

fifth edition

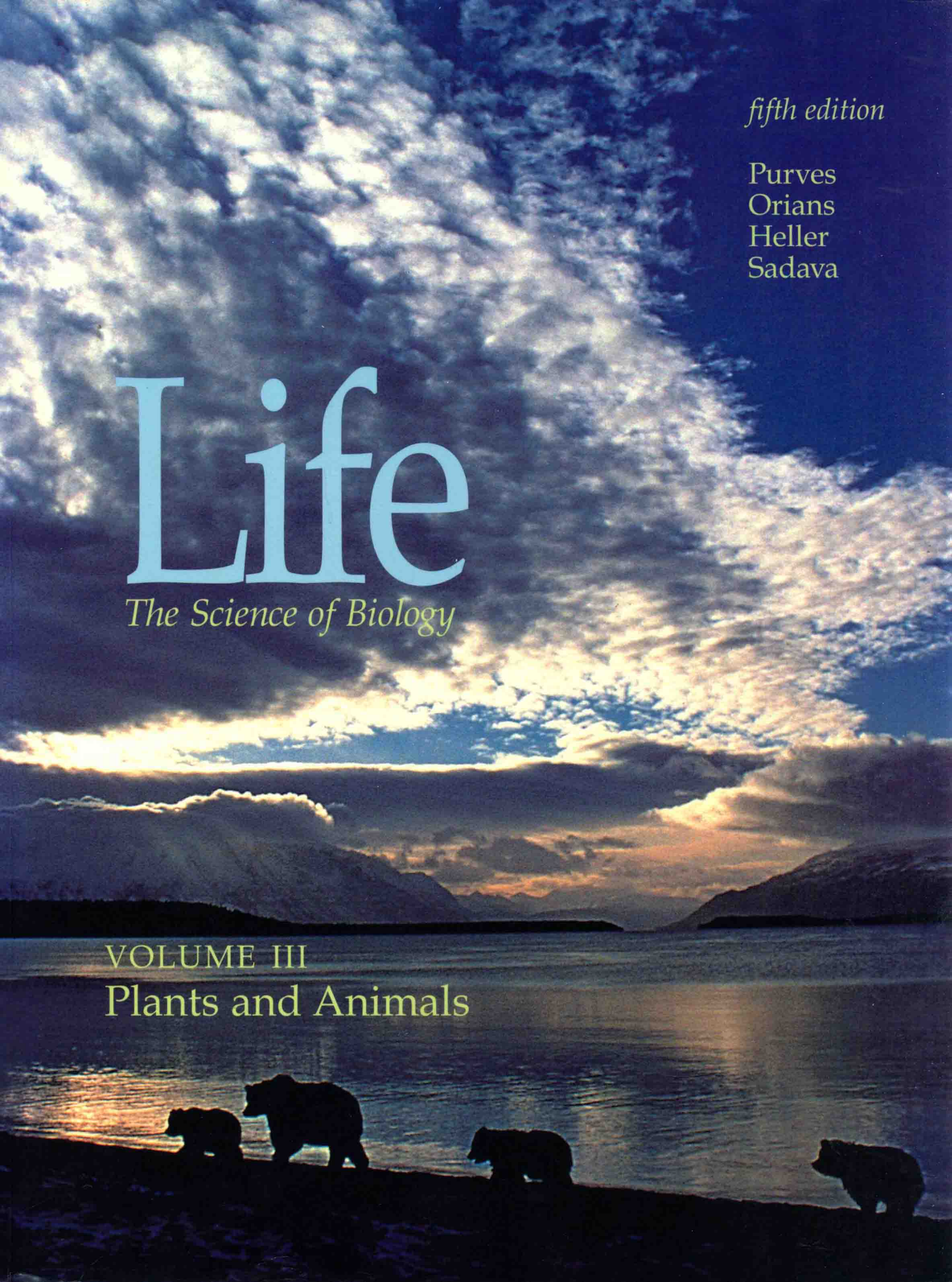
Purves
Orians
Heller
Sadava

Life

The Science of Biology

VOLUME III

Plants and Animals



FIFTH EDITION

Life

The Science of Biology

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The Cover

Grizzly bears (*Ursus arctos*) take many years to mature reproductively, and cubs remain with their mothers for several years. If their populations are to persist, adult bears must have access to rich food resources. Grizzly bears that live in coastal Alaska depend on salmon that swim up the rivers to spawn. Given that abundant, high-quality food, they grow to become the world's largest carnivorous mammal. Photograph by Michio Hoshino/Minden Pictures.

The Frontispiece

A sunset scene with nesting painted storks (*Mycteria leucocephalus*) taken in Bhakatpur, India. Photograph by Mike Powles/Woodfall Wild Images.

LIFE: The Science of Biology, Fifth Edition

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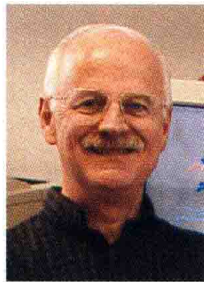
The Science of Biology



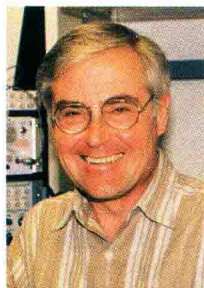
To Jean, Betty, Renu, and Angeline

About the Authors

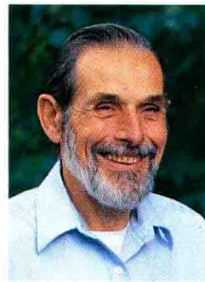
Bill Purves is Professor Emeritus of Biology as well as founder and former chair of the Department of Biology at Harvey Mudd College in Claremont, California. He received his Ph.D. from Yale University in 1959 under Arthur Galston. A fellow of the American Association for the Advancement of Science, 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.



Craig Heller is the Lorry Lokey/Business Wire Professor of Biological Sciences and Human Biology at Stanford University. He has served as Director of the popular interdisciplinary undergraduate program in Human Biology and is now Chairman of Biological Sciences. He is a fellow of the American Association for the Advancement of Science and received the Walter J. Gores Award for Excellence in Teaching. Dr. Heller received his Ph.D. from Yale University in 1970 and did postdoctoral work at Scripps Institution of Oceanography on how the brain regulates body temperature of mammals. His current research is on the neurobiology of sleep and circadian rhythms. Over the years Dr. Heller has done research on systems ranging from sleeping college students to diving seals to hibernating bears to meditating yogis. He teaches courses on animal and human physiology and neurobiology in Stanford's introductory core curriculum.



Gordon Orians is Professor Emeritus of Zoology 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, 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 and evolution, with research experience in behavioral ecology, plant–herbivore interactions, community structure, the biology of rare species, and environmental policy. He elected early retirement to be able to devote more time to writing and environmental policy activities.



David Sadava is the Pritzker Family Foundation Professor of Biology at Claremont McKenna, Pitzer, and Scripps, three of the Claremont Colleges. He received his Ph.D. from the University of California, San Diego in 1972 and has been at Claremont ever since. The author of textbooks on cell biology and on plants, genes and agriculture, Professor Sadava has done research in many areas of cell biology and biochemistry, ranging from developmental biology, to human diseases, to pharmacology. His current research concerns human lung cancer and its resistance to chemotherapy. Virtually all of the research articles he has published have undergraduates as coauthors. Professor Sadava teaches introductory biology and has recently developed a new course on the biology of cancer. For the last 15 years, Dr. Sadava has been a visiting professor in the Department of Molecular, Cellular, and Developmental Biology at the University of Colorado, Boulder.

Preface

This is an exciting time to be a biologist: our knowledge of living systems is expanding rapidly and our technologies for research improve daily. This fifth edition of *Life: The Science of Biology* has been an opportunity for us to communicate to students the excitement of modern biology by expanding and refining our coverage, by finding new ways to make important concepts more understandable and memorable, and by conveying the sense of adventure in biological research.

Our overriding goal continues to be to stimulate students' interests in biology. We have tried to do this by making underlying concepts clear and easy to grasp and showing their relevance to medical, agricultural, and environmental issues. Also, we want students to appreciate *how* we know rather than just *what* we know. To that end, we discuss scientific methods and show how experiments, field observations, and comparative methods help biologists formulate and test hypotheses. In the preparation of this edition, we have tried to introduce opportunities for students to think about concepts rather than just learning facts.

Themes and approaches that characterize the new edition

Throughout the book, we use several themes to link chapters and provide continuity. These themes, which are introduced in Chapter 1, include evolution, the experimental foundations of our knowledge, the flow of energy in the living world, the application and influence of molecular techniques, and human health considerations.

One of our approaches is to show how basic principles presented in earlier chapters apply in later chapters. For example, programmed cell death, also called apoptosis, has been a major focus of biological research in the past few years. This process is first presented in the context of cell reproduction (Chapter 9). Then we show its applications in development (Chapter 15), cancer (Chapter 17), and the immune system (Chapter 18). Another example is cladistics, introduced first in Chapter 22, and applied in subsequent chapters to show how evolutionary relationships help us understand a wide variety of biological problems.

A new organization enhances accessibility

In chapter after chapter, we have concentrated on making the descriptions, explanations, and applications more accessible to student readers. We have rewritten obscure or difficult passages, deleted some details, simplified the writing and illustrations, and shortened both paragraphs and sections. We have tried to tighten connections, improve transitions, and sharpen the focus. Many changes have been made in how information is distributed among the text, captions, figure labels, and a new feature of the illustrations—"balloon captions."

We have also taken a new approach to headings. We have tried to offer the reader more guidance in identifying, understanding, and interrelating key topics. We use two levels of heads (although occasionally a third level is introduced). Major heads divide the chapters into discrete topics, and second-level heads, now full sentences, identify the explicit focus of each subsection. In addition to providing a clear outline and introduction to covered topics, these "sentence heads" are useful to students for study and review.

To further guide the reader, we have provided explicit forecasts of concepts about to be discussed, both as part of the introduction to each chapter and as part of the introductions to most of the major sections within each chapter. This forecasting allows students to read with expectation and direction, better equipped to appreciate the implications of early topics and to see relationships among topics across the entire chapter.

Different students have different learning styles: some are more image-focused, others more text-focused. Line drawings and photographs have the advantages of directness, emphasis, and drama; on the other hand, text explanations provide explicit information and better describe events that occur through time. We have combined the strengths of both text and graphics through the abundant use of what we're calling "balloon captions." These brief statements are incorporated directly into the graphics and go beyond mere labeling to describe, define, or explain graphic elements. Thus, text becomes more intimately related to graphic representations and the graphics take on more significance. Balloon captions, sometimes numbered to clarify a sequence, guide the reader through the inevitable complexities of some figures; in other figures, balloons emphasize the most important features. This new feature has drawn extensive praise during the development of this edition, and we believe that students will find them highly effective aids to their learning.

A new format for the chapter summaries emphasizes the chapter outline, using major heads to distinguish and identify summary statements. The summary emphasizes major points but also includes specific references to key figures and tables where supporting details are found.

The seven parts: Content, changes, and themes

Each section of the book has undergone important changes. In Part One, The Cell, we eliminated some details and advanced topics, notably in Chapter 6 (Energy, Enzymes, and Metabolism), allowing us to develop certain key concepts such as allostery and cooperativity more clearly. New developments in such areas as protein folding are now introduced in a broad context so the student can relate them to other topics. When appropriate, we have tried to link biochemical and cellular phenomena to specific conditions and diseases that affect human health and well-being.

In Part Two, Information and Heredity, the first six chapters (Chapters 9–14) describe what we know and how we have gained some of this knowledge, and the final four (Chapters 15–18) describe its biological applications. The expression of DNA is dealt with separately in prokaryotes (Chapter 13) and eukaryotes (Chapter 14), and these principles are then used to describe the molecular analysis of development (Chapter 15), the manufacture of useful products via biotechnology (Chapter 16), the diagnosis and treatment of human genetic diseases (Chapter 17), and the production of antibodies (18). Because of its centrality to genetics and molecular biology, we now devote separate chapters to the structure and the role of DNA (Chapters 11 and 12, respectively).

The chapter on development (Chapter 15) in Part Two now concentrates entirely on molecular and genetic aspects of development; the cellular and tis-

sue aspects of embryology are presented in Chapter 40. In addition to applying the principles of molecular biology to recombinant DNA technologies, Chapter 16 emphasizes how these technologies are being used in agriculture and medicine. The “molecular revolution” that is just beginning in medicine, including the Human Genome Project, is the subject of an extensively updated chapter (Chapter 17).

In Part Three, Evolutionary Processes, we have expanded the treatment of cladistic methods to assess evolutionary relationships and show how cladograms are constructed and why knowing evolutionary relationships helps us better understand a wide array of biological problems, including human health problems. With this background, we are able to use phylogenetic trees in subsequent chapters to illustrate evolutionary patterns that range from individual molecules to phyla.

Part Three also includes an entirely new chapter (Chapter 23) on molecular evolution, one of the most exciting and vigorous fields in contemporary biology. Contributed by Peg Riley of Yale University, this chapter emphasizes both detailed molecular comparisons among species and their implications as to why and how molecules change over evolutionary time as organisms encounter and survive environmental challenges.

The results of molecular evolutionary studies have led us to a new emphasis on lineages in Part Four, The Evolution of Diversity, especially in our treatment of bacteria, archaea, and protists. Systematics is in ferment, and we try to impart some sense of current controversies in the field in Chapters 25 and 26. We explicitly treat today’s diversity of organisms as the product of evolution.

In Part Five of the fourth edition, we introduced a new chapter, The Biology of Flowering Plants, on plant responses to environmental challenges. It was so well received that we have enriched it with an up-to-date treatment of plant–pathogen interactions. This topic and others continue to emphasize the theme of evolution. Part Five also includes new findings on multiple phytochromes and on developmental mutants in *Arabidopsis*.

In response to requests from instructors, Part Six, The Biology of Animals, now features a chapter (Chapter 40) on animal embryology, which follows the chapter on animal reproduction. The coverage of neurobiology (Chapters 41–44) has been redesigned and expanded to include a new chapter (Chapter 43) on the organization and higher functions of the mammalian brain.

Our theme of human health concerns is manifest throughout Part Six. Chapter 47, on animal nutrition, includes new material on environmental toxicology, an emerging discipline we feel will be of increasing importance to the well-being of our planet.

In Part Seven, Ecology and Biogeography, we have further expanded our coverage of the role of experiments in helping biologists understand the complex interactions among organisms that structure ecological systems. New materials illustrate the role of phylogenetic analyses in behavioral ecology and biogeography. In Chapter 54 we have designed an original graphic method of displaying material on Earth’s biomes. This new and striking presentation enables students to visualize and quantify the differences and similarities in the dominant features of Earth’s major biomes.

We wish to thank a lot of people

We were all students and teachers long before we were textbook authors, and we want to help students in every way possible. In the next section, “To the Student,” we offer some advice that many of our own students have told us they found helpful.

Again, we have been fortunate to receive cogent and significant advice from the more than 60 colleagues who reviewed chapters or whole sections of

the book. Their names are listed after this Preface. Their reviews helped to shape many of the changes described above, ranging from the addition of new chapters to the many ways in which we worked to sharpen our story. We thank them all, and hope this new edition measures up to their expectations.

We were already indebted to J/B Woolsey Associates for the elegance and effectiveness of the art programs they developed for the third and fourth editions of this textbook. They have, of course, produced many new illustrations for this edition. However, rather than limiting ourselves to incremental changes in the existing art program, we have taken a major step forward this time with the introduction of the balloon captions. The success of this approach is the result of many factors. James Funston worked with authors and illustrators, offering input to virtually every pixel in the entire art program. John Woolsey and a dedicated team of artists led by Michael Demaray turned our ideas and suggestions into exciting new art.

James Funston, the developmental editor we chose to work with us on this edition, paid close attention to clarity and pedagogical focus. Stephanie Hiebert provided rigorous copy editing from beginning to end. Her sharp eye extended to the illustrations, and her polishing of and additions to the balloon copy often enhanced the clarity of the presentation. Carol Wigg once again coordinated and checked every change made by editors, artists and authors—indeed, she coordinated the entire preproduction process, and she applied her knowledge and talent to writing captions that tightly link the illustrations to key points in the text. We owe her more than we can say for her patience, persistence, and skill. Jane Potter, as photo researcher, found many new and exciting photographs to enhance the learning experience and enliven the appearance of the book as a whole.

We wish to thank the dedicated professionals in W. H. Freeman's marketing and sales group. Their efficiency and enthusiasm has helped bring *Life* to a wider audience. We appreciate their constant support and valuable marketing feedback. A large share of *Life's* success is due to their efforts in this publishing partnership.

Sinauer Associates provided the best publishing environment we can imagine. Their years of success in publishing biology books at the introductory, intermediate, and advanced levels result from their ability to envision a product and to guide, assist, and motivate authors through the long, demanding process. Remarkably, Andy Sinauer never ceases to extend helpful, and, above all, warm support to his authors.

Bill Purves Gordon Orians Craig Heller David Sadava

November, 1997

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To the Student

Welcome to the study of life! In our student days—and ever since—we have enjoyed studying the fascinating and fast-changing field of biology, and we hope that you will, too.

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. If a passage reminds you of something that has gone before, think about that, or even check back to refresh your memory. 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. The point of doing these things is that they will help you learn. 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. A summary identifies particular illustrations that you should study to help organize the material in your mind. It is essential that you study the cited illustrations and their captions as you review because important information that is covered in illustrations has been left out of the summary statements. Add concepts and details to the framework by reviewing the text. 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.

Use the self-quizzes and “Applying Concepts” questions at the end of each chapter. The self-quizzes are meant to help you understand some of the more detailed material and to help you sort out the information we have laid before you. Answers to all self-quizzes are in the back of the book. The concept questions, on the other hand, are often fairly open-ended and are intended to cause you to reflect on the material.

Two parts of a textbook that are, unfortunately, often underused or even ignored are the glossary and the index. Both can help you a great deal. When you are uncertain of the meaning of a term, check the glossary first—there are more than 1,500 definitions in it. If you don't find a term in the

glossary, or if you want a more thorough discussion of the term, use the index to find where it's discussed.

What if you'd like to pursue some of the topics in greater detail? At the end of each chapter there is a short, annotated list of supplemental readings. We have tried to choose readings from books and magazines, especially *Scientific American*, that should be available in your college library.

To provide another kind of help for students, we commissioned a CD-ROM (*Life 5.0*) covering the subject matter of Parts One and Two of this textbook. *Life 5.0* introduces and illustrates (often with unique animations) over 1700 key terms and concepts. You can access this information in several ways: via *Life* chapter reviews; via minicourses such as "Molecular Structure," "The Cell Cycle," and "DNA Replication"; or via a hyperlinked index. There are also several hundred self-quiz items and dozens of thought problems. You may have a copy of the disk inside the front cover of this book; if not, and if you would like to purchase one, contact **www.mona-group.com**. If you use the disk, explore its contents to see which of its tools best correspond to your needs.

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 CD-ROM can help by providing a different 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 and useful, 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 Gordon Orians Craig Heller David Sadava



Chapter 1

An Evolutionary Framework for Biology

We live on an ancient planet. People in some cultures believe that Earth has always existed—that it is eternal. In the Western world, however, people have long believed that Earth had a beginning, and a relatively recent one. In 1650 Irish Archbishop James Ussher, estimating from his close study of the Bible, calculated that Earth was created in 4004 B.C. Although not everyone agreed with his calculations, until the nineteenth century most people in the Western world shared Bishop Ussher's view that Earth was relatively young and that its entire history was chronicled in ancient texts.

During the nineteenth century, geologists and biologists accumulated evidence that Earth was much older, although they could not say exactly how old. Their evidence for an ancient Earth came primarily from the remains of organisms found in sedimentary rocks. The geologists' guiding concepts were simple: Rocks form slowly by the piling up of sediments, and younger rocks are deposited on top of older ones. A great canyon carved into sedimentary rocks may have a visible record of more than a billion years.

Preserved within some rocks were **fossils**—the remains of organisms that lived while the sediments were accumulating. When they compared older rocks with younger ones, geologists could detect slight but significant differences among similar fossil organisms. Furthermore, they found fossils of similar organisms at widely separated locations. By assuming that rocks at different locations containing the same type of fossil were of approximately the same age, early geologists determined the general order of events in the history of life on Earth. Although they could establish a sequence, these geologists had no method for determining the absolute ages of fossils.

One of the triumphs of twentieth-century science has been the development of methods to date materials formed in the past. The discovery that unstable forms (radioactive isotopes) of familiar atoms such as carbon and phosphorus decay at constant rates made it possible to date materials. Radioactive isotopes are incorporated into rocks and fossils in proportion to their presence in the environment when the rock solidified. Each type of radioactive isotope then begins to decay at its own constant rate, eventually becoming stable. Scientists can calculate the absolute ages of rocks from the proportions of radioactive and stable isotopes they contain.

Meanwhile, scientists in the fields of astronomy and physics, using data from the powerful telescopes and space probes that became available in the latter half of the twentieth century, have come to believe that our planet formed approximately 4 billion years ago. The earliest known fossils have been dated, using radioisotopes, as being 3.8 billion years old, so we know that life arose early in the history of Earth.

Evolutionary Milestones

The fullness of time is difficult for people to grasp. We all understand time spans measured in seconds, minutes, hours, days, years, and decades, but we find it difficult to comprehend millions, much less billions, of years. The following overview of the major evolutionary milestones is intended to provide a framework that presents life's characteristics as they will be covered in this book, and an overview of how these characteristics evolved during the history of life on Earth.

Life arose from nonlife

The first life must have come from nonlife. All matter, living and nonliving, is made up of chemicals. The smallest chemical units are atoms, which bond together into molecules (the properties of these molecules are the subject of Chapter 2). We think that the processes leading to life began nearly 4 billion years ago with interactions among small molecules that stored information in easy-to-copy sequences.

Chemical information became more complex when the information stored in these simple sequences resulted in the synthesis of larger molecules with complex but relatively stable shapes. Because they were both complex and stable, these molecules could participate in increasing numbers and kinds of chemical reactions. Certain types of large molecules—carbohydrates, lipids, proteins, and nucleic acids—are formed only by living systems, and they are found in all living systems. The properties and functioning of these complex *organic molecules* are the subject of Chapter 3.

About 3.8 billion years ago interacting systems of molecules came to be enclosed in compartments surrounded by *membranes*. Within these membrane-enclosed units, or *cells*, control was exerted over the entrance and retention of molecules, the chemical reactions taking place within the cell, and the exit of molecules. Cells and membranes are the subjects of Chapters 4 and 5.

Cells are so effective at capturing energy and replicating themselves—two fundamental characteristics of life—that since they evolved, cells have apparently outcompeted any noncellular life. The cell is the unit on which all life has been built.

An Englishman, Robert Hooke, built a simple microscope in 1665 and was the first person to observe cells. The cells he saw were those of cork, wood, and other dead plant materials, and they were empty. Living organisms that were fully contained in a single cell were first observed a few years later by the Dutch naturalist Antoni van Leeuwenhoek.

By 1839, microscopes had improved and enough living material had been observed that the German physiologist Theodor Schwann could assert that *all organisms consist of cells*. In 1858, the German physician Rudolf Virchow suggested that *all cells come from preexisting cells*. Experiments by the French chemist and microbiologist Louis Pasteur between 1859 and 1861 convinced most scientists that cells do not arise from noncellular material, but must come from other cells. In the modern world, life no longer arises from nonlife.

The first organisms were single cells

For 2 billion years all cells were small. They lived mostly autonomous lives, each separate from the other. Their lives were confined to the oceans, where they were shielded from lethal ultraviolet light. The relatively small amounts of genetic information that allowed these **prokaryotic cells** to replicate themselves and the biochemical machinery by which they obtained energy floated loose within an outer membrane. Some prokaryotes living today are similar to those that existed early in the evolution of living cells, several billion years ago (Figure 1.1).

To maintain themselves, to grow, and to reproduce, all organisms—whether they consist of one cell or tril-