulates events in both the cellular and humoral immune responses by binding to the antigen on an antigen-presenting cell; target of the HIV-I virus, the agent of AIDS. (Contrast with cytotoxic T cells.)

**T tubules** A system of tubules that runs throughout the cytoplasm of a muscle fiber, through which action potentials spread.

**taproot system** A root system typical of eudicots consisting of a primary root (*taproot*) that extends downward by tip growth and outward by initiating lateral roots. (Contrast with fibrous root system.)

**target cell** A cell with the appropriate receptors to bind and respond to a particular hormone or other chemical mediator.

**taste bud** A structure in the epithelium of the tongue that includes a cluster of chemoreceptors innervated by sensory neurons.

**TATA box** An eight-base-pair sequence, found about 25 base pairs before the starting point for transcription in many eukaryotic promoters, that binds a transcription factor and thus helps initiate transcription.

**taxon** (plural: taxa) [Gk. *taxis*: arrange, put in order] A biological group (typically a species or a clade) that is given a name.

**telencephalon** The outer, surrounding structure of the embryonic vertebrate forebrain, which develops into the cerebrum.

**telomerase** An enzyme that catalyzes the addition of telomeric sequences lost from chromosomes during DNA replication.

**telomeres** (tee' lo merz) [Gk. *telos*: end + *meros*: units, segments] Repeated DNA sequences at the ends of eukaryotic chromosomes.

**telophase** (tee' lo phase) [Gk. *telos*: end] The final phase of mitosis or meiosis during which chromosomes became diffuse, nuclear envelopes reform, and nucleoli begin to reappear in the daughter nuclei.

**template** A molecule or surface on which another molecule is synthesized in complementary fashion, as in the replication of DNA.

**template strand** In double-stranded DNA, the strand that is transcribed to create an RNA transcript that will be processed into a protein. Also

refers to a strand of RNA that is used to create a complementary RNA.

**temporal summation** In the production or inhibition of action potentials in a postsynaptic cell, the interaction of depolarizations or hyperpolarizations produced by rapidly repeated stimulation of a single point on the postsynaptic cell. (Contrast with spatial summation.)

**tendon** A collagen-containing band of tissue that connects a muscle with a bone.

**tepals** A sterile, modified, nonphotosynthetic leaf of an angiosperm flower that cannot be distinguished as a petal or a sepal.

**termination** In molecular biology, the end of transcription or translation.

**terminator** A sequence at the 3' end of mRNA that causes the RNA strand to be released from the transcription complex.

**terrestrial** (ter' reś' tree al) [L. *terra*: earth] Pertaining to or living on land. (Contrast with aquatic, marine.)

**tertiary structure** In reference to a protein, the relative locations in three-dimensional space of all the atoms in the molecule. The overall shape of a protein. (Contrast with primary, secondary, and quaternary structures.)

**test cross** Mating of a dominant-phenotype individual (who may be either heterozygous or homozygous) with a homozygous-recessive individual.

**testis** (tes' tis) (plural: testes) [L. *testis*: witness] The male gonad; the organ that produces the male gametes.

**tetanus** [Gk. *tetanos*: stretched] (1) A state of sustained maximal muscular contraction caused by rapidly repeated stimulation. (2) In medicine, an often fatal disease ("lockjaw") caused by the bacterium *Clostridium tetani*.

**tetrad** [Gk. *tettares*: four] During prophase I of meiosis, the association of a pair of homologous chromosomes or four chromatids.

**thalamus** [Gk. *thalamos*: chamber] A region of the vertebrate forebrain; involved in integration of sensory input.

**theory** [Gk. *theoria*: analysis of facts] A far-reaching explanation of observed facts that is supported by such a wide body of evidence, with no significant contradictory evidence, that it is scientifically accepted as a factual framework. Examples are Newton's theory of gravity and Darwin's theory of evolution. (Contrast with hypothesis.)

**thermoneutral zone** [Gk. *thermos*: temperature] The range of temperatures over which an endotherm does not have to expend extra energy to thermoregulate.

**thermophile** (ther' muh fyle) [Gk. *thermos*: temperature + *philos*: loving] An organism that lives exclusively in hot environments.

**thoracic cavity** [Gk. *thorax*: breastplate] The portion of the mammalian body cavity bounded by the ribs, shoulders, and diaphragm. Contains the heart and the lungs.

**thoracic duct** The connection between the lymphatic system and the circulatory system.

**threshold** The level of depolarization that causes an electrically excitable membrane to fire an action potential.

**thrombus** (throm' bus) [Gk. *thrombos*: clot] A blood clot that forms within a blood vessel and remains attached to the wall of the vessel. (Contrast with embolus.)

**thylakoid** (thigh la koid) [Gk. *thylakos*: sack or pouch] A flattened sac within a chloroplast. Thylakoid membranes contain all of the chlorophyll in a plant, in addition to the electron carriers of photophosphorylation. Thylakoids stack to form grana.

**thymine (T)** Nitrogen-containing base found in DNA.

**thymus** [Gk. *thymos*: warty] A ductless, glandular lymphoid tissue, involved in development of the immune system of vertebrates. In humans, the thymus degenerates during puberty.

**thyroid gland** [Gk. *thyreos*: door-shaped] A two-lobed gland in vertebrates. Produces the hormone thyroxin.

**thyrotropin** Hormone produced by the anterior pituitary that stimulates the thyroid gland to produce and release thyroxine. Also called thyroid-stimulating hormone (TSH).

**thyrotropin-releasing hormone (TRH)** Hormone produced by the hypothalamus that stimulates the anterior pituitary to release thyrotropin.

**thyroxine** Hormone produced by the thyroid gland; controls many metabolic processes.

**tidal volume** The amount of air that is exchanged during each breath when a person is at rest.

**tight junction** A junction between epithelial cells in which there is no gap between adjacent cells.

**tissue** A group of similar cells organized into a functional unit; usually integrated with other tissues to form part of an organ.

**tissue system** In plants, any of three organized groups of tissues—dermal tissue, vascular tissue, and ground tissue—that are established during embryogenesis and have distinct functions.

**titin** A protein that holds bundles of myosin filaments in a centered position within the sarcomeres of muscle cells. The largest protein in the human body.

**tonoplast** The membrane of the plant central vacuole.

**topsoil** The uppermost soil horizon; contains most of the organic matter of soil, but may be depleted of most mineral nutrients by leaching. Also called the A horizon.

**totipotent** [L. *toto*: whole, entire + *potens*: powerful] Possessing all the genetic information and other capacities necessary to form an entire individual. (Contrast with multipotent, pluripotent.)

**trachea** (tray' kee ah) [Gk. *trakhōia*: tube] A tube that carries air to the bronchi of the lungs of vertebrates. When plural (*tracheae*), refers to the major airways of insects.

**tracheary element** Either of two types of xylem cells—tracheids and vessel elements—that undergo apoptosis before assuming their transport function.

**tracheid** (tray' kee id) A type of tracheary element found in the xylem of nearly all vascular plants, characterized by tapering ends and walls that are pitted but not perforated. (Contrast with vessel element.)

**trade-off** The relationship between the fitness benefits conferred by an adaptation and the fitness costs it imposes. For an adaptation to be favored by natural selection, the benefits must exceed the costs.

**trait** In genetics, a specific form of a character: eye color is a character; brown eyes and blue eyes are traits. (Contrast with character.)

**transcription** The synthesis of RNA using one strand of DNA as a template.

**transcription factors** Proteins that assemble on a eukaryotic chromosome, allowing RNA polymerase II to perform transcription.

**transduction** (1) Transfer of genes from one bacterium to another by a bacteriophage. (2) In sensory cells, the transformation of a stimulus (e.g., light energy, sound pressure waves, chemical or electrical stimulants) into action potentials.

**transfection** Insertion of recombinant DNA into animal cells.

**transfer RNA (tRNA)** A family of double-stranded RNA molecules. Each tRNA carries a specific amino acid and anticodon that will pair with the complementary codon in mRNA during translation.

**transformation** (1) A mechanism for transfer of genetic information in bacteria in which pure DNA from a bacterium of one genotype is taken in through the cell surface of a bacterium of a different genotype and incorporated into the chromosome of the recipient cell. (2) Insertion of recombinant DNA into a host cell.

**transgenic** Containing recombinant DNA incorporated into the genetic material.

**translation** The synthesis of a protein (polypeptide). Takes place on ribosomes, using the information encoded in messenger RNA.

**translocation** (1) In genetics, a rare mutational event that moves a portion of a chromosome to a new location, generally on a nonhomologous chromosome. (2) In vascular plants, movement of solutes in the phloem.

**transmembrane protein** An integral membrane protein that spans the phospholipid bilayer.

**transpiration** [L. *spirare*: to breathe] The evaporation of water from plant leaves and stem, driven by heat from the sun, and providing the motive force to raise water (plus mineral nutrients) from the roots.

**transpiration-cohesion-tension mechanism** Theoretical basis for water movement in plants: evaporation of water from cells within leaves (transpiration) causes an increase in surface tension, pulling water up through the xylem. Cohesion of water occurs because of hydrogen bonding.

**transposable element** A segment of DNA that can move to, or give rise to copies at, another locus on the same or a different chromosome.

**transposon** Mobile DNA segment that can insert into a chromosome and cause genetic change.

**triglyceride** A simple lipid in which three fatty acids are combined with one molecule of glycerol.

**triploblastic** Having three cell layers.

**trisomic** Containing three rather than two members of a chromosome pair.

**tRNA** See transfer RNA.

**trochophore** (trok' o fore) [Gk. *trochos*: wheel + *phoreus*: bearer] A radially symmetrical larval form typical of annelids and mollusks, distinguished by a wheel-like band of cilia around the middle.

**trophic cascade** The progression over successively lower trophic levels of the indirect effects of a predator.

**trophic level** [Gk *trophes*: nourishment] A group of organisms united by obtaining their energy from the same part of the food web of a biological community.

**trophoblast** [Gk *trophes*: nourishment + *blastos*: sprout] At the 32-cell stage of mammalian development, the outer group of cells that will become part of the placenta and thus nourish the growing embryo. (Contrast with inner cell mass.)

**tropic hormones** Hormones produced by the anterior pituitary that control the secretion of hormones by other endocrine glands.

**tropomyosin** [troe poe my' oh sin] One of the three protein components of an actin filament; controls the interactions of actin and myosin necessary for muscle contraction.

**troponin** One of the three components of an actin filament; binds to actin, tropomyosin, and  $\text{Ca}^{2+}$ .

**troposphere** The lowest atmospheric zone, reaching upward from the Earth's surface approximately 10–17 km. Zone in which virtually all water vapor is located.

**true-breeding** A genetic cross in which the same result occurs every time with respect to the trait(s) under consideration, due to homozygous parents.

**trypsin** A protein-digesting enzyme. Secreted by the pancreas in its inactive form (trypsinogen), it becomes active in the duodenum of the small intestine.

**tubulin** A protein that polymerizes to form microtubules.

**tumor** [L. *tumor*: a swollen mass] A disorganized mass of cells. Malignant tumors spread to other parts of the body.

**tumor necrosis factor** A family of cytokines (growth factors) that causes cell death and is involved in inflammation.

**tumor suppressor** A gene that codes for a protein product that inhibits cell proliferation; inactive in cancer cells. (Contrast with oncogene.)

**turgor pressure** [L. *turgidus*: swollen] See pressure potential.

**turnover** In freshwater ecosystems, vertical movements of water that bring nutrients and dissolved  $\text{CO}_2$  to the surface and  $\text{O}_2$  to deeper water.

**tympanic membrane** [Gk. *tympanum*: drum] The eardrum.

## - U -

**ubiquinone** (yoo bic' kwi known) [L. *ubique*: everywhere] A mobile electron carrier of the mitochondrial respiratory chain. Similar to plastoquinone found in chloroplasts.

**ubiquitin** A small protein that is covalently linked to other cellular proteins identified for breakdown by the proteosome.

**ultimate cause** In ethology, the evolutionary processes that produced an animal's capacity and tendency to behave in particular ways. (Contrast with proximate cause.)

**uniporter** [L. *unus*: one + *portal*: doorway] A membrane transport protein that carries a single substance in one direction. (Contrast with antiporter, symporter.)

**unsaturated fatty acid** A fatty acid whose hydrocarbon chain contains one or more double bonds. (Contrast with saturated fatty acid.)

**upregulation** A process by which the abundance of receptors for a hormone increases when

hormone secretion is suppressed. (Contrast with downregulation.)

**upwelling zones** Areas of the ocean where cool, nutrient-rich water from deeper layers rises to the surface.

**uracil (U)** A pyrimidine base found in nucleotides of RNA.

**urea** A compound that is the main excreted form of nitrogen by many animals, including mammals.

**ureotelic** Pertaining to an organism in which the final product of the breakdown of nitrogen-containing compounds (primarily proteins) is urea. (Contrast with ammonotelic, uricotelic.)

**ureter** (your' uh tur) Long duct leading from the vertebrate kidney to the urinary bladder or the cloaca.

**urethra** (you ree' thrə) In most mammals, the canal through which urine is discharged from the bladder and which serves as the genital duct in males.

**uric acid** A compound that serves as the main excreted form of nitrogen in some animals, particularly those which must conserve water, such as birds, insects, and reptiles.

**uricotelic** Pertaining to an organism in which the final product of the breakdown of nitrogen-containing compounds (primarily proteins) is uric acid. (Contrast with ammonotelic, ureotelic.)

**urinary bladder** A structure in which urine is stored until it can be excreted to the outside of the body.

**urine** (you' rin) In vertebrates, the fluid waste product containing the toxic nitrogenous by-products of protein and amino acid metabolism.

**uterine cycle** In human females, the monthly cycle of events by which the endometrium is prepared for the arrival of a blastocyst. (Contrast with ovarian cycle.)

**uterus** (yo' ter us) [L. *utero*: womb] A specialized portion of the female reproductive tract in mammals that receives the fertilized egg and nurtures the embryo in its early development. Also called the womb.

## - V -

**vaccination** Injection of virus or bacteria or their proteins into the body, to induce immunization. The injected material is usually attenuated (weakened) before injection.

**vacuole** (vac' yew ole) Membrane-enclosed organelle in plant cells that can function for storage, water concentration for turgor, or hydrolysis of stored macromolecules.

**vagina** (vuh jine' uh) [L. sheath] In female animals, the entry to the reproductive tract.

**van der Waals forces** Weak attractions between atoms resulting from the interaction of the electrons of one atom with the nucleus of another. This type of attraction is about one-fourth as strong as a hydrogen bond.

**variable region** The portion of an immunoglobulin molecule or T-cell receptor that includes the antigen-binding site and is responsible for its specificity. (Contrast with constant region.)

**vas deferens** (plural: *vasa deferentia*) Duct that transfers sperm from the epididymis to the urethra.

**vasa recta** Blood vessels that parallel the loops of Henle and the collecting ducts in the renal medulla of the kidney.

**vascular** (vas' kew lar) [L. *vasculum*: a small vessel] Pertaining to organs and tissues that conduct fluid, such as blood vessels in animals and xylem and phloem in plants.

**vascular bundle** In vascular plants, a strand of vascular tissue, including xylem and phloem as well as thick-walled fibers.

**vascular cambium** (kam' bee um) [L. *cambiare*: to exchange] In plants, a lateral meristem that gives rise to secondary xylem and phloem.

**vascular tissue system** The transport system of a vascular plant, consisting primarily of xylem and phloem.

**vasopressin** See antidiuretic hormone.

**vector** (1) An agent, such as an insect, that carries a pathogen affecting another species. (2) A plasmid or virus that carries an inserted piece of DNA into a bacterium for cloning purposes in recombinant DNA technology.

**vegetal hemisphere** The lower portion of some animal eggs, zygotes, and embryos, in which the dense nutrient yolk settles. The *vegetal pole* is to the very bottom of the egg or embryo. (Contrast with animal hemisphere.)

**vegetative** Nonreproductive, nonflowering, or asexual.

**vegetative meristem** An apical meristem that produces leaves.

**vegetative reproduction** Asexual reproduction through the modification of stems, leaves, or roots.

**vein** [L. *vena*: channel] A blood vessel that returns blood to the heart. (Contrast with artery.)

**ventral** [L. *venter*: belly, womb] Toward or pertaining to the belly or lower side. (Contrast with dorsal.)

**ventricle** A muscular heart chamber that pumps blood through the lungs or through the body.

**venule** A small blood vessel draining a capillary bed that joins others of its kind to form a vein. (Contrast with arteriole.)

**vernization** [L. *vernalis*: spring] Events occurring during a required chilling period, leading eventually to flowering.

**vertebral column** [L. *vertere*: to turn] The jointed, dorsal column that is the primary support structure of vertebrates.

**very low-density lipoproteins (VLDLs)**

Lipoproteins that consist mainly of triglyceride fats, which they transport to fat cells in adipose tissues throughout the body; associated with excessive fat deposition and high risk for cardiovascular disease.

**vesicle** Within the cytoplasm, a membrane-enclosed compartment that is associated with other organelles; the Golgi complex is one example.

**vessel element** A type of tracheary element with perforated end walls; found only in angiosperms. (Contrast with tracheid.)

**vestibular system** (ves' bib' yew lar) [L. *vestibulum*: an enclosed passage] Structures within the inner ear that sense changes in position or momentum of the head, affecting balance and motor skills.

**vicariant event** (vey care' ee unt) [L. *vicus*: change] The splitting of a taxon's range by the imposition of some barrier to dispersal.

**villus** (vil' lus) (plural: *villi*) [L. *villus*: shaggy hair or beard] A hairlike projection from a membrane; for example, from many gut walls.

**virion** (veer' e on) The virus particle, the minimum unit capable of infecting a cell.

**virulence** [L. *virus*: poison, slimy liquid] The ability of a pathogen to cause disease and death.

**virus** Any of a group of ultramicroscopic particles constructed of nucleic acid and protein (and, sometimes, lipid) that require living cells in order to reproduce. Viruses evolved multiple times from different cellular species.

**vital capacity** The maximum capacity for air exchange in one breath; the sum of the tidal volume and the inspiratory and expiratory reserve volumes.

**vitamin** [L. *vita*: life] An organic compound that an organism cannot synthesize, but nevertheless requires in small quantities for normal growth and metabolism.

**vitelline envelope** The inner, proteinaceous protective layer of a sea urchin egg.

**viviparity** (vye vi par' uh tee) Reproduction in which fertilization of the egg and development of the embryo occur inside the mother's body. (Contrast with oviparity.)

**vivipary** Premature germination in plants.

**voltage-gated channel** A type of gated channel that opens or closes when a certain voltage exists across the membrane in which it is inserted.

**vomeronasal organ (VNO)** Chemosensory structure embedded in the nasal epithelium of amphibians, reptiles, and many mammals. Often specialized for detecting pheromones.

## - W -

**water potential** In osmosis, the tendency for a system (a cell or solution) to take up water from pure water through a differentially permeable membrane. Water flows toward the system with a more negative water potential. (Contrast with solute potential, pressure potential.)

**water vascular system** In echinoderms, a network of water-filled canals that functions in gas exchange, locomotion, and feeding.

**wavelength** The distance between successive peaks of a wave train, such as electromagnetic radiation.

**weathering** The mechanical and chemical processes by which rocks are broken down into soil particles.

**Wernicke's area** A region in the temporal lobe of the human brain that is involved with the sensory aspects of language.

**white blood cells** Cells in the blood plasma that play defensive roles in the immune system. Also called leukocytes.

**white matter** In the central nervous system, tissue that is rich in axons. (Contrast with gray matter.)

**wild-type** Geneticists' term for standard or reference type. Deviants from this standard, even if the deviants are found in the wild, are usually referred to as mutant. (Note that this terminology is not usually applied to human genes.)

**wood** Secondary xylem tissue.

## - X -

**xerophyte** (zee' row fyte) [Gk. *xerox*: dry + *phyton*: plant] A plant adapted to an environment with limited water supply.

**xylem** (zy' lum) [Gk. *xylon*: wood] In vascular plants, the tissue that conducts water and minerals; xylem consists, in various plants, of tracheids, vessel elements, fibers, and other highly specialized cells.

## - Y -

**yolk** [M.E. *yolke*: yellow] The stored food material in animal eggs, rich in protein and lipids.

**yolk sac** In reptiles, birds, and mammals, the extraembryonic membrane that forms from the endoderm of the hypoblast; it encloses and digests the yolk.

## - Z -

**zeaxanthin** A blue-light receptor involved in the opening of plant stomata.

**zona pellucida** A jellylike substance that surrounds the mammalian ovum when it is released from the ovary.

**zoospore** (zoe' o spore) [Gk. *zoon*: animal + *spora*: seed] In algae and fungi, any swimming spore. May be diploid or haploid.

**zygote** (zye' gote) [Gk. *zygotos*: yoked] The cell created by the union of two gametes, in which the gamete nuclei are also fused. The earliest stage of the diploid generation.

**zymogen** The inactive precursor of a digestive enzyme; secreted into the lumen of the gut, where a protease cleaves it to form the active enzyme.

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