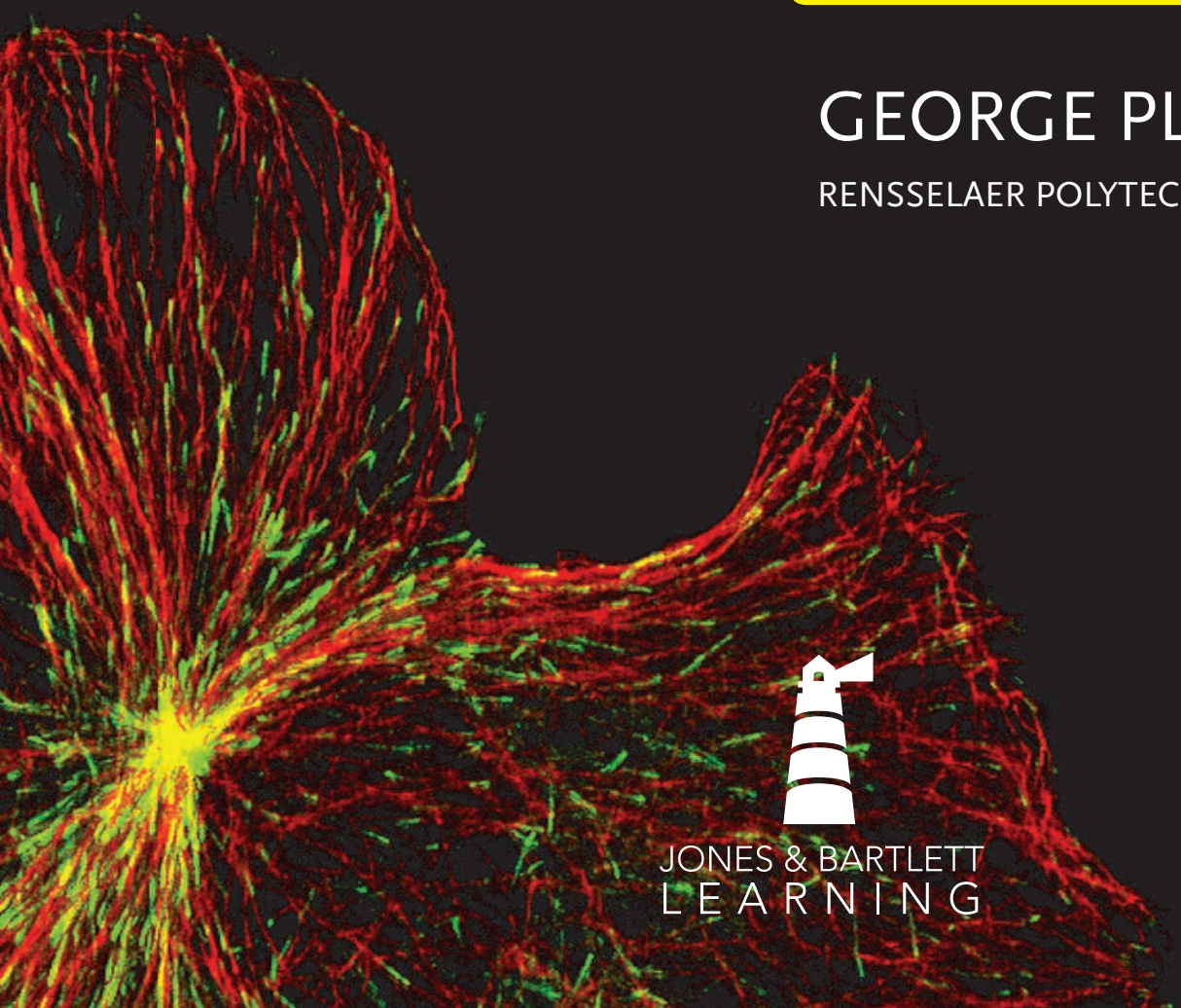
PRINCIPLES OF Cell Biology

SECOND EDITION

GEORGE PLOPPER

RENSSELAER POLYTECHNIC INSTITUTE



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05779-9

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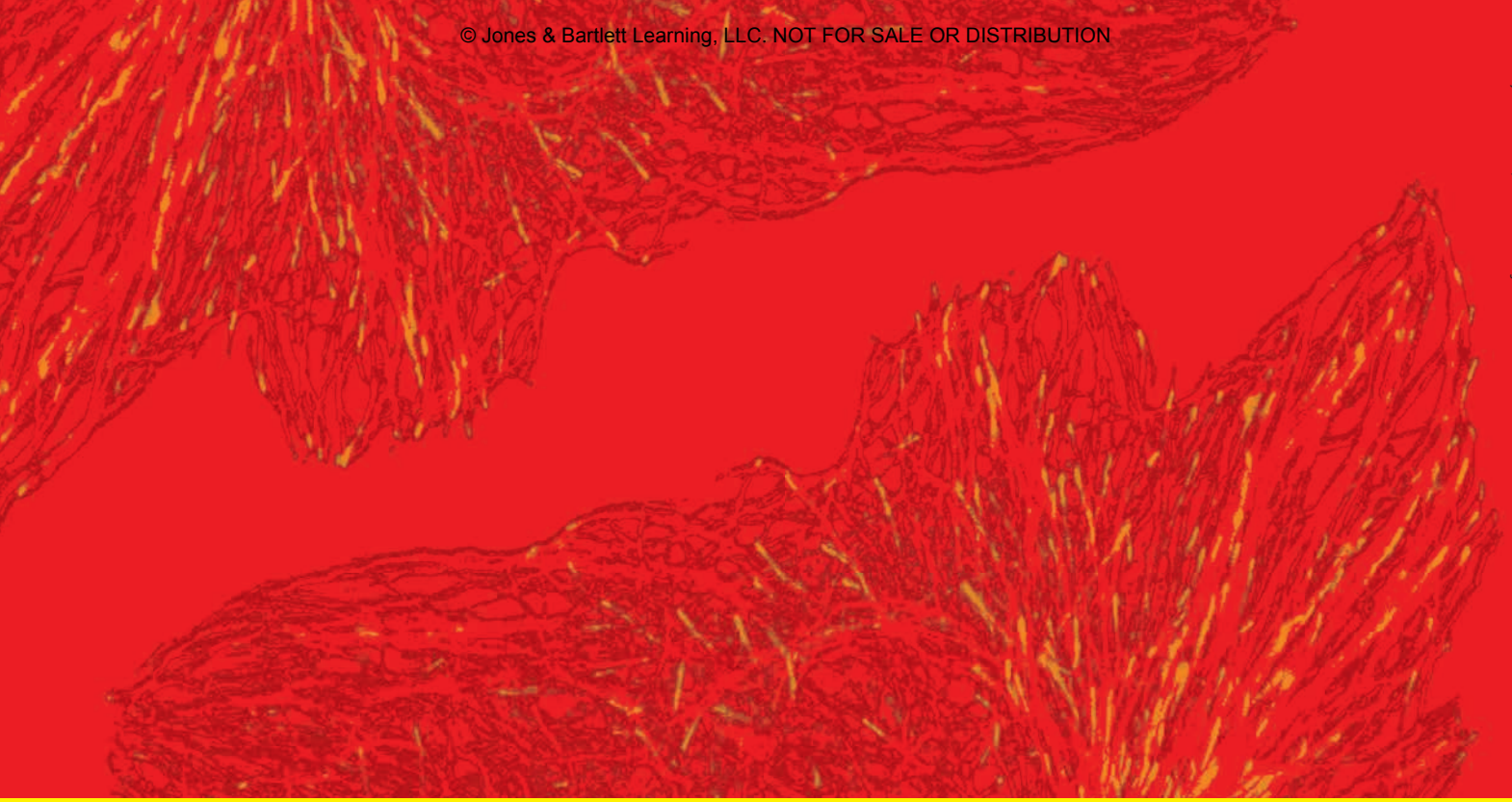
Cover Image: Courtesy of Brian O'Rourke,
Albert Einstein College of Medicine
Printing and Binding: Courier Companies
Cover Printing: Courier Companies

Library of Congress Cataloging-in-Publication Data
Plopper, George.
Principles of cell biology / George Plopper. — Second edition.
pages cm
Includes index.
ISBN 978-1-284-04760-8
1. Cytology—Textbooks. 2. Cytology—Study and teaching (Higher) I. Title.
QH581.2.P58 2013
571.6—dc23 2014008175

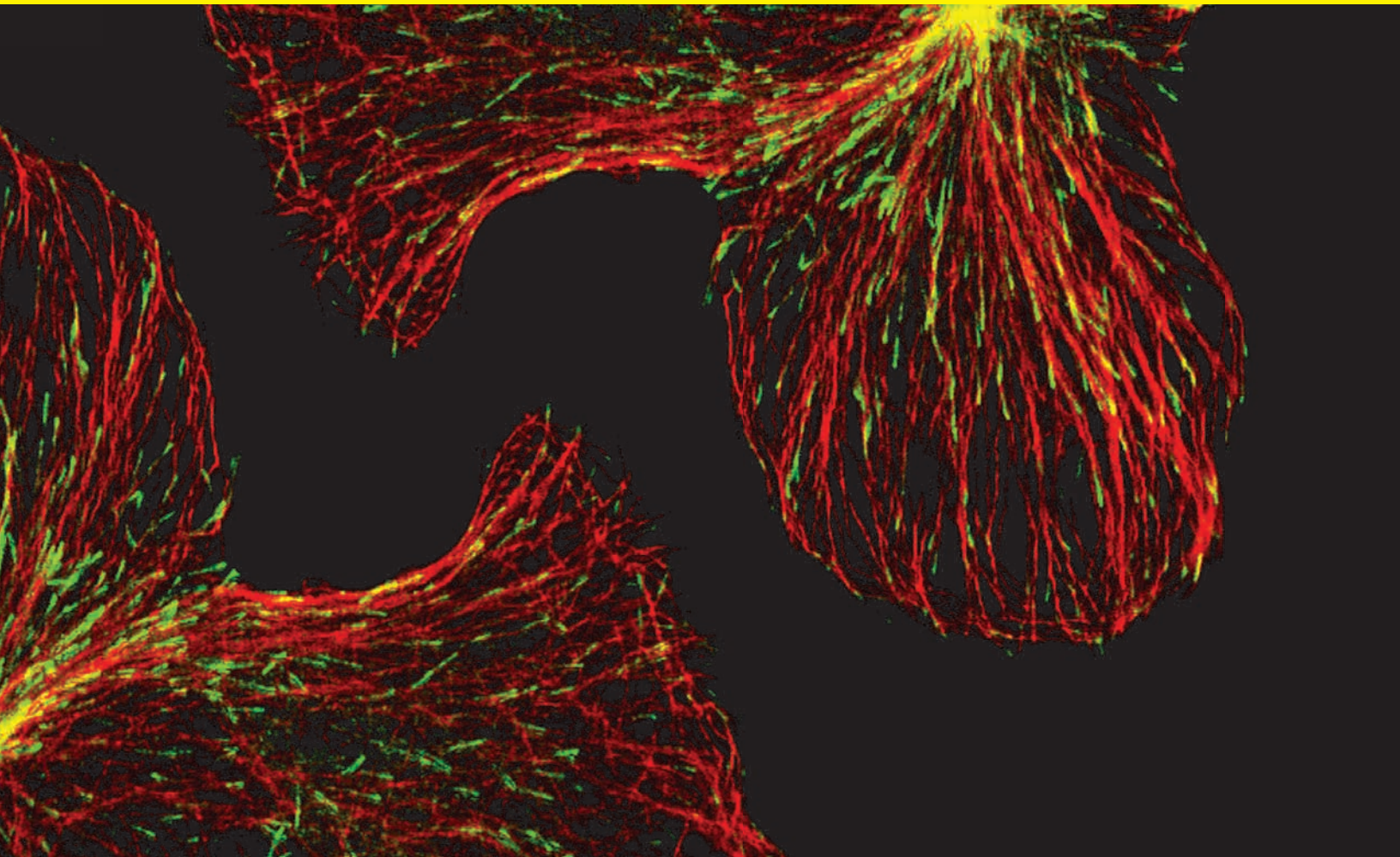
6048

Printed in the United States of America
18 17 16 15 14 10 9 8 7 6 5 4 3 2 1



Courtesy of Brian O'Rourke, Albert Einstein College of Medicine.

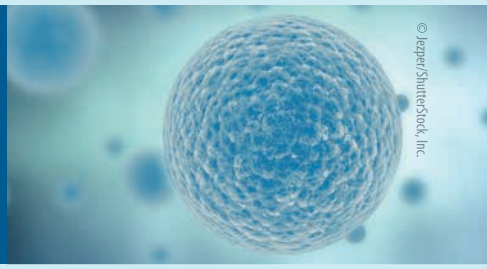
DEDICATED TO MY FAMILY:
Linda, Charlie, JoAnna, Suzanne, and Mark,
for a lifetime of support and encouragement.



Brief Table of Contents

Table of Contents

The Ten Principles of Cell Biology



Principle 1. Cells are always in motion.

Principle 2. Cells within tissues are physically contiguous with their surroundings.

Principle 3. DNA integrity is the top priority for all cells.

Principle 4. DNA encodes the function of RNAs and proteins.

Principle 5. The endomembrane system serves as the cellular import/export machinery for most macromolecules.

Principle 6. Chemical bonds and ion gradients are cellular fuel.

Principle 7. Signaling networks are the nervous system of a cell.

Principle 8. Protein complexes are cellular decision-making devices.

Principle 9. Progression through the cell cycle is the most vulnerable period in a cell's life.

Principle 10. Tissues form macroscopic equivalents of individual cells.

Preface

"Nothing in education is so astonishing as the amount of ignorance it accumulates in the form of inert facts."
—Henry Adams, *The Education of Henry Adams*

As the rate of discovering facts in the sciences continues to escalate, both students and instructors must confront the age-old problem of deciding what material matters most, especially at the introductory level. In my own experience, even the most enthusiastic students have great difficulty distinguishing essential facts in cell biology from more technical details. Given the heavy emphasis on memorization in most K–12 programs, many introductory-level college students resort to storing as much information as possible in short-term memory, only to discover later that they've missed the underlying concepts that give these facts their significance. In the past 20 years of teaching, I have spent as much time helping students navigate a conceptual path through the dense web of facts in cell biology as I have explaining the meaning of those facts. The purpose of this book is to help students build a conceptual framework for cell biology that will persist long after their coursework is complete.

Our Approach to Learning Cell Biology

The field of introductory cell biology enjoys a wealth of well-written texts by outstanding authors. Why write yet another introductory text? This book is needed for two important reasons. First, it overtly focuses on some of the underlying principles that illustrate both how cells function as well as how we study them. While many textbooks reference "principles" in their fields, few specifically identify these principles or explore them in detail. In contrast, this book identifies **10 specific principles of cell biology** (see page ix), and devotes a separate chapter to illustrate each one of them. As a result:

- We intentionally shift away from the traditional focus on technical details and toward a more integrative view of cellular activity that can be tailored to suit students with a broad range of backgrounds.
- Instructors have great freedom to organize technical subjects as they see fit while permitting students to build their own conceptual view of how cells solve problems. In short, because every cellular activity discussed in the text is tied directly to an overlying principle, these activities can be arranged and taught in many different combinations, at varying depths of detail, without losing focus on the Big Picture.
- Students develop a framework for evaluating facts as they encounter them, and this invites them to critically evaluate information as they learn. The principles in this book are not intended to be treated as laws, and are thus always subject to criticism and review.
- Instructors can capitalize on this organizing style to seamlessly merge supplemental material with the text as the field changes, or to emphasize specific subjects in a topics course.

- Professionals in the field can use these principles as starting points for identifying additional principles in cell biology and in other related fields, for comparing these principles in other fields of biology, and for developing a more integrated curriculum across multiple scales of biological organization. For example, mapping several courses to specific principles such as those identified in this text could assist in curriculum development and assessment at a department or program administrative level.

The second important distinguishing feature of this book is its informal, narrative writing style. This style is adopted to make even the most complex concepts accessible to students new to a scientific field, including stripping away some of the technical complexity that many introductory students find intimidating. Each chapter thus reflects my own lectures in introductory cell biology, in both style and content. Specifically, this includes:

- Liberal use of analogies that have proven effective over many years of teaching.
- Margin boxes throughout each chapter including studying tips, clarifications of apparent contradictions, explanations of naming schemes, FAQs, etc.
- Jargon is introduced gradually, after the concepts have been established, thereby de-emphasizing memorization of names.
- Ten principle-based chapters build on the foundation laid down in the first four chapters of the book, and include heavy emphasis on linking concepts across multiple chapters.
- Novel artwork is included, reflecting drawing exercises the author includes in his own lectures.

Audience

Principles of Cell Biology is written for introductory cell biology courses having an emphasis on eukaryotic cells, especially humans and other mammals. It is geared toward students in general biology, molecular biology, physiology, nursing, dental hygiene, and bioengineering. The book also provides a firm foundation for advanced programs in biological sciences, medicine, dentistry, and bioengineering.

Organization

The book consists of four chapters (1–4) that introduce the fundamental molecular building blocks of all cells: sugars, proteins, nucleic acids, and lipids. The remaining 10 chapters focus on explaining a single principle, supported by the topics typically discussed in cell biology courses. One important departure from most other books is that the topics of membrane transport and metabolism are covered in the same chapter (Chapter 10), though membrane transport is discussed in its own chapter subsection so it can be read independent of the metabolism sections if desired.

Through the use of cross-references, some chapters can be clustered into broader themes. Chapters 5 and 6 focus on the cytoskeleton and extracellular matrix, respectively, to explain how cells establish, maintain, and modify their shapes. Chapters 7–9 focus on DNA replication, transcription, translation, protein sorting, and the endomembrane system to illustrate the theme of information transfer from DNA to proteins. Chapters 11–13

use signal transduction as a unifying theme to illustrate the relationships among signaling pathways, control of gene expression, and cell growth/apoptosis. Finally, Chapter 14 evaluates the principles from earlier chapters at the tissue level, unifying the entire cell into a single functional unit of a multicellular organism.

Each chapter contains pedagogical features to assist instructors and facilitate student comprehension. These include:

- An introductory section, called The Big Picture, explains the learning objectives for the chapter, the relationship the chapter's subject matter shares with other chapters, and, in the last 10 chapters, introduces the Principle that the chapter illustrates.
- Every major section in each chapter includes a bulleted list of key concepts.
- Each chapter contains Concept Check questions at the end of major sections to test comprehension of the section, with answers provided at the end of the chapter. The test bank includes exam questions that link to these concept check questions.
- End-of-chapter questions ask students to integrate material across chapter sections and across different chapters.

Acknowledgments

Just as cell biology is a collaborative science, creating and publishing this textbook is the product of my extensive collaboration with the outstanding editorial and production team at Jones & Bartlett Learning, artists, my professional colleagues, and the external reviewers. I offer my deepest thanks to everyone who helped take this project from its very humble beginning to the finished product. This list includes, but is not limited to, the following individuals: Cathy Esperti, Erin O'Connor, Matt Kane, Raven Heroux, Lauren Miller, and Lou Bruno. Special thanks are extended to Elizabeth Morales, who developed the art program. Special thanks to Dr. Jeffrey Pommerville, who let me use his "To the Student" section for this book. Thanks are also extended to Sheldon R. Gordon of Oakland University and Sara G. Cline of Athens State University for their assistance with writing test questions for the book.

The author and publisher would like to thank the following individuals for serving as reviewers in the preparation of this *Second Edition*:

Jennifer L. Bath, Concordia College
Wade Bell, Virginia Military Institute
Ken Cao, University of Maryland College Park
Claudette P. Davis, George Mason University
Erastus C. Dudley, Huntingdon College
David E. Featherstone, University of Illinois at Chicago
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Sheldon R. Gordon, Oakland University
Charles H. Mallery, University of Miami
Bob Morris, Wheaton College
Dina L. Newman, Rochester Institute of Technology
Mark Running, University of Louisville
Robert Seiser, Roosevelt University

Thanks are also extended to those who have previously reviewed *Principles of Cell Biology:*

Soohyoun Ahn, Arkansas State University
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Carol Castaneda, Indiana University Northeast
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Hongmin Qin, Texas A&M University
Eric Sikorski, University of Tampa

Finally, I wish to thank my current and former students, who simultaneously ask the utmost of me and provide much of the inspiration and imaginative ideas to spur me on. I salute you and look forward to hearing your ideas for making this text as effective and enjoyable as possible.

George Plopper

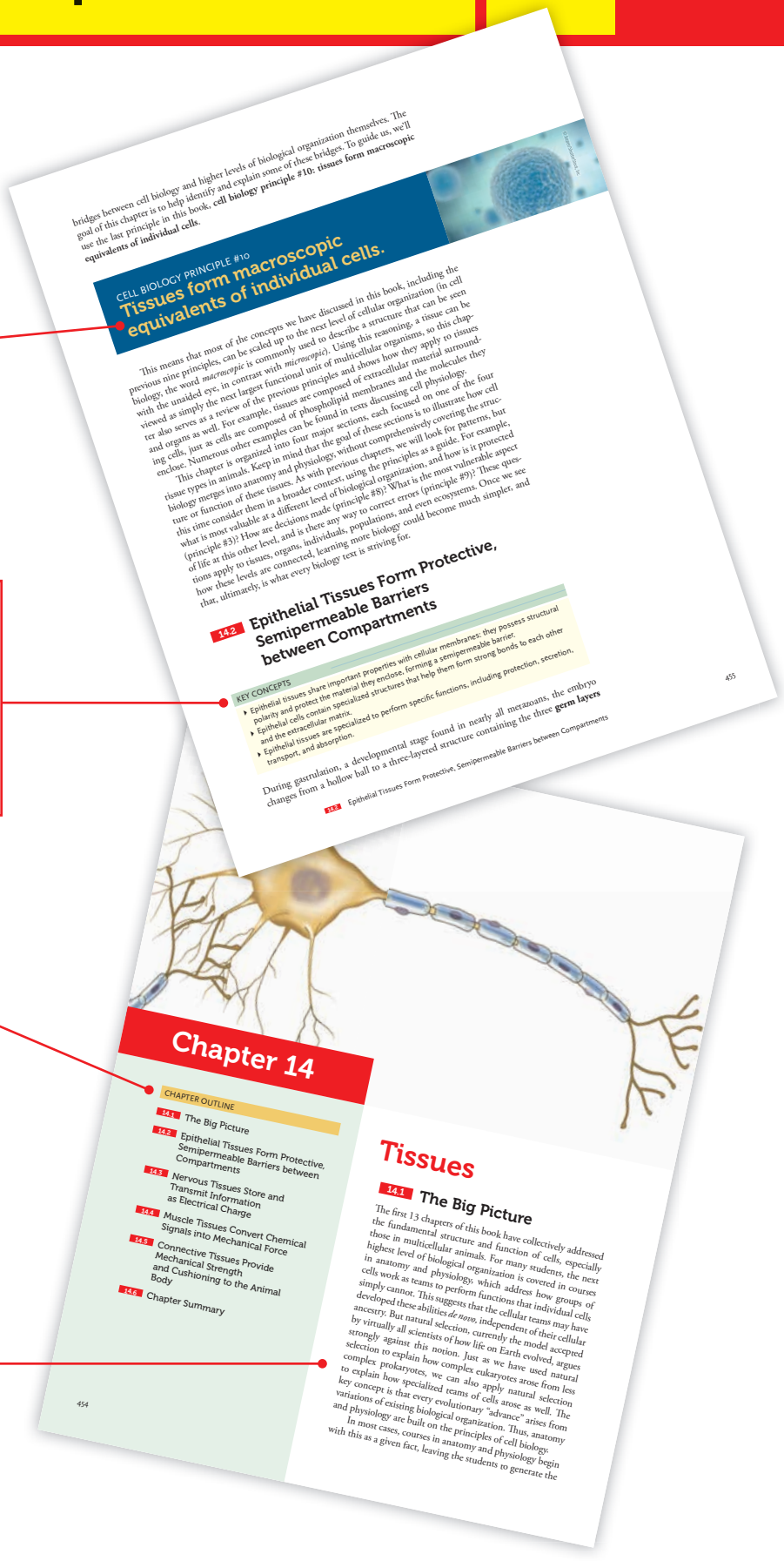
The Student Experience

The 10 Principles of Cell Biology—The *Second Edition* has been thoroughly redesigned to better identify and illuminate the 10 Principles of Cell Biology (page ix). This breakdown into 10, easy-to-understand principles provides students with the formula for understanding how cells function as well as how we study them.

Key Concepts—A list of Key Concepts at the start of each section provides a framework of the core cell biology concepts for students as they read through the section. Students should refer back to the Key Concepts as they progress through the section and eventually to the Concept Check question.

Chapter Outlines—Along with The Big Picture, a Chapter Outline is included at the start of every chapter. This list succinctly identifies the sections readers will encounter as they progress through a chapter. It provides students with a clear understanding of the overarching topics that pertain to the cell biology principle under discussion.

The Big Picture—Written in a conversational tone, The Big Picture opens every chapter and identifies and explains the objectives of the chapter. Students should carefully read it to guide their focus before diving into the chapter. As they progress through the chapter, they should think critically about these objectives to ensure they fully understand the cell biology principle being covered.

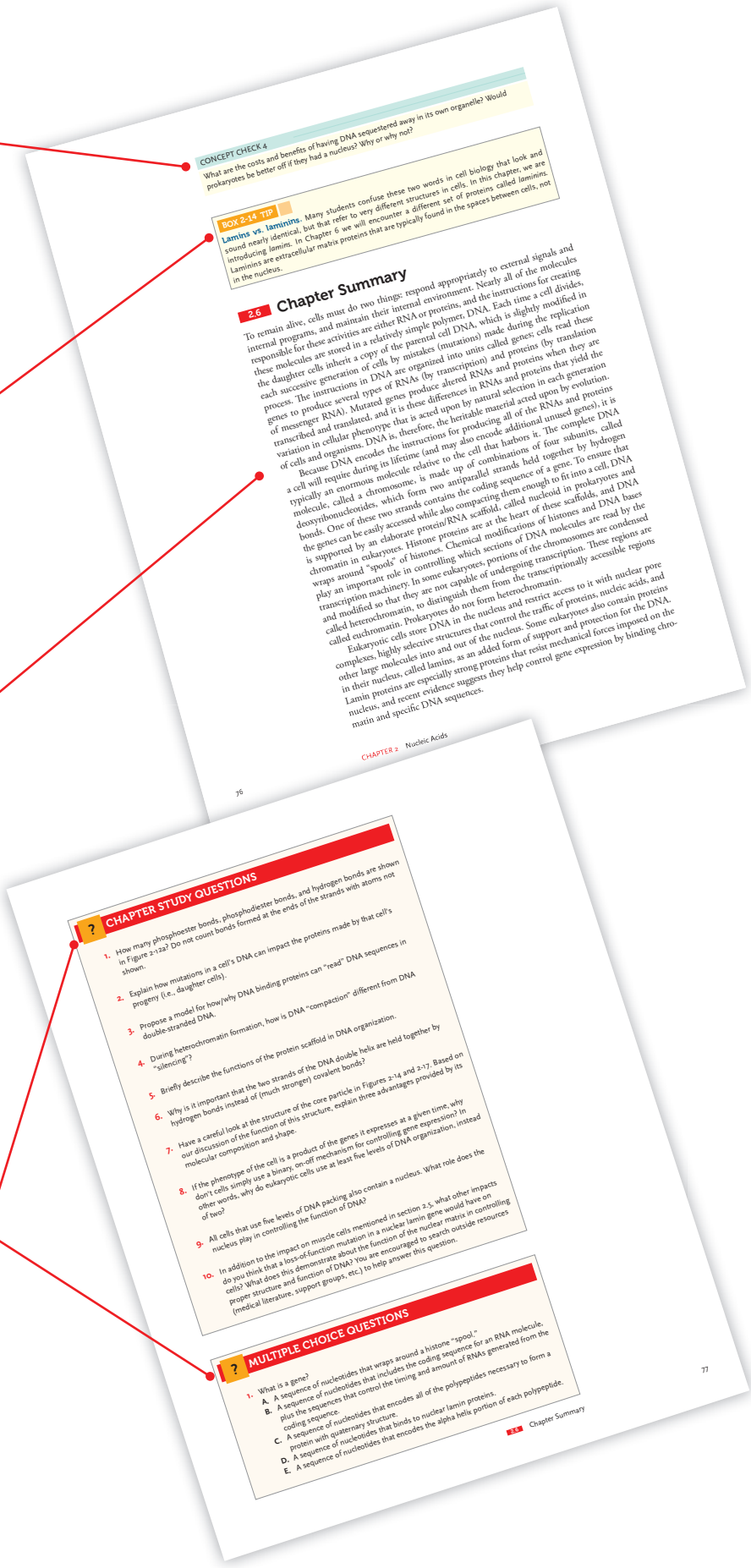


Concept Checks—Each section opens with a list of key concepts to help guide readers' focus and concludes with a Concept Check question. Answers are provided in the back of the book so students can instantly check their comprehension of section material.

Box Tips—Helpful boxes throughout each chapter include study tips, clarifications of apparent contradictions, explanations of naming schemes, FAQs, and more. These boxes clarify and complement section and chapter material as well as offer additional interesting cell biology information.

Chapter Summaries—To ensure readers thoroughly grasp the important concepts, each chapter concludes with a comprehensive Chapter Summary to provide students with a clear understanding of the cell biology principle under discussion. Students can review the summary before diving into the chapter to direct their study and can also use it as a study tool to prepare for course lectures and exams.

Chapter Study Questions—New, thought-provoking, end-of-chapter questions, including open-ended and multiple choice, integrate material across chapter sections and assess students' retention of core cellular concepts. The answers are at the back of the book, providing students with a complete learning and study solution.


CONCEPT CHECK 4

What are the costs and benefits of having DNA sequestered away in its own organelle? Would prokaryotes be better off if they had a nucleus? Why or why not?

BOX 2-14 TIP

Lamins vs. laminins. Many students confuse these two words in cell biology that look and sound nearly identical, but that refer to very different structures in cells. In this chapter, we are introducing *lamins*. In Chapter 6 we will encounter a different set of proteins called *laminins*. Laminins are extracellular matrix proteins that are typically found in the spaces between cells, not in the nucleus.

2.6 Chapter Summary

To remain alive, cells must do two things: respond appropriately to external signals and internal programs, and maintain their internal environment. Nearly all of the molecules responsible for these activities are either RNA or proteins, and the instructions for creating these molecules are stored in a relatively simple polymer, DNA. Each time a cell divides, the daughter cells inherit a copy of the parental cell DNA, which is slightly modified in each successive generation of cells by mistakes (mutations) made during the replication process. The instructions in DNA are organized into units called genes; cells read these genes to produce several types of RNAs (by transcription) and proteins when they are transcribed and translated, and it is these differences in RNAs and proteins that yield the variation in cellular phenotype that is acted upon by natural selection in each generation of cells and organisms. DNA is, therefore, the heritable material acted upon by evolution.

Because DNA encodes the instructions for producing all of the RNAs and proteins a cell will require during its lifetime (and may also encode additional unused genes), it is typically an enormous molecule relative to the cell that harbors it. The complete DNA molecule, called a chromosome, is made up of combinations of four subunits, called deoxyribonucleotides, which form two antiparallel strands held together by hydrogen bonds. One of these two strands contains the coding sequence of a gene. To ensure that the genes can be easily accessed while also compacting them enough to fit into a cell, DNA is supported by an elaborate protein/RNA scaffold, called nucleoid in prokaryotes and chromatin in eukaryotes. Histone proteins are at the heart of these scaffolds, and DNA wraps around "spools" of histones. Chemical modifications of histones and DNA bases play an important role in controlling which sections of DNA molecules are read by the transcription machinery. In some eukaryotes, portions of the chromosomes are condensed and modified so that they are not capable of undergoing transcription. These regions are called heterochromatin, to distinguish them from the transcriptionally accessible regions called euchromatin. Prokaryotes do not form heterochromatin.

Eukaryotic cells store DNA in the nucleus and restrict access to it with nuclear pore complexes, highly selective structures that control the traffic of proteins, nucleic acids, and other large molecules into and out of the nucleus. Some eukaryotes also contain proteins in their nucleus, called lamins, as an added form of support and protection for the DNA. Lamin proteins are especially strong proteins that resist mechanical forces imposed on the nucleus, and recent evidence suggests they help control gene expression by binding chromatin and specific DNA sequences.

CHAPTER 2 Nucleic Acids 76

CHAPTER STUDY QUESTIONS

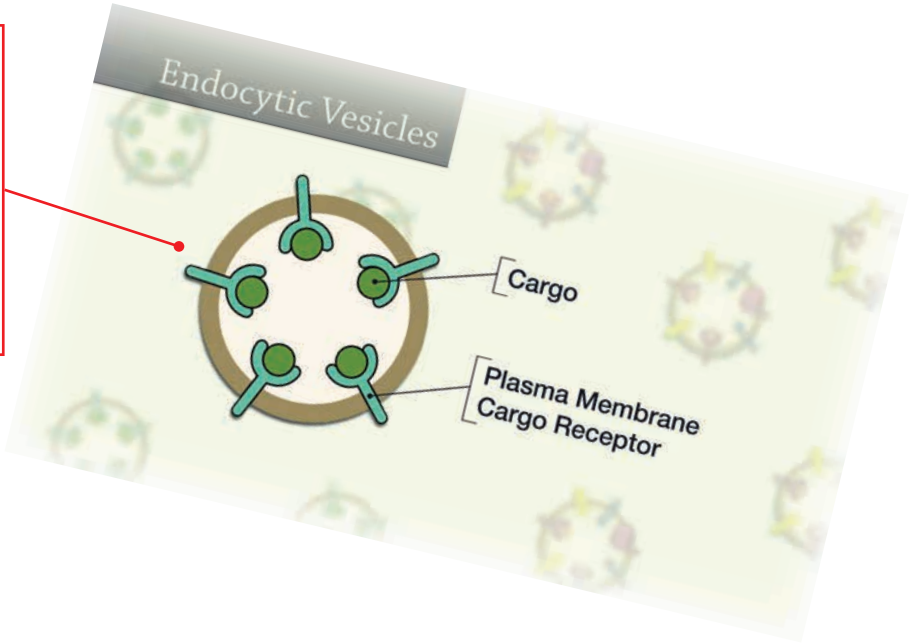
1. How many phosphoester bonds, phosphodiester bonds, and hydrogen bonds are shown in Figure 2-12a? Do not count bonds formed at the ends of the strands with atoms not shown.
2. Explain how mutations in a cell's DNA can impact the proteins made by that cell's progeny (i.e., daughter cells).
3. Propose a model for how/why DNA binding proteins can "read" DNA sequences in double-stranded DNA.
4. During heterochromatin formation, how is DNA "compaction" different from DNA "silencing"?
5. Briefly describe the functions of the protein scaffold in DNA organization.
6. Why is it important that the two strands of the DNA double helix are held together by hydrogen bonds instead of (much stronger) covalent bonds?
7. Have a careful look at the structure of the core particle in Figures 2-14 and 2-17. Based on our discussion of the function of this structure, explain three advantages provided by its molecular composition and shape.
8. If the phenotype of the cell is a product of the genes it expresses at a given time, why don't cells simply use a binary, on-off mechanism for controlling gene expression? In other words, why do eukaryotic cells use at least five levels of DNA organization, instead of two?
9. All cells that use five levels of DNA packing also contain a nucleus. What role does the nucleus play in controlling the function of DNA?
10. In addition to the impact on muscle cells mentioned in section 2.5, what other impacts do you think that a loss-of-function mutation in a nuclear lamin gene would have on cells? What does this demonstrate about the function of the nuclear matrix in controlling proper structure and function of DNA? You are encouraged to search outside resources (medical literature, support groups, etc.) to help answer this question.

MULTIPLE CHOICE QUESTIONS

1. What is a gene?
   A. A sequence of nucleotides that wraps around a histone "spool."
   B. A sequence of nucleotides that includes the coding sequence for an RNA molecule, plus the sequences that control the timing and amount of RNAs generated from the coding sequence.
   C. A sequence of nucleotides that encodes all of the polypeptides necessary to form a protein with quaternary structure.
   D. A sequence of nucleotides that binds to nuclear lamin proteins.
   E. A sequence of nucleotides that encodes the alpha helix portion of each polypeptide.

2.6 Chapter Summary 77

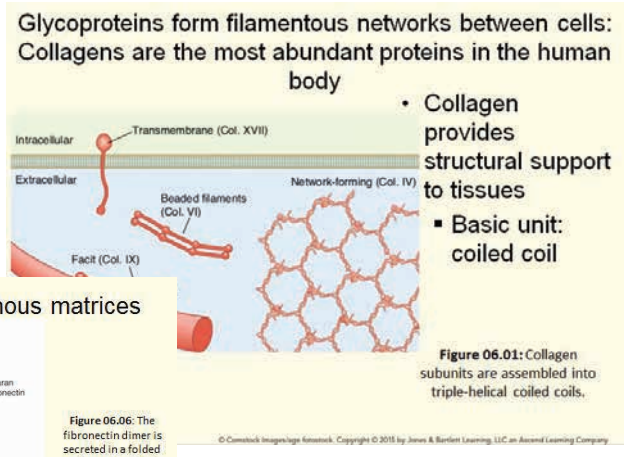
Animations—To visually assist readers in understanding key cellular processes, Jones & Bartlett Learning has developed interactive cellular biology animations. These engaging animations bring fascinating cell biology phenomena to life! Each interactive animation guides students through cellular processes and gauges students' understanding with exercises and assessment questions.

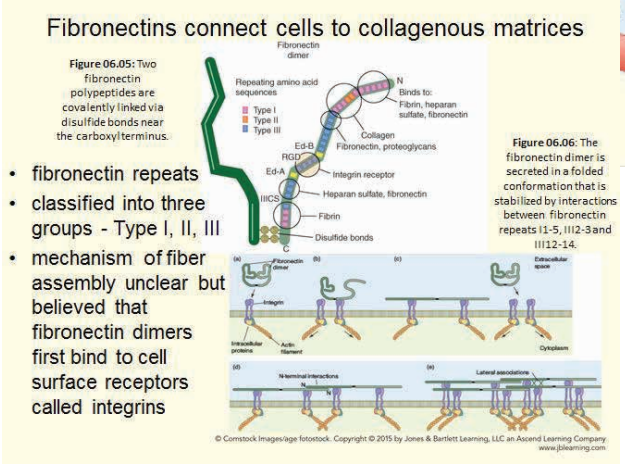


Teaching Tools

The following Teaching Tools are available to assist qualified instructors with preparations for their course.

- The **Image Bank** provides the illustrations, photographs, and tables (to which Jones & Bartlett Learning holds the copyright or has permission to reproduce digitally). You can quickly and easily copy individual images or tables into your existing lecture slides.
- The **Lecture Outlines in PowerPoint format**, developed by the author, provide lecture notes and images for each chapter of *Principles of Cell Biology, Second Edition.* Instructors with the Microsoft PowerPoint software can customize the outlines, art, and order of presentation.
- An extensive Test Bank is also available.





About the Author

Courtesy of Linda Plopper

George Plopper is a Professor in the Department of Biology at Rensselaer Polytechnic Institute in Troy, New York. He received his Bachelor of Arts in General Biology from the University of California, San Diego. He completed his PhD in Cell & Developmental Biology at Harvard University, then completed his postdoctoral training in Cell Biology at The Scripps Research Institute in La Jolla, California. Dr. Plopper served as Assistant Professor at The University of Nevada, Las Vegas before moving to his present position at Rensselaer Polytechnic Institute. He has taught cell biology to undergraduate and graduate students since 1985, receiving four teaching awards. He was named a National Academies Education Fellow in the Life Sciences by the National Academy of Sciences in 2004.

A Note to the Students

To the Student—Study Smart

Your success in cell biology—or any college or university course—will depend on your ability to study effectively and efficiently. Therefore, this textbook was designed with you, the student, in mind. The text's organization will help you improve your learning and understanding and, ultimately, your grades. The learning design illustrated below reflects this organization. Study it carefully, and, if you adopt the flow of study shown, you should be a big step ahead in your preparation and understanding of cell biology—and for that matter any subject you are taking.

When I was an undergraduate student, I hardly ever read the "To the Student" section (if indeed one existed) in my textbooks because the section rarely contained any information of importance. This one does, so please read on.

In college, I was a mediocre student until my junior year. Why? Mainly because I did not know how to study properly, and, more importantly, I did not know how to read a textbook effectively. My textbooks were filled with highlighted sentences without any plan on how I would use this "emphasized" information. In fact, most textbooks *assume* you know how to read a textbook properly. I didn't and you might not, either.

Reading a textbook is difficult if you are not properly prepared. So you can take advantage of what I learned as a student and have learned from instructing thousands of students; I have worked hard to make this text user friendly with a reading style that is not threatening or complicated. Still, there is a substantial amount of information to learn and understand, so having the appropriate reading and comprehension skills is critical. Therefore, I encourage you to spend 20 minutes reading this section, as I am going to give you several tips and suggestions for acquiring those skills. Let me show you how to be an active reader.

Be a Prepared Reader

Before you jump into reading a section of a chapter in this text, prepare yourself by finding the place and time and having the tools for study.

Place. Where are you right now as you read these lines? Are you in a quiet library or at home? If at home, are there any distractions, such as loud music, a blaring television, or screaming kids? Is the lighting adequate to read? Are you sitting at a desk or lounging on the living room sofa? Get where I am going? When you read for an educational purpose—that is, to learn and understand something—you need to maximize the environment for reading. Yes, it should be comfortable, but not to the point that you will doze off.

Time. All of us have different times during the day when we best perform a certain skill, be it exercising or reading. The last thing you want to do is read when you are tired or simply not "in tune" for the job that needs to be done. You cannot learn and understand the information if you fall asleep or lack a positive attitude. I have kept all of the chapters in this text about the same length so you can estimate the time necessary for each and plan your reading accordingly. If you have done your preliminary survey of the chapter or chapter section, you can determine about how much time you will need. If 40 minutes is needed to read—and comprehend (see below)—a section of a chapter, find the place

and time that will give you 40 minutes of uninterrupted study. Brain research suggests that most people's brains cannot spend more than 45 minutes in concentrated, technical reading. Therefore, I have avoided lengthy presentations and instead have focused on smaller sections, each with its own heading. These should accommodate shorter reading periods.

Reading Tools. Lastly, as you read this, what study tools do you have at your side? Do you have a highlighter or pen for emphasizing or underlining important words or phrases? Notice the text has wide margins that allow you to make notes or to indicate something that needs further clarification. Do you have a pencil or pen handy to make these notes? Or, if you do not want to "deface" the text, make your notes in a notebook. Lastly, some students find having a ruler is useful to prevent their eyes from wandering on the page and to read each line without distraction.

Be an Explorer Before You Read

When you sit down to read a section of a chapter, do some preliminary exploring. Look at the section head and subheadings to get an idea of what is discussed. Preview any diagrams, photographs, tables, graphs, or other visuals used. They give you a better idea of what is going to occur. We have used a good deal of space in the text for these features, so use them to your advantage. They will help you learn the written information and comprehend its meaning. Do not try to understand all the visuals, but try to generate a mental "big picture" of what is to come. Familiarize yourself with any symbols or technical jargon that might be used in the visuals.

The end of each chapter contains a **Summary** for that chapter. It is a good idea to read the summary before delving into the chapter, even though it is at the end. That way you will have a framework for the chapter before filling in the nitty-gritty information.

Be a Detective as You Read

Reading a section of a textbook is not the same as reading a novel. With a textbook, you need to uncover the important information (the terms and concepts) in the forest of words on the page. So, the first thing to do is read the complete paragraph. When you have determined the main ideas, highlight or underline them. However, I have seen students highlighting the entire paragraph in yellow, including every *a, the,* and *and.* This is an example of highlighting before knowing what is important. So, I have helped you out somewhat. Important terms and concepts are in **boldface** followed by the definition (or the definition might be in the glossary). So only highlight or underline with a pen essential ideas and key phrases—not complete sentences, if possible.

What if a paragraph or section has no boldfaced words? How do you find what is important here? From an English course, you may know that often the most important information is mentioned first in the paragraph. If it is followed by one or more examples, then you can backtrack and know what was important in the paragraph. In addition, I have added section "speed bumps" (called **Concept and Reasoning Checks**) to let you test your learning and understanding before getting too far ahead in the material. These checks also are clues to what was important in the section you just read.

Be a Repetitious Student

Brain research has shown that each individual can only hold so much information in short-term memory. If you try to hold more, then something else needs to be

removed—sort of like a full computer disk. So that you do not lose any of this important information, you need to transfer it to long-term memory—to the hard drive, if you will. In reading and studying, this means retaining the term or concept; so, write it out in your notebook *using your own words.* Memorizing a term does not mean you have learned the term or understood the concept. By writing it out in your own words, you are forced to think and actively interact with the information. This repetition reinforces your learning.

Be a Patient Student

In textbooks, you cannot read at the speed that you read your email or a magazine story. There are unfamiliar details to be learned and understood—and this requires being a patient, slower reader. Identifying the important information from a textbook chapter requires you to *slow down* your reading speed. Speed-reading is of no value here. It may help to go back and re-read sections as your general understanding of the topic improves. I use many cross-references in this book, and suggest you take the time to look up the referenced material in other chapters.

Know the What, Why, and How

Have you ever read something only to say, "I have no idea what I read!"? As I've already mentioned, reading a cell biology text is not the same as reading *Sports Illustrated* or *People* magazine. In these entertainment magazines, you read passively for leisure or perhaps amusement. In *Principles of Cell Biology,* you must read actively for learning and understanding—that is, for *comprehension.* This can quickly lead to boredom unless you engage your brain as you read—that is, be an active reader. Do this by knowing the *what, why,* and *how* of your reading.

- *What* is the general topic or idea being discussed? This often is easy to determine because the section heading might tell you. If not, then it will appear in the first sentence or beginning part of the paragraph.
- *Why* is this information important? If I have done my job, the text section will tell you why it is important or the examples provided will drive the importance home. These surrounding clues further explain why the main idea was important.
- *How* do I "mine" the information presented? This was discussed under "Be a Detective as You Read."

Have a Debriefing Strategy

After reading the material, be ready to debrief. Verbally summarize what you have learned. This will start moving the short-term information into the long-term memory storage—that is, *retention.* Any notes you made concerning confusing material should be discussed as soon as possible with your instructor. A lot of cell biology is represented visually, so allow time to draw out diagrams. Again, repetition makes for easier learning and better retention.

In many professions, such as sports, music, or the theater, the name of the game is practice, practice, practice. The hints and suggestions I have given you form a skill that requires practice to perfect and use efficiently. Be patient, things will not happen overnight; perseverance and willingness though will pay off with practice. You might also check with your college or university academic (or learning) resource center. These folks will have more ways to help you to read a textbook better and to study well overall.

Send Me a Note

In closing, I would like to invite you to write me and let me know what is good about this textbook so I can build on it and what may need improvement so I can revise it. I can be reached at the Department of Biology, Rensselaer Polytechnic Institute, 110 8th St, Troy, NY, 12180. Feel free to email me at: ploppg@rpi.edu.

I wish you great success in your cell biology course. Welcome!
—Dr. Plopper

Website: http://www.rpi.edu/~ploppg