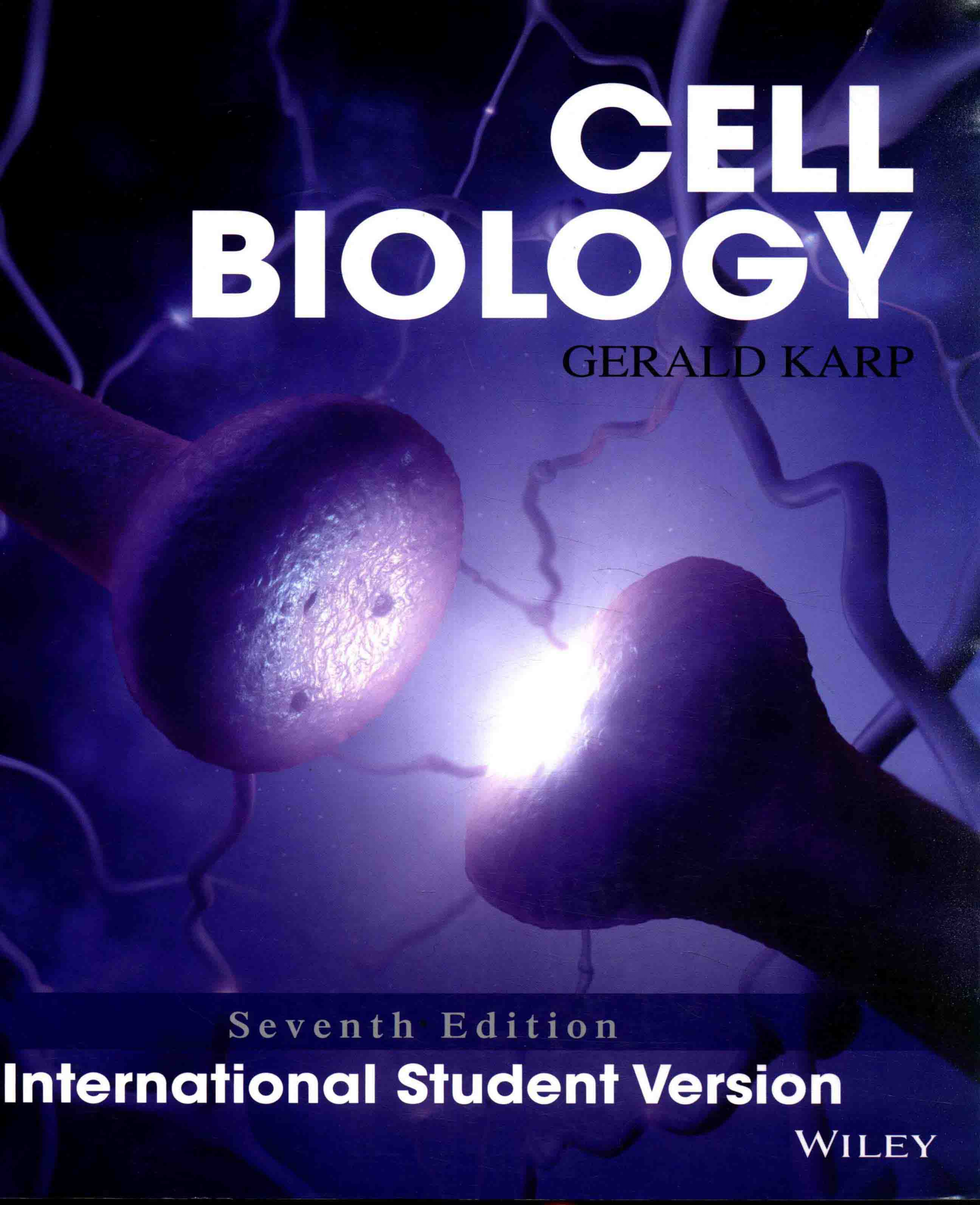
CELL BIOLOGY

GERALD KARP



Seventh Edition

International Student Version

WILEY

Cell Biology

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藏书章

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Chapter 6 was revised in collaboration with

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DEPARTMENT OF BIOLOGICAL SCIENCES
VANDERBILT UNIVERSITY

WILEY

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Nobel Prizes Awarded for Research in Cell and Molecular Biology Since 1958

Year	*Recipient**	*Prize*	*Area of Research*	*Pages in Text*
2012	John B. Gurdon	M & P**	Animal cloning, nuclear reprogramming	247
	Shinya Yamanaka		Cell reprogramming	22, 253
	Brian K. Kobilka	Chemistry	G protein-coupled receptors	621
	Robert J. Lefkowitz			
2011	Bruce A. Beutler	M & P	Innate immunity	700
	Jules A. Hoffmann			
	Ralph M. Steinman		Dendritic cells and Adaptive immunity	707
2009	Venkatraman Ramakrishnan	Chemistry	Ribosome structure and function	213
	Thomas A. Steitz			
	Ada E. Yonath			
	Eliazbeth H. Blackburn	M & P	Telomeres and telomerase	239
	Carol W. Greider			
	Jack W. Szostak			
2008	Francoise Barré-Sinoussi	M & P	Discovery of HIV	24
	Luc Montagnier			
	Harald zur Hausen		Role of HPV in cancer	668
	Martin Chalfie	Chemistry	Discovery and development of GFP	459, 737
	Osamu Shimomura			
	Roger Tsien			
2007	Mario R. Capecchi	M & P	Development of techniques for knockout mice	778
	Martin J. Evans			
	Oliver Smithies			
2006	Andrew Z. Fire	M & P	RNA Interference	189, 780
	Craig C. Mello			
	Roger D. Kornberg	Chemistry	Transcription in eukaryotes	167, 228
2004	Richard Axel	M & P	Olfactory receptors	634
	Linda B. Buck			
	Aaron Ciechanover	Chemistry	Ubiquitin and proteasomes	275
	Avram Hershko			
	Irwin Rose			
2003	Peter Agre	Chemistry	Structure of membrane channels	336, 338
	Roderick MacKinnon			
2002	Sydney Brenner	M & P	Introduction of *C. elegans* as a model organism	18
	John Sulston			
	H. Robert Horvitz		Apoptosis in *C. elegans*	657
	John B. Fenn	Chemistry	Electrospray ionization in MS	758
	Koichi Tanaka		MALDI in MS	758
	Kurt Wüthrich		NMR analysis of proteins	57
2001	Leland H. Hartwell	M & P	Control of the cell cycle	576, 611
	Tim Hunt			
	Paul Nurse			
2000	Arvid Carlsson	M & P	Synaptic transmission and signal transduction	354 617
	Paul Greengard			
	Eric Kandel			
1999	Günter Blobel	M & P	Protein trafficking	467
1998	Robert Furchgott	M & P	NO as intercellular messenger	655
	Louis Ignarro			
	Ferid Murad			

Year	*Recipient**	*Prize*	*Area of Research*	*Pages in Text*
1997	Jens C. Skou	Chemistry	Na^+/K^+-ATPase	343
	Paul Boyer		Mechanism of ATP synthesis	387
	John Walker			
	Stanley B. Prusiner	M & P	Protein nature of prions	66
1996	Rolf M. Zinkernagel Peter C. Doherty	M & P	Recognition of virus-infected cells by the immune system	727
1995	Edward B. Lewis Christiane Nüsslein-Volhard Eric Wieschaus	M & P	Genetic control of embryonic development	EP12
1994	Alfred Gilman Martin Rodbell	M & P	Structure and function of GTP-binding (G) proteins	624
1993	Kary Mullis	Chemistry	Polymerase chain reaction (PCR)	769
	Michael Smith		Site-directed mutagenesis (SDM)	778
	Richard J. Roberts Phillip A. Sharp	M & P	Intervening sequences	178
1992	Edmond Fischer Edwin Krebs	M & P	Alteration of enzyme activity by phosphorylation/dephosphorylation	115, 627
1991	Erwin Neher Bert Sakmann	M & P	Measurement of ion flux by patch-clamp recording	338
1990	Joseph E. Murray E. Donnall Thomas	M & P	Organ and cell transplantation in human disease	716, 20
1989	J. Michael Bishop Harold Varmus	M & P	Cellular genes capable of causing malignant transformation	695
	Thomas R. Cech Sidney Altman	Chemistry	Ability of RNA to catalyze reactions	211
1988	Johann Deisenhofer Robert Huber Hartmut Michel	Chemistry	Bacterial photosynthetic reaction center	404
1987	Susumu Tonegawa	M & P	DNA rearrangements responsible for antibody diversity	713
1986	Rita Levi-Montalcini Stanley Cohen	M & P	Factors that affect nerve outgrowth	565
1985	Michael S. Brown Joseph L. Goldstein	M & P	Regulation of cholesterol metabolism and endocytosis	505
1984	Georges Köhler Cesar Milstein	M & P	Monoclonal antibodies	782
	Niels K. Jerne		Antibody formation	704
1983	Barbara McClintock	M & P	Mobile elements in the genome	142
1982	Aaron Klug	Chemistry	Structure of nucleic acid-protein complexes	79
1980	Paul Berg	Chemistry	Recombinant DNA technology	764
	Walter Gilbert Frederick Sanger		DNA sequencing technology	771
	Baruj Bennacerraf Jean Dausset George D. Snell	M & P	Major histocompatibility complex	716
1978	Werner Arber Daniel Nathans Hamilton O. Smith	M & P	Restriction endonuclease technology	764
	Peter Mitchell	Chemistry	Chemiosmotic mechanism of oxidative phosphorylation	373
1976	D. Carleton Gajdusek	M & P	Prion-based diseases	66
1975	David Baltimore Renato Dulbecco Howasrd M. Temin	M & P	Reverse transcriptase and tumor virus activity	694

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Year	*Recipient**	*Prize*	*Area of Research*	*Pages in Text*
1974	Albert Claude Christian de Duve George E. Palade	M & P	Structure and function of internal components of cells	461
1972	Gerald Edelman Rodney R. Porter	M & P	Immunoglobulin structure	711
	Christian B. Anfinsen	Chemistry	Relationship between primary and tertiary structure of proteins	63
1971	Earl W. Sutherland	M & P	Mechanism of hormone action and cyclic AMP	627
1970	Bernard Katz Ulf von Euler	M & P	Nerve impulse propagation and transmission	351
	Luis F. Leloir	Chemistry	Role of sugar nucleotides in carbohydrate synthesis	471
1969	Max Delbrück Alfred D. Hershey Salvador E. Luria	M & P	Genetic structure of viruses	23, 156
1968	H. Gobind Khorana Marshall W. Nirenberg	M & P	Genetic code	196
	Robert W. Holley		Transfer RNA structure	199
1966	Peyton Rous	M & P	Tumor viruses	694
1965	Francois Jacob Andre M. Lwoff Jacques L. Monod	M & P	Bacterial operons and messenger RNA	218, 162
1964	Dorothy C. Hodgkin	Chemistry	X-ray structure of complex biological molecules	758
1963	John C. Eccles Alan L. Hodgkin Andrew F. Huxley	M & P	Ionic basis of nerve membrane potentials	350
1962	Francis H. C. Crick James D. Watson Maurice H. F. Wilkins	M & P	Three-dimensional structure of DNA	127
	John C. Kendrew Max F. Perutz	Chemistry	Three-dimensional structure of globular proteins	58
1961	Melvin Calvin	Chemistry	Biochemistry of CO_2 assimilation during photosynthesis	412
1960	F. MacFarlane Burnet Peter B. Medawar	M & P	Clonal selection theory of antibody formation	704
1959	Arthur Kornberg Severo Ochoa	M & P	Synthesis of DNA and RNA	284, 197
1958	George W. Beadle Joshua Lederberg Edward L. Tatum	M & P	Gene expression	161
	Frederick Sanger	Chemistry	Primary structure of proteins	55

*In a few cases, corecipients whose research was in an area outside of cell and molecular biology have been omitted from this list.
**Medicine and Physiology

To Patsy and Jenny

About the Author

Gerald C. Karp received a bachelor's degree from UCLA and a Ph.D. from the University of Washington. He conducted postdoctoral research at the University of Colorado Medical Center before joining the faculty at the University of Florida. Gerry is the author of numerous research articles on the cell and molecular biology of early development. His interests have included the synthesis of RNA in early embryos, the movement of mesenchyme cells during gastrulation, and cell determination in slime molds. For 13 years, he taught courses in molecular, cellular, and developmental biology at the University of Florida. During this period, Gerry coauthored a text in developmental biology with N. John Berrill and authored a text in cell and molecular biology. Finding it impossible to carry on life as both full-time professor and author, Gerry gave up his faculty position to concentrate on the revision of this textbook every three years.

About the Cover

Preface to the Seventh Edition

Before I began work on the *first* edition of this text, I drew up a number of basic guidelines regarding the type of book I planned to write.

- I wanted a text suited for an introductory course in cell and molecular biology that ran either a single semester or 1–2 quarters. I set out to draft a text of about 800 pages that would not overwhelm or discourage students at this level.
- I wanted a text that elaborated on fundamental concepts, such as the relationship between molecular structure and function, the dynamic character of cellular organelles, the use of chemical energy in running cellular activities and ensuring accurate macromolecular biosynthesis, the observed unity and diversity at the macromolecular and cellular levels, and the mechanisms that regulate cellular activities.
- I wanted a text that was grounded in the experimental approach. Cell and molecular biology is an experimental science and, like most instructors, I believe students should gain some knowledge of how we know what we know. With this in mind, I decided to approach the experimental nature of the subject in two ways. As I wrote each chapter, I included enough experimental evidence to justify many of the conclusions that were being made. Along the way, I described the salient features of key experimental approaches and research methodologies. Chapters 12 and 13, for example, contain introductory sections on techniques that have proven most important in the analysis of cytomembranes and the cytoskeleton, respectively. I included brief discussions of selected experiments of major importance in the body of the chapters to reinforce the experimental basis of our knowledge. I placed the more detailed aspects of methodologies in a final "techniques chapter" because (1) I did not want to interrupt the flow of discussion of a subject with a large tangential section on technology and (2) I realized that different instructors prefer to discuss a particular technology in connection with different subjects.

  For students and instructors who wanted to explore the experimental approach in greater depth, I included an Experimental Pathways at the end of most chapters. Each of these narratives describes some of the key experimental findings that have led to our current understanding of a particular subject that is relevant to the chapter at hand. Because the scope of the narrative is limited, the design of the experiments can be considered in some detail. The figures and tables provided in these sections are often those that appeared in the original research article, which provides the reader an opportunity to examine original data and to realize that its analysis is not beyond their means. The Experimental Pathways also illustrate the stepwise nature of scientific discovery, showing how the result of one study raises questions that provide the basis for subsequent studies.
- I wanted a text that was interesting and readable. To make the text more relevant to undergraduate readers, particularly premedical students, I included The Human Perspective. These sections illustrate that virtually all human disorders can be traced to disruption of activities at the cellular and molecular level. Furthermore, they reveal the importance of basic research as the pathway to understanding and eventually treating most disorders. In Chapter 5, for example, The Human Perspective describes how small synthetic siRNAs may prove to be an important new tool in the treatment of cancer and viral diseases, including AIDS. In this same chapter, the reader will learn how the action of such RNAs were first revealed in studies on plants and nematodes. It becomes evident that one can never predict the practical importance of basic research in cell and molecular biology. I have also tried to include relevant information about human biology and clinical applications throughout the body of the text.
- I wanted a high-quality illustration program that helped students visualize complex cellular and molecular processes. To meet this goal, many of the illustrations have been "stepped-out" so that information can be more easily broken down into manageable parts. Events occurring at each step are described in the figure legend and/or in the corresponding text. I also sought to include a large number of micrographs to enable students to see actual representations of most subjects being discussed. Included among the images are many fluorescence micrographs that illustrate either the dynamic properties of cells or provide a means to localize a specific protein or nucleic acid sequence. Wherever possible, I have tried to pair line art drawings with micrographs to help students compare idealized and actual versions of a structure.

The most important changes in the seventh edition can be delineated as follows:

- Each of the illustrations has been carefully scrutinized and a large number of drawings have been modified with the goal of achieving greater consistency and quality. Particular attention has been paid to the continuity of color and rendering style for each structure and element, as they are represented within each figure, and throughout the book.
- The illustration program for the seventh edition includes a new feature called Figure in Focus. The premise of this feature is to highlight one of the chapter's key topics in a visually interesting way. Focusing attention on these figures, through the use of line art, 3D molecular models, and micrographs, provides a clear visual explanation of one of the chapter's core concepts.
- The body of information in cell and molecular biology is continually changing, which provides much of the excitement we all feel about our selected field. Even though only three years have passed since the publication of the sixth edition, nearly every discussion in the text has been modified to a greater or lesser degree. This has been done without allowing the chapters to increase significantly in length.
- Altogether, the seventh edition contains more than 100 new micrographs and computer-derived images, all of which were provided by the original source.

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- Clinical Connections Questions by Sarah VanVickle-Chavez, Washington University in St. Louis.
- Experimental Pathways Questions by Joel Piperberg, Millersville University.
- NEW Figure in Focus feature by Anthony Contento, SUNY Oswego, New podcasts & assessment questions accompany selected figures, highlighting important concepts & processes.

Book Companion Site (www.wiley.com/college/karp)

For the Student

- *Quizzes* for student self-testing.
- Answers to the end-of chapter Analytic Questions.
- Additional reading resources provide students with an extensive list of additional useful sources of information.
- Experimental Pathways for Chapters 6, 7, 9, 10, 11, 13, and 15.

For the Instructor

- Biology Visual Library; all images in jpg and PowerPoint formats.
- Instructor's Manual; Test Bank; Lecture PowerPoint Presentations.

Instructor Resources are password protected.

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I am especially thankful to the many biologists who have contributed micrographs for use in this book; more than any other element, these images bring the study of cell biology to life on the printed page. Finally, I would like to apologize in advance for any errors that may occur in the text, and express my heartfelt embarrassment. I am grateful for the constructive criticism and sound advice from the following reviewers of the most recent editions:

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To the Student

At the time I began college, biology would have been at the bottom of a list of potential majors. I enrolled in a physical anthropology course to fulfill the life science requirement by the easiest possible route. During that course, I learned for the first time about chromosomes, mitosis, and genetic recombination, and I became fascinated by the intricate activities that could take place in such a small volume of cellular space. The next semester, I took Introductory Biology and began to seriously consider becoming a cell biologist. I am burdening you with this personal trivia so you will understand why I wrote this book and to warn you of possible repercussions.

Even though many years have passed, I still find cell biology the most fascinating subject to explore, and I still love spending the day reading about the latest findings by colleagues in the field. Thus, for me, writing a text on cell biology provides a reason and an opportunity to keep abreast with what is going on throughout the field. My primary goal in writing this text is to help generate an appreciation in students for the activities in which the giant molecules and minuscule structures that inhabit the cellular world of life are engaged. Another goal is to provide the reader with an insight into the types of questions that cell and molecular biologists ask and the experimental approaches they use to seek answers. As you read the text, think like a researcher; consider the evidence that is presented, think of alternate explanations, plan experiments that could lead to new hypotheses.

You might begin this approach by looking at one of the many electron micrographs that fill the pages of this text. To take this photograph, you would be sitting in a small, pitch-black room in front of a large metallic instrument whose column rises several meters above your head. You are looking through a pair of binoculars at a vivid, bright green screen. The parts of the cell you are examining appear dark and colorless against the bright green background. They are dark because they've been stained with heavy metal atoms that deflect a fraction of the electrons within a beam that is being focused on the viewing screen by large electromagnetic lenses in the wall of the column. The electrons that strike the screen are accelerated through the evacuated space of the column by a force of tens of thousands of volts. One of your hands may be gripping a knob that controls the magnifying power of the lenses. A simple turn of this knob can switch the image in front of your eyes from that of a whole field of cells to a tiny part of a cell, such as a few ribosomes or a small portion of a single membrane. By turning other knobs, you can watch different parts of the specimen glide across the screen, giving you the sensation that you're driving around inside a cell.

Because the study of cell function requires the use of considerable instrumentation, such as the electron microscope just described, the investigator is physically removed from the subject being studied. To a large degree, cells are like tiny black boxes. We have developed many ways to probe the boxes, but we are always groping in an area that cannot be fully illuminated. A discovery is made or a new technique is developed and a new thin beam of light penetrates the box. With further work, our understanding of the structure or process is broadened, but we are always left with additional questions. We generate more complete and sophisticated constructions, but we can never be sure how closely our views approach reality. In this regard, the study of cell and molecular biology can be compared to the study of an elephant as conducted by six blind men in an old Indian fable. The six travel to a nearby palace to learn about the nature of elephants. When they arrive, each approaches the elephant and begins to touch it. The first blind man touches the side of the elephant and concludes that an elephant is smooth like a wall. The second touches the trunk and decides that an elephant is round like a snake. The other members of the group touch the tusk, leg, ear, and tail of the elephant, and each forms his impression of the animal based on his own limited experiences. Cell biologists are limited in a similar manner as to what they can learn by using a particular technique or experimental approach. Although each new piece of information adds to the preexisting body of knowledge to provide a better concept of the activity being studied, the total picture remains uncertain.

Before closing these introductory comments, let me take the liberty of offering the reader some advice: Don't accept everything you read as being true. There are several reasons for urging such skepticism. Undoubtedly, there are errors in this text that reflect the author's ignorance or misinterpretation of some aspect of the scientific literature. But, more importantly, we should consider the nature of biological research. Biology is an empirical science; nothing is ever proved. We compile data concerning a particular cell organelle, metabolic reaction, intracellular movement, etc., and draw some type of conclusion. Some conclusions rest on more solid evidence than others. Even if there is a consensus of agreement concerning the "facts" regarding a particular phenomenon, there are often several possible interpretations of the data. Hypotheses are put forth and generally stimulate further research, thereby leading to a reevaluation of the original proposal. Most hypotheses that remain valid undergo a sort of evolution and, when presented in the text, should not be considered wholly correct or incorrect.

Cell biology is a rapidly moving field and some of the best hypotheses often generate considerable controversy. Even though this is a textbook where one expects to find material that is well tested, there are many places where new ideas are presented. These ideas are often described as models. I've included such models because they convey the current thinking in the field, even if they are speculative. Moreover, they reinforce the idea that cell biologists operate at the frontier of science, a boundary between the unknown and known (or thought to be known). Remain skeptical.

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