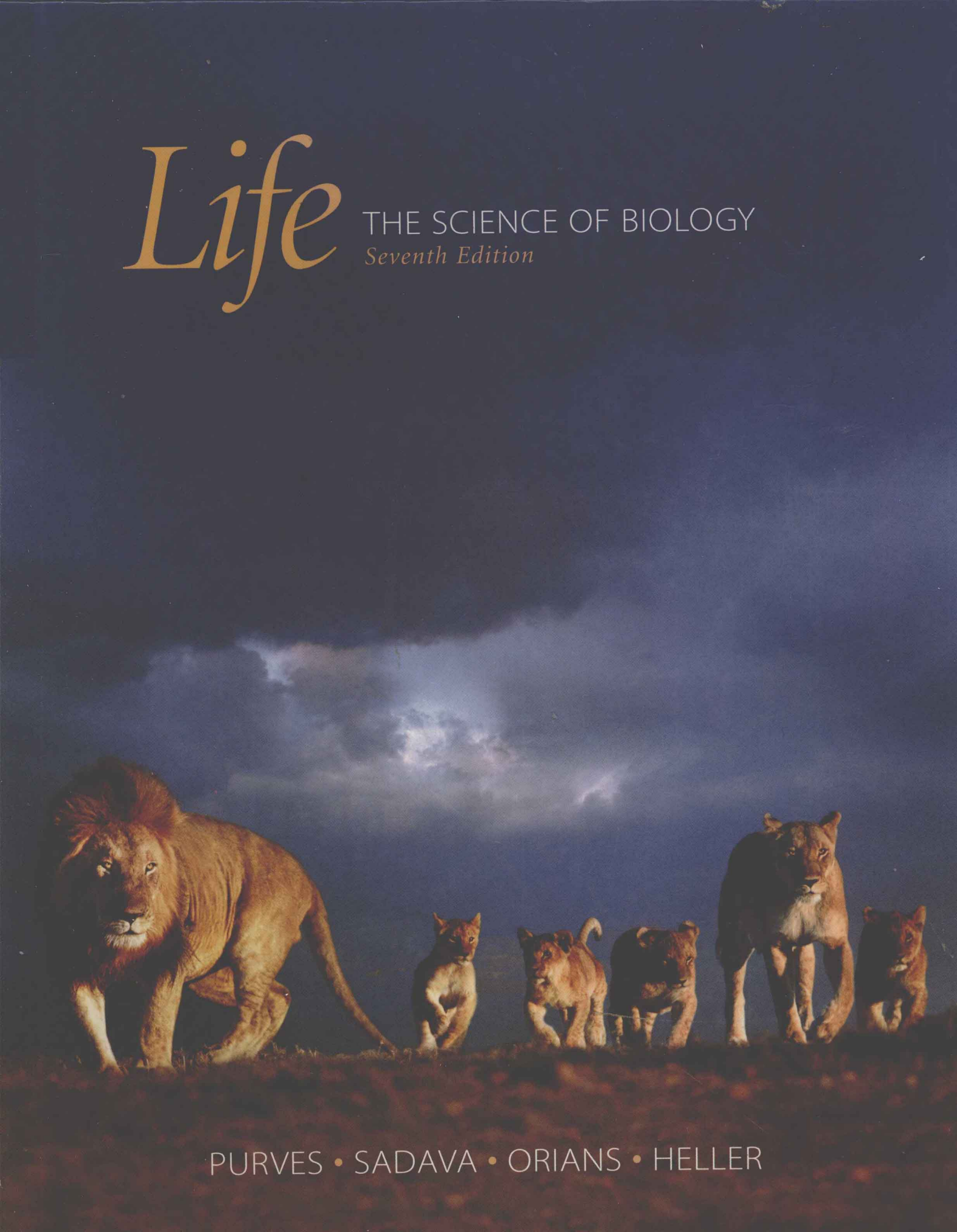
Life

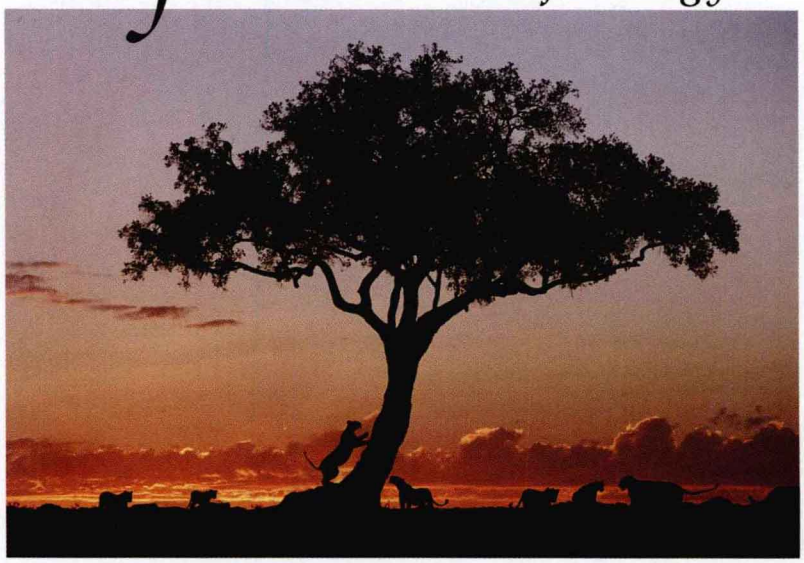
THE SCIENCE OF BIOLOGY

Seventh Edition



PURVES • SADAVA • ORIANS • HELLER

Life *The Science of Biology*



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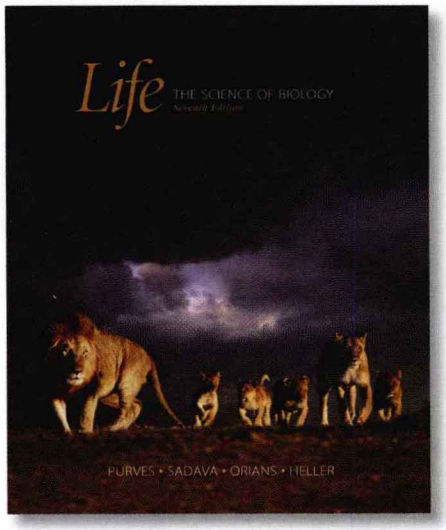

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Life

The Science of Biology

SEVENTH EDITION

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David Sadava *The Claremont Colleges • Claremont, California*

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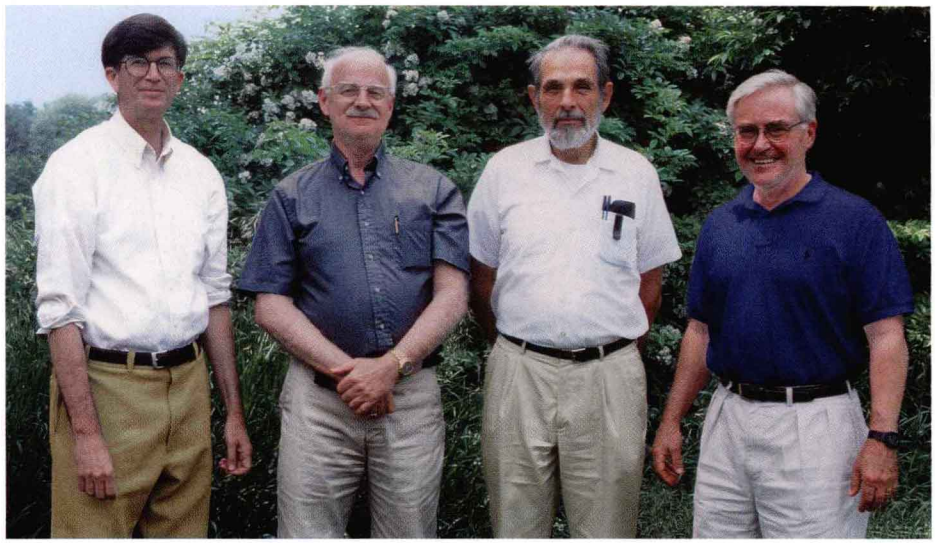
H. Craig Heller *Stanford University • Stanford, California*

To our students, especially the 25,000 we have collectively instructed in introductory biology over the years

About the Authors



David Sadava Bill Purves Gordon Orians Craig Heller

Bill Purves is Professor Emeritus of Biology as well as founder and former chair of the Department of Biology at Harvey Mudd College in Claremont, California. He received his Ph.D. from Yale University in 1959 under Arthur Galston. A fellow of the American Association for the Advancement of Science, Professor Purves has served as head of the Life Sciences Group at the University of Connecticut, Storrs, and as chair of the Department of Biological Sciences, University of California, Santa Barbara, where he won the Harold J. Plous Award for teaching excellence. His research interests focus on the chemical and physical regulation of plant growth and flowering. Professor Purves elected early retirement in 1995, after teaching introductory biology for 34 consecutive years, in order to turn his skills to writing and producing multimedia for introductory biology students.

David Sadava is the Pritzker Family Foundation Professor of Biology at the Keck Science Center of Claremont McKenna, Pitzer, and Scripps, three of The Claremont Colleges. Professor Sadava teaches and has taught courses to undergraduates in biotechnology, biochemistry, cell biology, molecular biology, plant biology, introductory biology, and cancer biology. In addition, he has taught courses in cancer to nonacademic staff members. He is a visiting professor in the Division of Biology at Caltech, and a visiting scientist in medical oncology at the City of Hope Medical Center. He is the author or coauthor of five books on cell biology and on plants, genes, and crop biotechnology. His research has resulted in over 50 papers, many coauthored with undergraduates, on topics ranging from plant biochemistry to pharmacology of narcotic analgesics to human genetic diseases. For the past decade, he and his collaborators have investigated multi-drug resistance in human small-cell lung carcinoma cells with a view to understanding and overcoming this clinical challenge.

Gordon Orians is Professor Emeritus of Biology at the University of Washington. He received his Ph.D. from the University of California, Berkeley in 1960 under Frank Pitelka. Professor Orians has been elected to the National Academy of Sciences and the American Academy of Arts and Sciences, and is a Foreign Fellow of the Royal Netherlands Academy of Arts and Sciences. He was President of the Organization for Tropical Studies, 1988–1994, and President of the Ecological Society of America, 1995–1996. He is a recipient of the Distinguished Service Award of the American Institute of Biological Sciences. Professor Orians is a leading authority in ecology, conservation biology, and evolution. His research on behavioral ecology, plant–herbivore interactions, community structure, and environmental policy has taken him to six continents. He now devotes full time to writing and to helping apply scientific information to environmental decision-making.

Craig Heller is the Lorry I. Lokey/Business Wire Professor in Biological Sciences and Human Biology at Stanford University. He earned his Ph.D. from the Department of Biology at Yale University in 1970, and then spent two years as a Postdoctoral Fellow at Scripps Institute of Oceanography studying how the brain regulates body temperature in mammals. Dr. Heller has taught at Stanford since 1972, served as Director of the Program in Human Biology, Chairman of the Biological Sciences Department, and Associate Dean of Research. Dr. Heller is a fellow of the American Association for the Advancement of Science and a recipient of the Walter J. Gores Award for excellence in teaching. His research focus is on the neurobiology of sleep and circadian rhythms, mammalian hibernation, the regulation of body temperature, and the physiology of human performance. Over the years, Dr. Heller has done research on systems ranging from sleeping college students to diving seals to hibernating bears to exercising athletes.

Preface

Like populations, textbooks evolve. Not only must the content change, but our goals must be rethought as well. We have tried, in this Seventh Edition of *Life*, to emphasize those things that will best prepare students for their future careers. The store of biological knowledge increases ever more rapidly. This requires us to seek a careful balance between thoroughness of coverage and appropriate treatment of the process, or processes, of science. We have retained and expanded the emphasis on experiment—on how things were and are learned. The emphasis remains on concepts. However, because different instructors emphasize different topics, and because a key role of the textbook is as a "place to look things up," this book is comprehensive as well. We provide sufficient detail to meet most needs without making the book too voluminous. We have enhanced our emphasis on an evolutionary theme, and have added new material on such important cutting-edge topics as evolutionary developmental biology ("evo–devo") and earth systems.

Experimental Focus

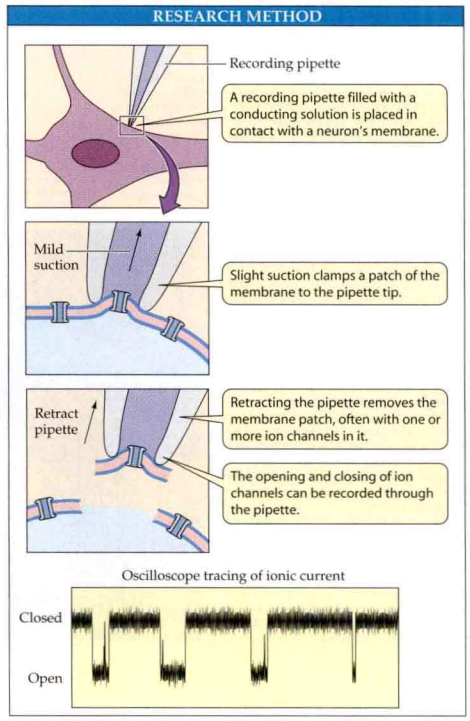
Since the First Edition of this book, we have been committed to answering the question, "How do we know?" As the book has evolved, this commitment has steadily deepened.

Obviously, we can't provide the experimental or observational evidence for every fact or theory we discuss. However, we have selected the key experiments underlying some of the most important biological principles. Some are very recent, at the cutting edge of current research; others are classics. To supplement and highlight the text discussions, we have created unique Experiment figures that show how experiments, field observations, and comparative methods help biologists formulate and test hypotheses. Other figures highlight some of the many laboratory and field methods used to do this research. In this edition there are more than 100 Experiment and Research Method figures (examples at right). In addition, we have 20 new Experiment tutorials on www.thelifewire.com, the Website/CD that was created for *Life*.

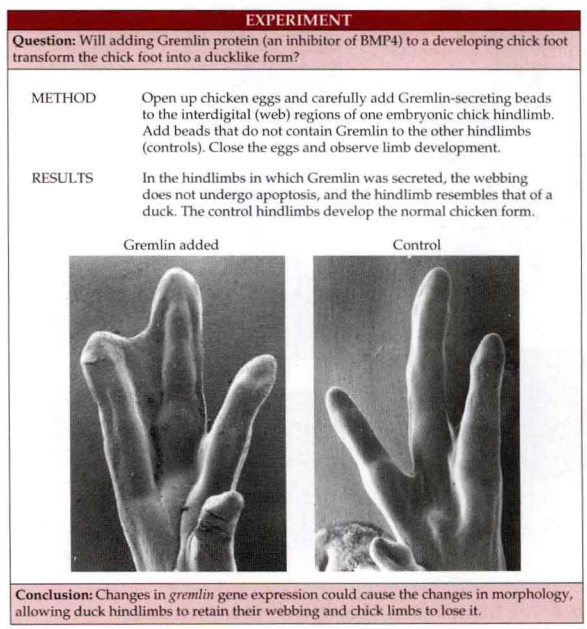
We hope that, in tandem with the frequent discussions of experimental evidence, these figures and tutorials will help students understand and appreciate the nature of biology as a vital, ongoing experimental science.

New Chapters, A New Unit, and New Essays

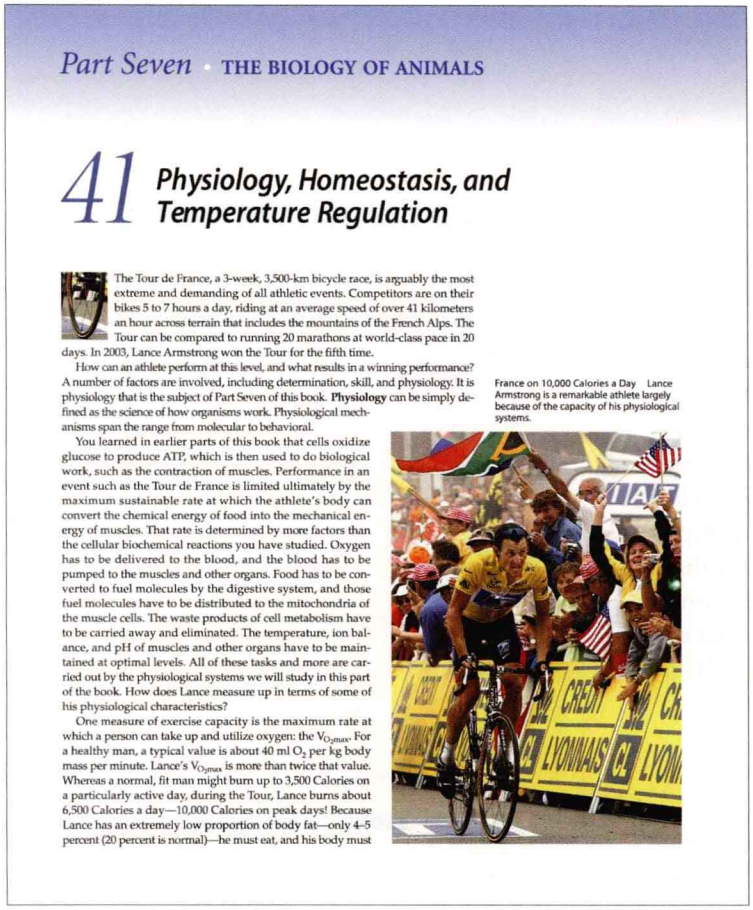
This edition features two new chapters that reflect current trends in biological research. Chapter 21 ("Development and Evolutionary Change") introduces students to evolutionary developmental biology, a rapidly growing field that deals with how the molecular genetics of the developing organism affects the evolution of complex morphology and biochemistry. In addition, the interaction of environment and embryogenesis on the ultimate form of an organism is covered at length.



44.11 Patch Clamping The patch clamping technique can record the opening and closing of a single ion channel.



21.7 Changing the Form of an Appendage In this experiment, chick hindlimbs exposed to Gremlin-secreting beads developed ducklike webbed feet.



Part Seven · THE BIOLOGY OF ANIMALS

41 Physiology, Homeostasis, and Temperature Regulation

The Tour de France, a 3-week, 3,500-km bicycle race, is arguably the most extreme and demanding of all athletic events. Competitors are on their bikes 5 to 7 hours a day, riding at an average speed of over 41 kilometers an hour across terrain that includes the mountains of the French Alps. The Tour can be compared to running 20 marathons at world-class pace in 20 days. In 2003, Lance Armstrong won the Tour for the fifth time.

How can an athlete perform at this level, and what results in a winning performance? A number of factors are involved, including determination, skill, and physiology. It is physiology that is the subject of Part Seven of this book. **Physiology** can be simply defined as the science of how organisms work. Physiological mechanisms span the range from molecular to behavioral.

You learned in earlier parts of this book that cells oxidize glucose to produce ATP, which is then used to do biological work, such as the contraction of muscles. Performance in an event such as the Tour de France is limited ultimately by the maximum sustainable rate at which the athlete's body can convert the chemical energy of food into the mechanical energy of muscles. That rate is determined by more factors than the cellular biochemical reactions you have studied. Oxygen has to be delivered to the blood, and the blood has to be pumped to the muscles and other organs. Food has to be converted to fuel molecules by the digestive system, and those fuel molecules have to be distributed to the mitochondria of the muscle cells. The waste products of cell metabolism have to be carried away and eliminated. The temperature, ion balance, and pH of muscles and other organs have to be maintained at optimal levels. All of these tasks and more are carried out by the physiological systems we will study in this part of the book. How does Lance measure up in terms of some of his physiological characteristics?

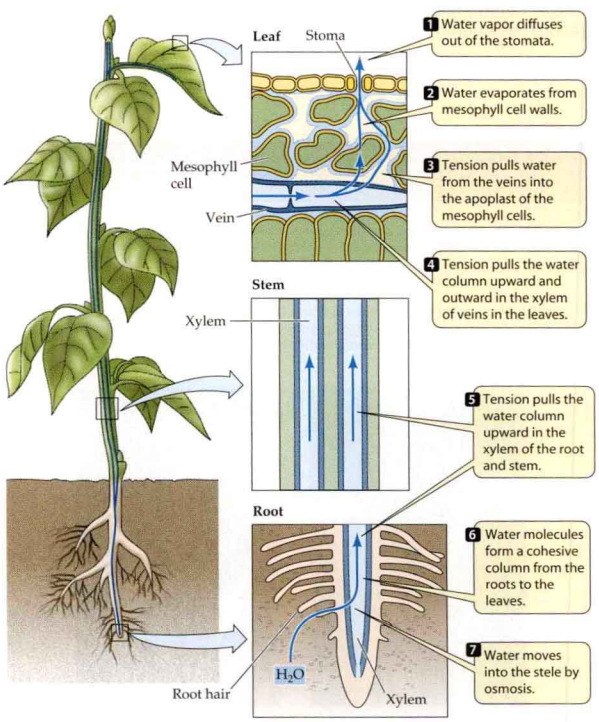
One measure of exercise capacity is the maximum rate at which a person can take up and utilize oxygen: the V_{O_2max}. For a healthy man, a typical value is about 40 ml O_2 per kg body mass per minute. Lance's V_{O_2max} is more than twice that value. Whereas a normal, fit man might burn up to 3,500 Calories on a particularly active day, during the Tour, Lance burns about 6,500 Calories a day—10,000 Calories on peak days! Because Lance has an extremely low proportion of body fat—only 4–5 percent (20 percent is normal)—he must eat, and his body must

France on 10,000 Calories a Day Lance Armstrong is a remarkable athlete largely because of the capacity of his physiological systems.

Chapter 58 ("Earth System Science") introduces students to the new field focusing on Earth as a whole, studying great cycles of materials, inputs of solar energy, and the interactions between living organisms and the physical environment that determine how Earth as a planet functions today.

We have reorganized our treatment of developmental biology to create a new unit, Part Three, Development. Developmental biology is the subdiscipline of biology that draws from a great span of other subdisciplines, from molecular biology to ecology. Thus our new unit begins with updated chapters on "Differential Gene Expression in Development" and "Animal Development: From Genes to Organism," and concludes with the new Chapter 21. This unit leads naturally forward from Part Two, Information and Heredity, and progresses to a transition to Part Four, Evolutionary Processes.

We believe that another mission in the training of new scientists is to make them aware of the links between science and society. New for the Seventh Edition are eight essays, each of which concludes a Part of *Life*. We invited eight eminent humanists and social scientists to address a topic that bridges biology and an important ethical, moral, philosophical, or economic issue. For example, Bonnie Steinbock, SUNY Albany, examines some of the ethical implications arising from today's latest research activities in her essay, "What Are the Moral Issues Surrounding Stem Cell Therapy?" which concludes Part Three, Development.



36.8 The Transpiration–Cohesion–Tension Mechanism
Transpiration causes evaporation from mesophyll cell walls, generating tension on the xylem. Cohesion among water molecules in the xylem transmits the tension from the leaf to the root, causing water to move from the soil to the atmosphere.

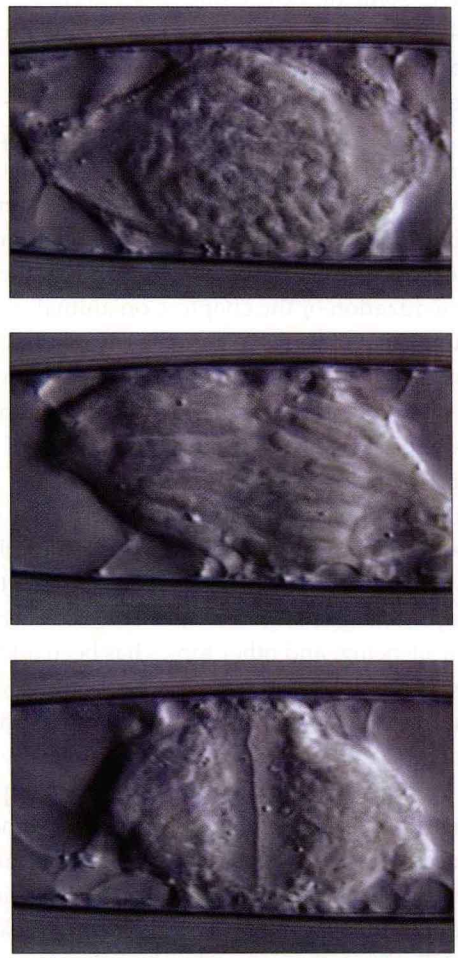
Pedagogy

In addition to our attention to updates and enhancements of content, we have again set as a major goal making the presentation as clear and helpful as possible for the student. Here are some of the ways in which we intend to make the reader's work easier and more effective:

- Every chapter begins with a short story (example above) to grab the reader's interest and encourage further exploration of the chapter's content.
- We have increased the number of bulleted lists (like this one) that highlight key points.
- All second-level headings (the workhorses) are declarative sentences that describe at a glance the text and figures that follow.
- We have added more interim summaries and bridges between topics to keep the reader on track.
- All chapter summaries include references to key figures and now also provide convenient links to the appropriate tutorials and activities on the Website/CD.
- Responding to adopters' requests, we have put the Self-Quizzes back in the text, since some students prefer to access them directly in the chapters.
- Each chapter concludes with four or five "For Discussion" items that help the reader synthesize the chapter's main concepts.
- The balloon captions (example at left) that we introduced in the Fifth Edition are now further streamlined and positioned for maximum pedagogical effectiveness.

Although our much-praised art program appears very similar to the Sixth Edition's, it has undergone a very significant pedagogical upgrade. Our new artist, Elizabeth Morales, who has been illustrating biology textbooks for more than 20 years, worked with each author to evaluate the effectiveness of every piece of line art in the book. The result is many hundreds of simplifications and improvements in clarity.

Media and New Video Collection



The Seventh Edition media and supplements are built around two main goals: (1) to provide the student with a collection of tools to help digest and truly understand the vast amount of material presented in this textbook; and (2) to provide the instructor with the richest possible collection of resources to aid in effectively teaching the course: preparing, presenting the lecture, providing course materials online, and assessing student comprehension.

Working with a dozen contributing authors and an experienced scientific multimedia studio, we have put together an outstanding package that is built specifically for this textbook. For example, the collection of over 100 in-depth animated tutorials was created using textbook art as the basis for the animations, and the introductions, conclusions, and quizzes were matched in level, terminology, and content to the Seventh Edition of *Life*.

In our continuing effort to provide instructors with outstanding visual resources for the lecture, and in response to many requests from biology professors, we are introducing a new feature for the Seventh Edition: "Seeing Life: Video Sequences in Biology." This collection of approximately 200 outstanding video segments (over two hours of footage that spans the book's coverage; example at right) can help capture the attention and imagination of your students with stunning moving images of biological phenomena. Each video segment is fully narrated.

(For a detailed description of all the media and supplements available for the Seventh Edition, please turn to "*Life*'s Supplements" on page xvi.)

The Eight Parts

Part One, The Cell, leads from basic chemistry to cell structure, membranes, and energetics. Chapters 3 ("Large Molecules") and 4 ("Cells: The Basic Units of Life") now integrate ideas on the origin and evolution of cells. The discussion of thermodynamics in Chapter 6 has been reduced and is now focused on biological applications. The art in the chapters on respiration and photosynthesis has been streamlined for clarity.

Part Two, Information and Heredity, retains the order of principles of genetics and molecular biology in the first chapters followed by applications of them in the later chapters. We have updated all of the material on genomics, and added newly emerging approaches of study, including RNA interference.

Part Three, Development, brings together and integrates topics in developmental biology to build upon the detailed treatment of genetics in Part Two and set the stage for the discussions of evolutionary processes in Part Four. We show how new insights into the ways in which genes and environment interact to yield the forms of adult organisms are providing important new perspectives on the origins of evolutionary novelties.

Part Four, Evolutionary Processes, begins with an overview of the history of life on Earth, followed by a detailed treatment of the evolutionary mechanisms and processes that are being investigated to explain those patterns. Chapter 25 ("Constructing and Using Phylogenies") has been updated to incorporate the most recent methods of inferring evolutionary relationships among organisms. Chapter 26 ("Molecular and Genomic Evolution") describes some of the exciting new information on how the genomes of organisms have evolved and how processes of genomic evolution help us understand the evolution of the diversity of life.

Part Five, The Evolution of Diversity, has been updated to reflect current views on phylogeny. We have retained the strong evolutionary thread, emphasizing lineages over some classically defined groups. The treatment of flowering plants other than monocots and eudicots has been upgraded. We have retained the organization of the chapters on animal diversity to reflect the three great lineages of animals—Lophotrochozoans, Ecdysozoans, and Deuterostomes—while incorporating new information on evolutionary relationships among animals revealed by new fossil finds and improved methods of inferring phylogenetic relationships.

In Part Six, The Biology of Flowering Plants, we have improved the explanations of bulk flow in xylem and phloem by modifying and simplifying the art and focusing the text more directly on key mechanisms. New material on clock genes, auxin carriers, RNA silencing, and other topics has been added.

Part Seven, The Biology of Animals, is about how animals work. Although we give major coverage of human physiology, we try to embed it in the background of comparative animal physiology. We have made an effort to offer a complete and broad coverage of physiology while still introducing the student to new advances. For example, the story of the molecular mechanism of the biological clock has advanced very rapidly since the last edition of this book. The genetic control of sexual behavior in fruit flies is another example where the two ends of the biological spectrum—molecular to behavioral—are coming together. As in previous editions, throughout Part Seven, we bring the student back to issues of control and regulation. These are the most central concepts in all of physiology.

Part Eight, Ecology and Biogeography, has been substantially reorganized and updated. Chapter 53 ("Behavioral Ecology") now emphasizes how the decisions that individual animals make can influence population dynamics and community structure. Chapter 54 ("Population Ecology") is organized around the key questions about populations that ecologists attempt to answer. Chapter 55 ("Communities and Ecosystems") combines and integrates material that was separated into two chapters in the Sixth Edition, providing a more integrated treatment of those topics. Chapter 57 ("Conservation Biology") now gives more emphasis on how science is used in the service of conserving Earth's biological diversity. Finally, the new chapter on "Earth System Science" (Chapter 58) introduces students to this rapidly developing field that looks at Earth as a whole.

Full Book or Paperbacks

We again provide *Life* both as the full book and as a cluster of paperbacks. For the Seventh Edition, the new Part Three is an additional fourth paperback. Thus, instructors who want to use less than the whole book, or who want their students to have more portable units, can choose from these split volumes:

- Volume I, The Cell and Heredity, includes: Part One, The Cell (Chapters 2–8); and Part Two, Information and Heredity (Chapters 9–18).
- Volume II, Evolution, Diversity, and Ecology, includes: Part Four, Evolutionary Processes (Chapters 22–26); Part Five, The Evolution of Diversity (Chapters 27–34); and Part Eight, Ecology and Biogeography (Chapters 53–58).
- Volume III, Plants and Animals, includes: Part Six, The Biology of Flowering Plants (Chapters 35–40); and Part Seven, The Biology of Animals (Chapters 41–52).
- Volume IV, Development, includes Part Three, Development (Chapters 19–21)

Note that Volumes I, II, and III include the book's front matter, Glossary, and Index plus Chapter 1.

There Are Many People To Thank

When we met in Sunderland with the key editorial and marketing people from Sinauer Associates and W. H. Freeman to plan this Seventh Edition, we determined that a central goal would be to involve and seek advice from a greater number of our teaching colleagues. This turned out to be a rich idea. We now have more than twice as many instructors to thank for their help in crafting this edition. We began the process by recruiting adopters of the Sixth Edition to report on what worked and what could be improved. With this input, we created the plan for the Seventh Edition and wrote the first drafts. Then, every chapter was reviewed by at least five introductory biology teachers. In addition to checking for accuracy and clarity, they helped us make decisions on material to cut or add. Many productive e-mail exchanges took place at this stage to the book's benefit.

After the chapters and final art were put into page proofs, we built in another round of reviews to help catch and eliminate lingering errors. This final check also provided suggestions for making the text and figures more precise. Finally, and concurrently with the manuscript and accuracy reviews, we got critical scrutiny of all of the animations, tutorials, and activities for the book's Website. We heartily thank all of the people who contributed these reviews. It's a demanding process but there is no doubt that a better book and supporting media have resulted because of it.

We wish to especially thank Scott Gilbert for providing an excellent draft of the new Chapter 21 on evolution and development.

As mentioned earlier, our new artist, Elizabeth Morales, has also made a very large contribution by assuring that *Life*'s extensive illustration program is as effective as possible. Many of the concepts that are illustrated in the book are complex. It takes an illustrator with Elizabeth's talent to render them both artistically and with maximum clarity.

The exact same team that worked with or within Sinauer Associates on the Sixth Edition on the many facets of editing the book was on board again. James Funston provided forceful and insightful developmental editing. Norma Roche contributed her elegant copy editing. Carol Wigg yet again deftly coordinated the entire editorial process and crafted many of the new captions. Jeff Johnson once again delivered the elegant interior and cover designs and coordinated the layout process. Susan McGlew orchestrated the mammoth reviewing process described above. And David McIntyre produced another dazzling array of new photographs for our selection.

W. H. Freeman's marketing and sales group has again succeeded in bringing *Life* to a wider audience. They are both effective ambassadors and skillful transmitters of information. We depend on their expertise and energy to keep us in touch with how *Life* is perceived by its users.

The constant asset we have had in our efforts to produce a better and better book to help students learn and appreciate the science of *Life* has been Andy Sinauer. For over 34 years Andy has run a company that produces the highest quality books in the biological sciences. His strategy has been to maintain a staff of talented, dedicated people and to give each book his personal attention from recruitment of authors to marketing. We feel that we have had more than our fair share of Andy's attention. He is the constant motivator to find ways to make our book and the teaching of biology more effective. He gently but firmly keeps us on track, and he is always ready to deal with the biggest crisis or the smallest detail. Andy, we are fortunate to work with you and we greatly appreciate all you have done to make *Life* a book of which we are exceedingly proud.

Bill Purves ***David Sadava*** ***Gordon Orians*** ***Craig Heller***

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To the Student

There are a few things you can do to help you get the most from this book and from your course. For openers, read the book actively—don't just read passively, but do things that force you to think as you read. If we pose questions, stop and think about them. Ask questions of the text as you go. Do you understand what is being said? Does it relate to something you already know? Is it supported by experimental or other evidence? Does that evidence convince you? How does this passage fit into the chapter as a whole? Annotate the book—write down comments in the margins about things you don't understand, or about how one part relates to another, or even when you find an idea particularly interesting. People remember things they think about much better than they remember things they have read passively. Highlighting is passive; copying is drudge work; questioning and commenting are active and well worthwhile.

"Read" the illustrations actively too. You will find the balloon captions in the illustrations especially useful—they are there to guide you through the complexities of some topics and to highlight the major points.

The chapter summaries will help you quickly review the high points of what you have read. They also identify particular illustrations that you should study to help organize the material in your mind. Add concepts and details to the framework by reviewing the text. Also in the summaries are keyed reminders of the tutorials and activities on the book's website. A way to review the material in slightly more detail after reading the chapter is to go back and look at the boldfaced terms. You can use the boldfaced terms to pose questions—and see if you can answer those questions. The boldfacing will probably be more useful on a second reading than on the first.

The "Self-Quiz" in each chapter is a convenient way to measure your mastery of the material. All answers are at the end of the book. Use the "For Discussion" questions that end each chapter. These questions are usually open-ended and are intended to cause you to reflect on the material.

The glossary and the index can help you a great deal. When you are uncertain of the meaning of a term, check the glossary first—it has more than 1,500 definitions. If you don't find a term in the glossary or you want a more thorough discussion of it, use the index to find where it's discussed.

The Website

The Seventh Edition Student Website (www.thelifewire.com; also available on CD at your instructor's request) is designed to help you learn the vast amount of material we are presenting in this book in a variety of ways. Throughout the book, you will see this icon on headings and figure titles. Wherever you see the icon, you will find a corresponding animated tutorial or activity on the website. They will reinforce your understanding of the key concepts presented in the book. Another important feature of the website is the extensive set of Interactive Quizzes. These quizzes incorporate figures from the book, thorough answer feedback, and links to electronic versions of book pages. There is a second quiz for each chapter, the Online Quiz, the results of which can be emailed to your instructor if he/she requests. Also on the website are key terms flashcards, a full glossary (with audio pronunciations of difficult terms), suggested readings, and two useful documents: Math for Life and Student Survival Skills. The website has been built with you in mind, we hope you find it to be an important resource in your study of introductory biology.

What If the Going Gets Tough?

Most students occasionally have difficulty in courses, including biology courses. If you find that you are slipping behind in the course, or if a particular topic is giving you an unreasonable amount of trouble, here are some useful steps you might take. First, the basics: attend class, take careful lecture notes, and read the textbook assignments. Second, note that one of the most important roles of studying is to discover what you don't know, so that you can do something about it. Use the index, the glossary, the chapter summaries, and the text itself to try to answer any questions you have and to help you organize the material. Make a habit of looking over your lecture notes within 24 hours of when you take them—find out right away what points are unclear, and get them straightened out in your mind. The website can help by providing an additional perspective.

If none of these self-help remedies does the trick, get help! Other students are often a good source of help, because they are dealing with the material at the same level as you are. Study groups can be very useful, as long as the participants are all committed to learning the material. Tutors are almost always helpful, as are faculty members. The main thing is to get help when you need it. It is not a good idea to be strong and silent and drift into a low grade.

But don't make the grade the point of this or any other course. You are in college to learn, to pursue interesting subjects, and to enjoy the subjects you are pursuing. We hope you'll enjoy the pursuit of biology.

Bill Purves ***David Sadava*** ***Gordon Orians*** ***Craig Heller***

Life's Supplements

For the Student

Student Website: www.thelifewire.com

(Also available as a CD optionally bundled with the book)

The *Life,* Seventh Edition Website offers the student a wealth of in-depth, self-directed review material. With the help of three contributing authors and an experienced scientific multimedia design studio, we've created a collection of resources that take advantage of the flexibility and interactivity of the electronic medium to help the student master the many complex concepts presented in the textbook. Features of the site include:

- **Interactive Summaries:** This is the most convenient way to review the entire chapter. The summary contains links to all the key figures from the chapter as well as all of the relevant animated tutorials and activities.
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