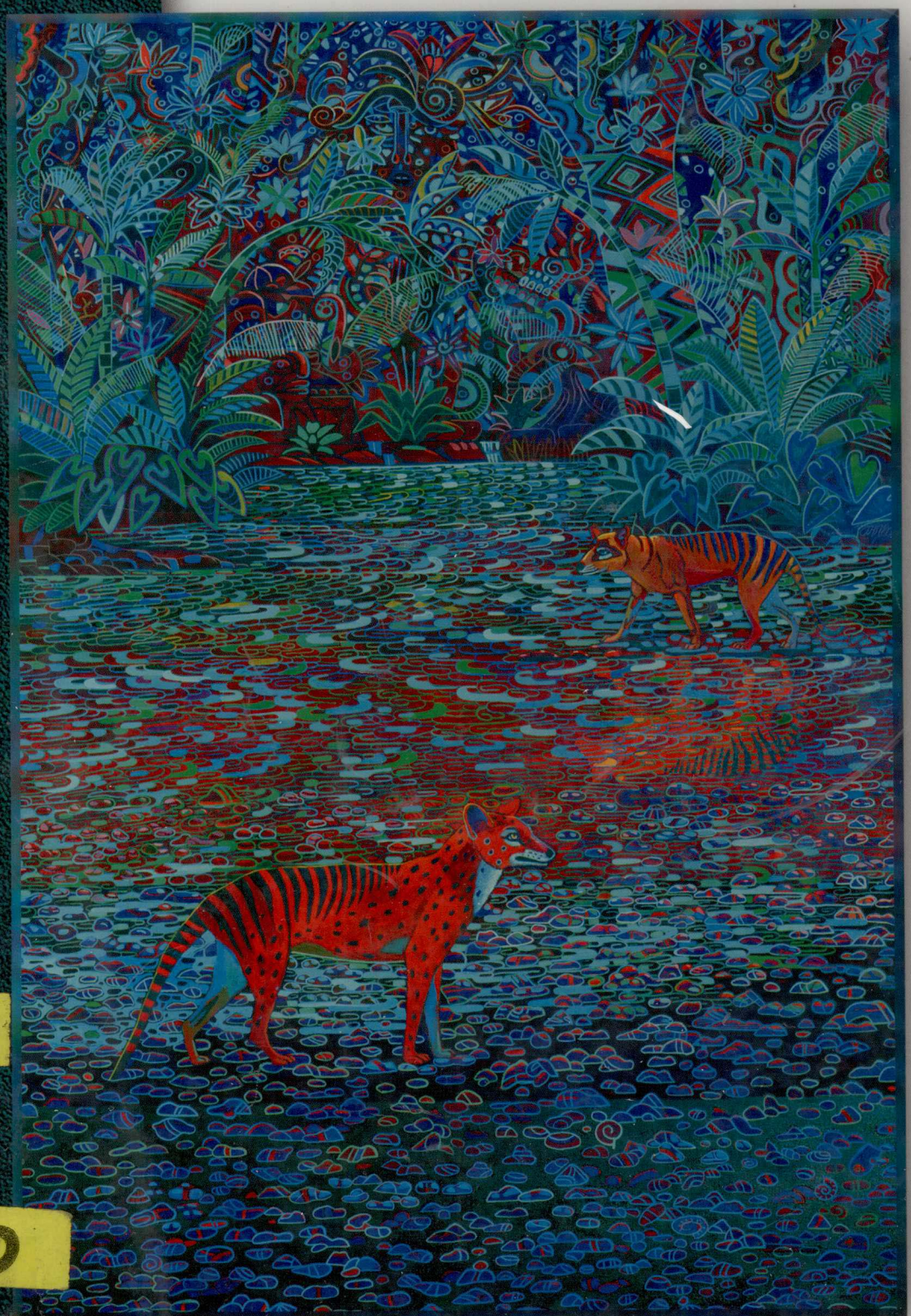
SIXTH EDITION

BIOLOGY



RAVEN
JOHNSON

BIOLOGY

Sixth Edition

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McGraw-Hill Higher Education
A Division of The McGraw-Hill Companies

BIOLOGY, SIXTH EDITION

Published by McGraw-Hill, a business unit of The McGraw-Hill Companies, Inc., 1221 Avenue of the Americas, New York, NY 10020.

2 3 4 5 6 7 8 9 0 VNH/VNH 0 9 8 7 6 5 4 3 2 1

ISBN 0-07-303120-8
ISBN 0-07-112261-3 (ISE)

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Typeface: *10/12 Janson*
Printer: *Von Hoffmann Press, Inc.*

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Library of Congress Cataloging-in-Publication Data

Raven, Peter H.
Biology / Peter H. Raven, George B. Johnson.—6th ed.
p. cm.
Includes bibliographical references and index.
ISBN 0-07-303120-8
1. Biology. I. Johnson, George B. (George Brooks), 1942- . II. Title.

QH308.2 .R38 2002
570—dc21

2001030052
CIP

INTERNATIONAL EDITION ISBN 0-07-112261-3

www.mhhe.com

Preface

We enter a new century with this sixth edition of *Biology*, one that is exploding with excitement in biology. This first year of the new millennium has seen the completion of the Human Genome Project, with the full sequence of the human genome now available for research and exploration. Embryonic stem cells were cloned for the first time in the year 2000, and offer the potential for curing a wide range of ills, from spinal cord injuries to diabetes. Golden rice, a genetically modified crop to which has been added a battery of genes that overcome deficiencies in vitamin A and iron, was planted for the first time in Asian fields. Neurobiologists for the first time caught a glimpse of the molecular basis of learning. Even taxonomy, that bastion of conservative judgments, seems to be undergoing a sea change, with molecular phylogenies forcing the redrawing of many family trees, from angiosperm plants to insects and other arthropods.

There probably has never been a more exciting time to learn biology. Adding together the years, Dr. Raven and I have been teaching biology for more than 70 years, neither of us can remember any time as fraught with promise as today. We started teaching in the sixties, also exciting times. In those revolutionary years the black box surrounding the gene machine was stripped away, revealing for the first time how DNA achieves the constancy and diversity that are the hallmarks of life. For 40 years researchers have been amplifying that picture, learning in ever-greater detail how life works.

In the last few decades, the pace of biological research has accelerated, as we have learned for the first time how to manipulate genes. In agriculture this has led to waves of controversy, in medicine to advances universally applauded. But no matter how one views genetic engineering, no one questions that it is changing the science of biology in profound ways.

What is important about these changes in biology, what excites us like no past year, is the potential to influence our health, and that of our world. Biology as a science can—indeed, must—be more than simply a trip to the zoo, an investigation of what living things are like and how they work. These things are important parts of biology, of course, the knowledge that provides the core of the science. But it can't stop there. The knowledge of biology that has been gained, especially in the last decade, provides us with a tool of unprecedented power to improve the human condition and lessen human impact on the world we share with life's other creatures.

It is with this sense of a science alive with promise that we set out in the first year of this new century to produce the sixth edition of *Biology*.

Significant Enhancements to the Sixth Edition

Every revision of a successful text starts with a plan to update areas where advances have occurred. Thus the initial plans for this sixth edition of *Biology* were to correct any errors detected by its many users, and to incorporate new findings in rapidly advancing areas of research. In publishing terms, this was to have been a "light" revision. However, that is not what happened. Inspired by the suggestions of reviewers, we found ourselves adding chapters, overhauling the way in which key chapters were organized, adding material and then more material—soon we were knee-deep in a significant revision.

Much of the focus of this sixth edition revision was on evolution, ecology, and botany, areas where there was an opportunity for exciting improvement. To revise these chapters, we recruited two young energetic biologists to provide fresh perspective. They brought with them new approaches, fresh ideas, and up-to-date knowledge of their areas of expertise. Indeed, it has been so much fun to work with them that in future editions they will join us as full coauthors of the text.

Ecology and Evolution

Professor Jonathan Losos, our colleague at Washington University, has revised the evolution and ecology sections of the text, bringing more experimental science into our discussions. Presentation of the experimental data used to derive key conclusions and concepts is key to this revision. Our goal is to better aid students to understand how the concepts arose from the research. For this reason, you will see that graphs and charts are more plentiful in these chapters.

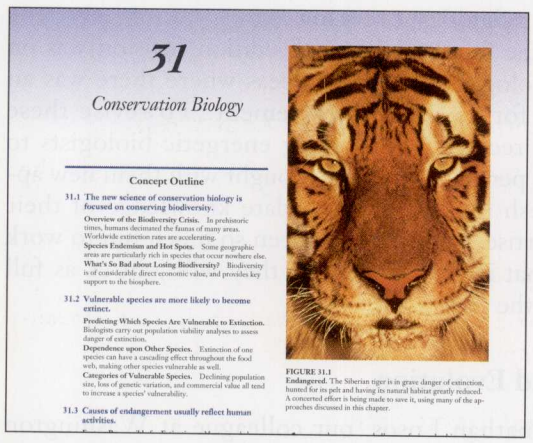
Botany

Professor Susan Singer of Carleton College has revised the botany chapters. The botany sections have benefited from a new approach where plant development takes center stage. A plant developmental biologist, she has placed the traditional discussions of evolutionary influences on plant form and function into a developmental context. Thus while evolution is still presented as the underlying explanation for the character of vascular tissue, seeds, flowers, and fruits, the developmental processes that produce these organs are now given more prominence. This does not lessen the evolutionary character of the treatment, but

rather serves to amplify it. Throughout all the botany chapters, there is an enhanced emphasis on the molecular aspects of plant life. Understanding the molecular underpinnings of plant form and function allows students to more clearly understand the evolutionary changes that have shaped them.

New Chapter: Conservation Biology (Chapter 31)

In the fifth edition, we presented a discussion of conservation biology on the *Biology* web site, as an "enhancement chapter." The response to this material was so overwhelming that we have included such a chapter in this edition of our text. In our own classroom teaching we find students to be keenly aware of the problems of dwindling natural resources, and the need to tackle the issue concretely. We feel a chapter focusing on conservation biology will be appreciated by students and useful to professors.


31

Conservation Biology

Concept Outline

31.1 The new science of conservation biology is focused on conserving biodiversity.

Overview of the Biodiversity Crisis. In prehistoric times, humans decimated the faunas of many areas. Worldwide extinction rates are accelerating.

Species Endemism and Hot Spots. Some geographic areas are particularly rich in species that occur nowhere else.

What's So Bad about Losing Biodiversity? Biodiversity is of considerable direct economic value, and provides key support to the biosphere.

31.2 Vulnerable species are more likely to become extinct.

Predicting Which Species Are Vulnerable to Extinction. Biologists carry out population viability analyses to assess danger of extinction.

Dependence upon Other Species. Extinction of one species can have a cascading effect throughout the food web, making other species vulnerable as well.

Categories of Vulnerable Species. Declining population size, loss of genetic variation, and commercial value all tend to increase a species' vulnerability.

31.3 Causes of endangerment usually reflect human activities.

FIGURE 31.1
Endangered. The Siberian tiger is in grave danger of extinction, hunted for its pelt and having its natural habitat greatly reduced. A concerted effort is being made to save it, using many of the approaches discussed in this chapter.

Genomics "Enhancement Chapter"

The rapidly advancing field of genomics is so key to the future of biology that we felt it necessary to discuss it in some way in this sixth edition. Including a chapter in the text seemed rather pointless—so much of what we would cover will have changed after the first year. So we turn again to an "enhancement chapter." We used enhancement chapters to expand information for the fifth edition of *Biology*, and as you see from above, after fine-tuning the conservation biology chapter, we now include it in this edition. The enhancement chapter on genomics can be found at *http://www/mhhe.com/raven6* This new chapter expands upon the discussion of gene technology to present and explain the advances now being made with genomics. While the chapter discusses the technology involved and the genomes that have been uncoded, it focuses on the significance of this information to biology as a science, and on what it could mean to the future of medicine, agriculture, and many other fields.

Real People Doing Real Science

We have added an inquiry-based learning experience at the beginning of every Part that walks a student through the process of scientific inquiry by examining a particular experiment. We have titled this feature "Real People Doing Real Science." After briefly reviewing the significance of the experimental question being addressed, we take the student through the actual experiment, discussing experimental design in depth, and then briefly describe the results and conclusion. This is but the first part of the learning experience. The student is then directed to the *Biology* sixth edition web site for an in-depth examination of the experiment. There a student can read the actual published research paper, allowing students to become more familiar with the primary literature. Then the student can carry out a "Virtual Experiment" where he or she is able to manipulate the parameters of the experiment and obtain data for analysis. We provide on-line questions and discussions to help the student better understand the thought process behind the experiment.


To explore this experiment further, go to the Virtual Lab at www.mhhe.com/raven6/vlab8.mhtml

A Thorough Revision

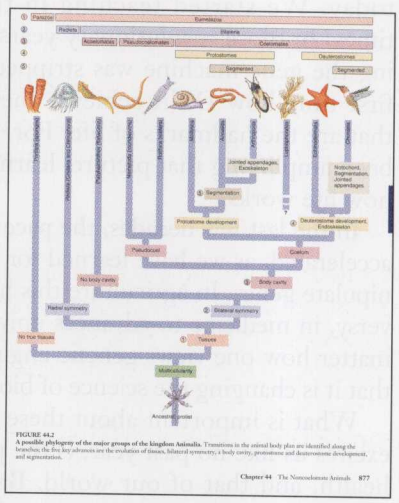


FIGURE 44.2
A possible phylogeny of the major groups of the kingdom Animalia. Transitions in the animal body plan are identified along the branches; the five key advances are the evolution of tissues, bilateral symmetry, a body cavity, protostome and deuterostome development, and segmentation.

Chapter 44 The Noncoelomate Animals 877

In addition to the extensive revisions of the ecology, evolution, and botany sections of the text, and the new chapter on conservation biology, we have thoroughly revised the rest of the text as well. Many chapters now sport radically different organizations, benefiting from extensive reviewer input. Pedagogy has been improved as well. We have included phylogenetic guideposts throughout the discussions of diversity to clarify for the student where each group fits in the tree of life. (You will find these guideposts in chapters 35, 36, 37, and 44–48.)

The Chemical Building Blocks of Life (Chapter 3)

The organization of this chapter has been turned on its head, presenting lipids before carbohydrates. This gives a greatly improved sense of the relative biological importance of these macromolecules, and actually makes the material easier to learn.

The Origin and Early History of Life (Chapter 4)

The discussion of ideas about the origin of life is now much more open-ended, stressing competing hypotheses and the key role of assumptions for which there is little data.

Photosynthesis (Chapter 10)

The internal organization of this chapter has been reworked to make it easier for students to understand how the many concepts covered in this chapter relate to one another.

Patterns of Inheritance (Chapter 13)

This chapter has been reorganized to incorporate the discussion of human genetics earlier in the chapter and then to use human examples as a means of explaining Mendelian principles.

Cellular Mechanisms of Development (Chapter 17)

We have moved the discussion of cellular development up earlier in the text, immediately following the discussion of gene expression, to reinforce key molecular concepts.

Altering the Genetic Message (Chapter 18)

Many recent advances in cancer research are highlighted, with greater emphasis on genes governing metastasis and angiogenesis.

Gene Technology (Chapter 19)

New topics such as biochips and transgenic rice have been included and rapidly advancing areas such as stem cells and ethics and regulations have been updated.

The Evidence for Evolution (Chapter 21)

We have expanded this chapter to include a complete discussion of the evolution of the horse, and have expanded the discussion of artificial selection as a means of showing the power of selection on the evolution of species.

Population Ecology (Chapter 24)

We have added and expanded the discussions of population distributions, ranges, dispersal mechanisms and human effects in examples replete with actual data.

Animal Behavior (Chapter 26) and Behavioral Ecology (Chapter 27)

We have amplified these two chapters, moving them to the ecology section, a more logical place to teach these topics.

Dynamics of Ecosystems (Chapter 28)

We have greatly expanded discussions of interactions among trophic levels and the controversial matter of how species richness influences community stability.

The Biosphere (Chapter 29)

We have expanded the discussion of evolutionary responses to environmental variation.

Evolutionary History of Plants (Chapter 37)

We now include a discussion of the green algal origin of all plants.

The Plant Body (Chapter 38)

We include a discussion of the genes involved in development of stomata, trichomes, root tissues and leaves.

How Plants Grow in Response to Their Environment (Chapter 41)

This chapter was extensively reworked and many new topics were added and expanded such as acid growth hypothesis of auxin actions, plant defense responses, cytokinin involvement in organ regeneration and crown gall tumors, brassinosteroids and oligosaccharins, transgenic tomatoes, initiating flowering, and circadian clocks.

The Noncoelomate Animals (Chapter 44)

This chapter now includes a molecular reevaluation of the evolution of the metazoan body plan.

Arthropods (Chapter 46)

New molecular data calls into question traditional classification of arthropods based on external characteristics.

Locomotion (Chapter 50)

We have added a discussion of modes of locomotion that ties together the concepts presented in the chapter.

Circulation (Chapter 52)

We have added a section on heart disease, explaining that heart disease is preventable and begins with establishing a heart-healthy lifestyle early.

Sensory Systems (Chapter 55)

We have broadened the coverage in this chapter to include more examples of nonmammalian sensory systems.

The Immune System (Chapter 57)

This chapter has been completely reorganized to improve clarity and understanding. The presentation of topics now more logically follows the process of the immune response in the body.

Real People Doing Real Science

Each of the fourteen parts of this text is introduced with a detailed look at an experiment—not a famous one, but rather the kind of experiment that real scientists do each day. There is no better way for a student to appreciate how scientific progress occurs than to get down in the trenches with the researchers doing the work.

Part I Kellar Autumn (Lewis & Clark College) and **Robert Full** (University of California, Berkeley)—*Unraveling the Mystery of How Geckos Defy Gravity.*

Part II Richard Cyr (Pennsylvania State University)—*How Do the Cells of a Growing Plant Know in Which Direction to Elongate?*

Part III Andrew Webber (Arizona State University)—*How Do Proteins Help Chlorophyll Carry Out Photosynthesis?*

Part IV Julian Adams (University of Michigan)—*Why Do Some Genes Maintain More Than One Common Allele in a Population?*

Part V Randall Johnson (University of California, San Diego)—*Can Cancer Tumors Be Starved to Death?*

Part VI John Endler (University of California, Santa Barbara) and **David Reznick** (University of California, Riverside)—*Catching Evolution in Action.*

Part VII Mark Boyce (University of Alberta, Edmonton)—*Why Do Tropical Songbirds Lay Fewer Eggs?*

Part VIII Andrew Blaustein (Oregon State University)—*Identifying the Environmental Culprit Harming Amphibians.*

Part IX Michael Houghton (Chiron)—*Discovering the Virus Responsible for Hepatitis C.*

Part X Robert Boyd (Auburn University) and **Scott Martens** (University of California, Davis)—*Why Do Some Plants Accumulate Toxic Levels of Metals?*

Part XI John Schiefelbein (University of Michigan)—*The Control of Patterning in Plant Root Development.*

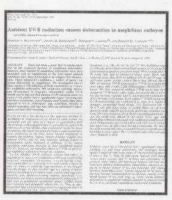
Part XII Jon Harrison (Arizona State University)—*How Honeybees Keep Their Cool.*

Part XIII Elizabeth Brainerd (University of Massachusetts, Amherst)—*Why Some Lizards Take a Deep Breath.*

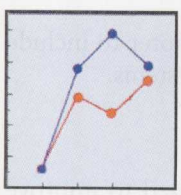
Part XIV Louis Guillette (University of Florida)—*Are Pollutants Affecting the Sexual Development of Florida's Alligators?*

Virtual Lab

To allow students to explore further, each of these fourteen experiments is linked to a far richer presentation on the internet. As an example, consider Part VIII, an experiment attempting to gain a better understanding of why many amphibian populations today are exhibiting decreasing numbers and numerous individuals with severe developmental deformities. By going to the *BIOLOGY* 6/e virtual lab devoted to this experiment (www.mhhe.com/raven6/vlab8.mhtml), a student can:

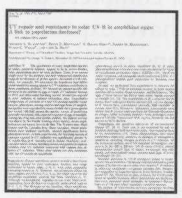


READ THE ORIGINAL RESEARCH PAPER Blaustein, Andrew R. et al., "Ambient UV-B radiation causes deformities in amphibian embryos," *Proc. Natl. Acad. Sci. USA* 1997 vol. 94: 13735–13737.

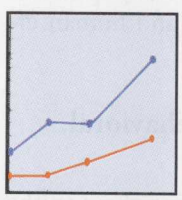


RUN A VIRTUAL EXPERIMENT EXPLORING THE ORIGINAL PAPER The student runs a virtual experiment, collects and plots data, and answers questions about the significance of the results.

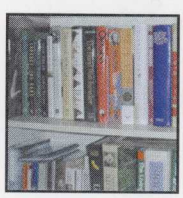
MEET THE INVESTIGATOR An interview with the principle investigator, Andrew Blaustein, with a short bio and links to his home page and publication list.



READ A RELATED PAPER Blaustein, Andrew et al., "UV repair and resistance to solar UV-B in amphibian eggs: A link to population declines?" *Proc. Natl. Acad. Sci. USA* 1994 vol. 91:1791–1795.



RUN A VIRTUAL EXPERIMENT EXPLORING THE RELATED PAPER The student is presented with a second hypothesis, to be tested with another virtual experiment.



READINGS AND ADDITIONAL RESOURCES Links to other related papers, to web sites of interest, and to relevant "*ON SCIENCE*" articles written by the author George Johnson.

Acknowledgments

William C. Ober and Claire Garrison have again enhanced the art program for this text with many new and revised full-color illustrations. Bill's artistic skills, knowledge of biology, and experience gained from an earlier career as a practicing physician have enriched this text through six of its editions. Claire practiced pediatric and obstetric nursing before turning to scientific illustration as a full-time career. Texts illustrated by Bill and Claire have received national recognition and won awards from the Association of Medical Illustrators, American Institute of Graphic Arts, Chicago Book Clinic, Printing Industries of America, and Bookbuilders West. They are also recipients of the Art Directors Award.

Our goal for *Biology* has always been to present the science in an interesting and engaging manner while maintaining a comprehensive and authoritative text. This is a lofty goal considering the mountains of information and research authors must go through just to update the text from one edition to the next. This sixth edition would not have been possible without the contributions of many. As you will see on the title page and the "Meet the Authors" section of this Preface, two new contributors joined us for the revision of this new edition of *Biology*. Jonathan Losos brought major contributions to the evolution and ecology sections, increasing the authoritativeness of the text by adding more original research to the discussions. Susan Singer had the formidable responsibility of reevaluating the botany sections to give the chapters a new and more current approach. Without Jonathan and Susan, this sixth edition would not have been possible. Eric Strauss also provided extensive reviews of the diversity chapters with recommendations for revision and modifications. His comments were greatly appreciated. The visuals are so important in a biology textbook and the superb illustrations were conceived and rendered by Bill Ober and Claire Garrison. We also thank Don and Joan Murie of Meyers Photo-Art for their excellent research of new photographs for this and past editions. Of course we are also indebted to our colleagues from across the country and around the globe that provided numerous suggestions on how to improve the sixth edition. Every one of you has our heartfelt thanks.

A major feature of *Biology* continues to be the presentation of the information into conceptual modules. It is no small feat to take the information written by four individuals along with their suggestions for figures and tables and present it in a conceptual module. This formidable task would not have been possible without the efforts of Megan Jackman, our off-site developmental editor. Her intelligence and perseverance played a major role in the high quality of this book. Liz Sievers joined our off-site development team during the revision process, and her help and support was greatly appreciated. As any author knows, a textbook is made not by a writer but by a publishing team, a group of people that guide the raw book written by the authors through a year-long process of reviewing, editing, fine-tuning, and production. This edition was particularly fortunate in its book team, led by Patrick Reidy, sponsoring editor, Lu Ann Weiss, developmental editor, Peggy Selle, project manager, Stuart Paterson, design manager, Lori Hancock, photo research coordinator, and many, many more people behind the scenes.

As always, we have had the support of wives and family who have seen less of us than they might like because of the pressures of getting this revision done. They have become accustomed to the many hours this book draws us away from them, a hidden price of textbook writing of which they are fully aware.

Acknowledgments would not be complete without thanking the generations of students who have used the many editions of this text. They have taught us at least as much as we have taught them.

Finally, we need to thank our reviewers. Every text owes a great deal to those faculty across the country who review it. Serving as sensitive antennae for errors and sounding boards for new approaches, reviewers are among the most valuable tools at an author's disposal. Many improvements in this edition are the direct result of their suggestions. Every one of them has our sincere thanks.

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Kevin Winterling *Emory & Henry College*
E. William Wischusen *Louisiana State University and Agricultural and Mechanical College*
Kenneth Wunch *Tulane University*
Mark L. Wygoda *McNeese State University*
Roger Young *Drury College*

In June 1999, at the McGraw-Hill General Biology Symposium in St. Louis, Missouri, a talented group of instructors helped us map out a plan for the revision:

Ruth Beattie *University of Kentucky*
Douglas Gaffin *University of Oklahoma*
Jon C. Glase *Cornell University*
Randy Hampton *University of California-San Diego*
Marielle Hoefnagels *University of Oklahoma*
Laurie Iten *Purdue University*
Randall S. Johnson *University of California-San Diego*
Jonathan Losos *Washington University*
Michael Meighan *University of CA-Berkeley*
Craig Peebles *University of Pittsburgh*
Susan Singer *Carleton College*
Eric Strauss *Boston College*

We wish to thank our supplement authors who worked relentlessly to prepare new materials and who so kindly provided feedback on the page proofs of *Biology*, Sixth Edition:

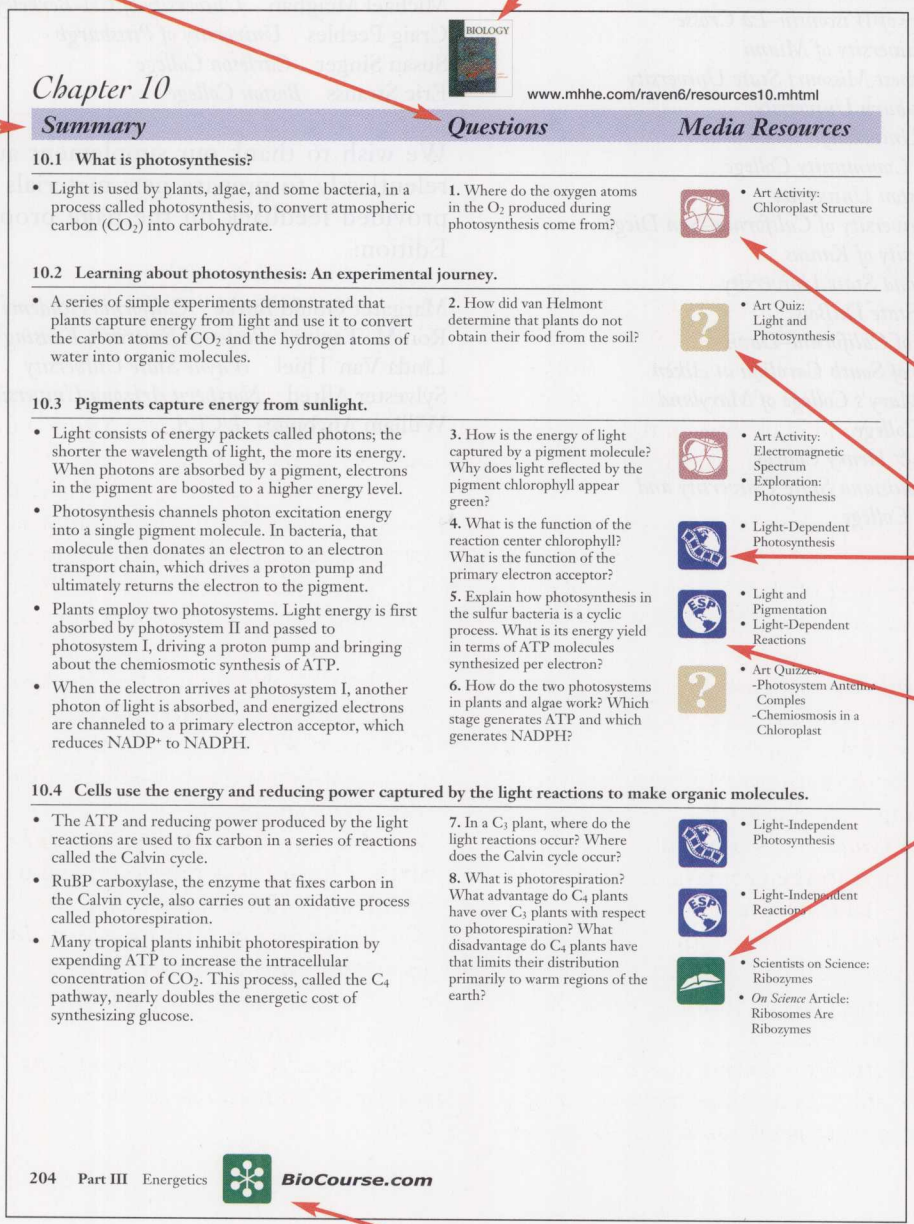
Margaret Gould Burke *California Academy of Sciences*
Ron M. Taylor *Professor Emeritus, Lansing Community College*
Linda Van Thiel *Wayne State University*
Sylvester Allred *Northern Arizona University*
William Anyonge *UCLA*

A Guide to the Learning System

Summary, Questions, and Media Resources

Located at the end of each chapter, the Summary Page links to an abundance of chapter-related learning tools.

- A link to the full collection of media resources by using the URL next to the *Biology*, Sixth Edition book cover icon at the top of the page.
- Questions for students to answer, reinforcing those most important points
- Summaries of each section, bringing together key concepts of that chapter.



Chapter 10

www.mhhe.com/raven6/resources10.mhtml

Summary	*Questions*	*Media Resources*
10.1 What is photosynthesis?		
• Light is used by plants, algae, and some bacteria, in a process called photosynthesis, to convert atmospheric carbon (CO_2) into carbohydrate.	**1.** Where do the oxygen atoms in the O_2 produced during photosynthesis come from?	• Art Activity: Chloroplast Structure
10.2 Learning about photosynthesis: An experimental journey.		
• A series of simple experiments demonstrated that plants capture energy from light and use it to convert the carbon atoms of CO_2 and the hydrogen atoms of water into organic molecules.	**2.** How did van Helmont determine that plants do not obtain their food from the soil?	• Art Quiz: Light and Photosynthesis
10.3 Pigments capture energy from sunlight.		
• Light consists of energy packets called photons; the shorter the wavelength of light, the more its energy. When photons are absorbed by a pigment, electrons in the pigment are boosted to a higher energy level. • Photosynthesis channels photon excitation energy into a single pigment molecule. In bacteria, that molecule then donates an electron to an electron transport chain, which drives a proton pump and ultimately returns the electron to the pigment. • Plants employ two photosystems. Light energy is first absorbed by photosystem II and passed to photosystem I, driving a proton pump and bringing about the chemiosmotic synthesis of ATP. • When the electron arrives at photosystem I, another photon of light is absorbed, and energized electrons are channeled to a primary electron acceptor, which reduces $NADP^+$ to NADPH.	**3.** How is the energy of light captured by a pigment molecule? Why does light reflected by the pigment chlorophyll appear green? **4.** What is the function of the reaction center chlorophyll? What is the function of the primary electron acceptor? **5.** Explain how photosynthesis in the sulfur bacteria is a cyclic process. What is its energy yield in terms of ATP molecules synthesized per electron? **6.** How do the two photosystems in plants and algae work? Which stage generates ATP and which generates NADPH?	• Art Activity: Electromagnetic Spectrum • Exploration: Photosynthesis • Light-Dependent Photosynthesis • Light and Pigmentation • Light-Dependent Reactions • Art Quizzes: -Photosystem Antenna Comples -Chemiosmosis in a Chloroplast
10.4 Cells use the energy and reducing power captured by the light reactions to make organic molecules.		
• The ATP and reducing power produced by the light reactions are used to fix carbon in a series of reactions called the Calvin cycle. • RuBP carboxylase, the enzyme that fixes carbon in the Calvin cycle, also carries out an oxidative process called photorespiration. • Many tropical plants inhibit photorespiration by expending ATP to increase the intracellular concentration of CO_2. This process, called the C_4 pathway, nearly doubles the energetic cost of synthesizing glucose.	**7.** In a C_3 plant, where do the light reactions occur? Where does the Calvin cycle occur? **8.** What is photorespiration? What advantage do C_4 plants have over C_3 plants with respect to photorespiration? What disadvantage do C_4 plants have that limits their distribution primarily to warm regions of the earth?	• Light-Independent Photosynthesis • Light-Independent Reactions • Scientists on Science: Ribozymes • *On Science* Article: Ribosomes Are Ribozymes

- A list of awesome media tools for learning that tie in to each section of the chapter.
  - —Activities such as art labeling, and exploration activities
  - —Art Quizzing
  - —Animations from Life Science Animations and Johnson Explorations
  - —ESP (Essential Study Partner) modules
  - —Readings about Scientists on Science, Student Research, Historic Experiments, and a wide range of articles by George Johnson called *On Science* Articles
- A link to a comprehensive warehouse of life science materials, professional, and student resources using the BioCourse icon at the bottom of the page.

Brief Contents

Section A. General Principles

Section B. Organismal Biology

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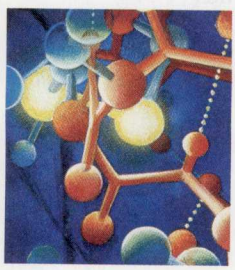
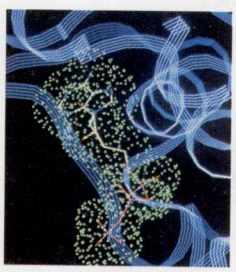
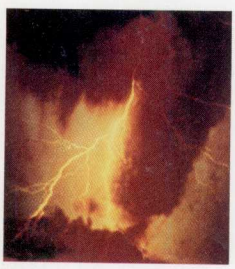
Chemical Biology

Part I The Origin of Living Things

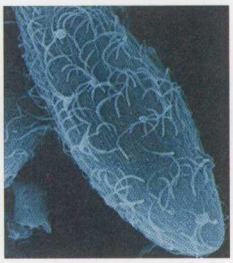


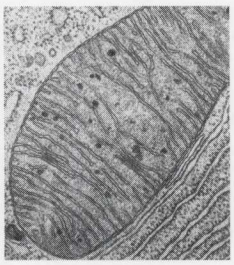


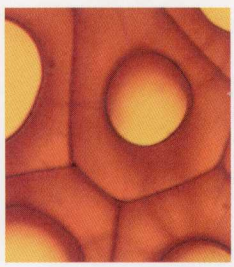


Cell Biology

Part II Biology of the Cell





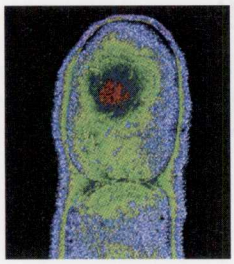


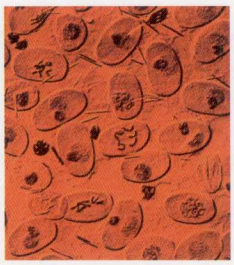
Cell Biology

Part III Energetics

Genetics

Part IV Reproduction and Heredity





Part V Molecular Genetics