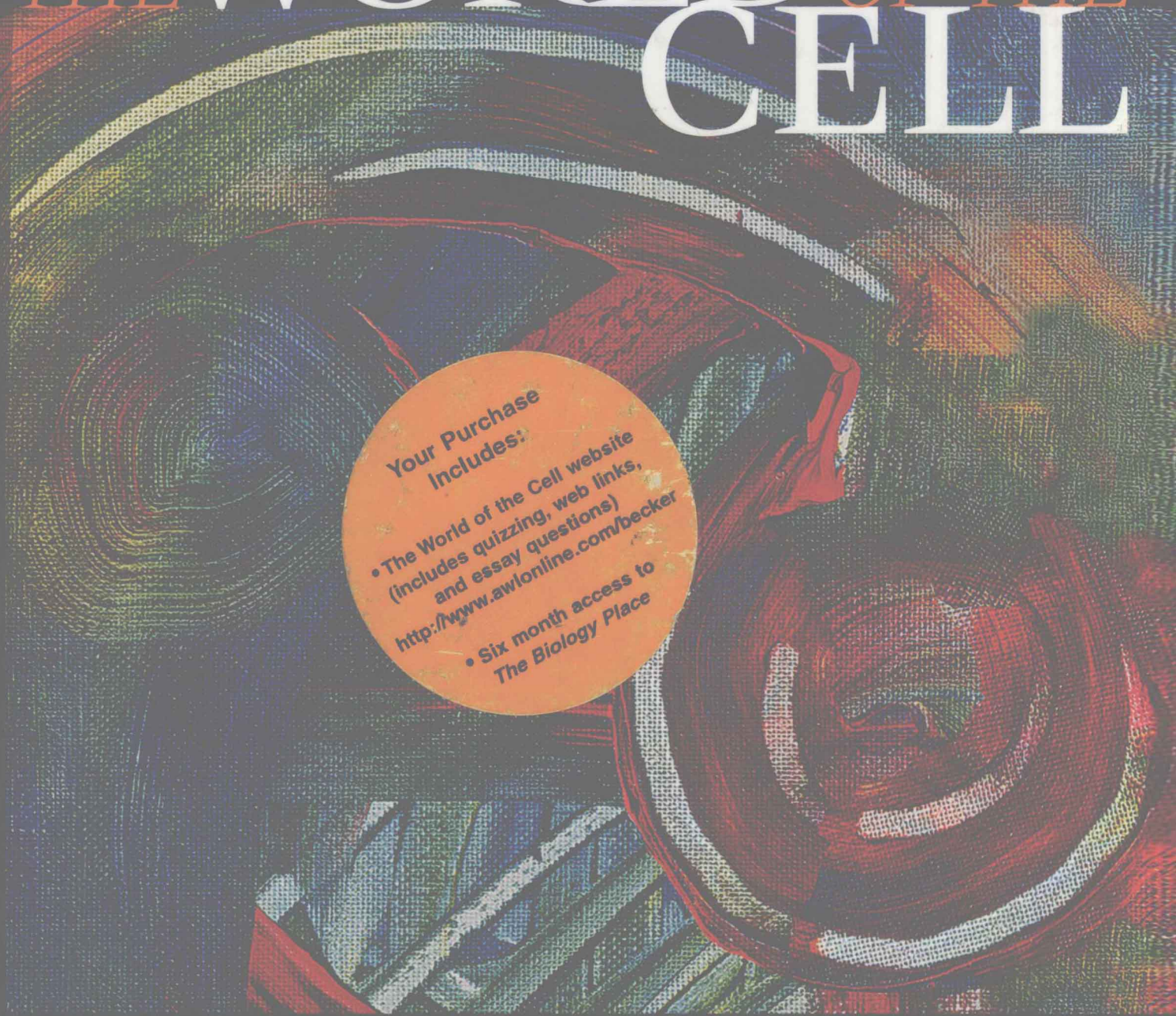
FOURTH EDITION

THE WORLD OF THE CELL



BECKER • KLEINSMITH • HARDIN

THE WORLD OF THE CELL

Fourth Edition

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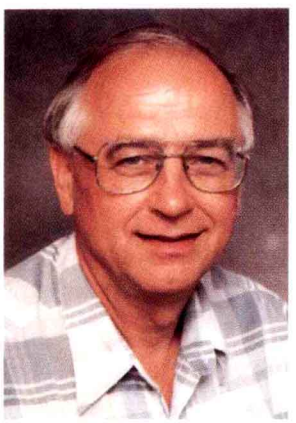
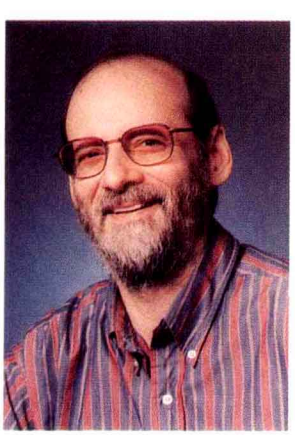
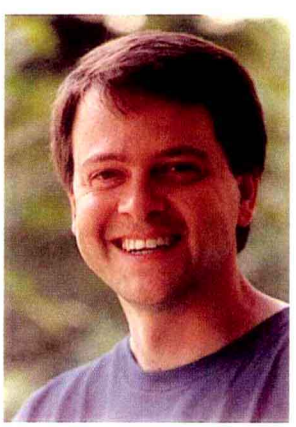


Wayne M. Becker teaches cell biology at the University of Wisconsin, Madison. His interest in textbook writing grew out of notes, outlines, and problem sets that he assembled for his students, culminating in *Energy and the Living Cell,* a paperback text on bioenergetics published in 1977, and *The World of the Cell,* the first edition of which appeared in 1986. He earned all his degrees at the University of Wisconsin, Madison. All three degrees are in biochemistry, an orientation that is readily discernible in his textbooks. His research interests have been in plant molecular biology, focused specifically on the regulation of the expression of genes that encode enzymes of the photorespiratory pathway. His interests in teaching, learning, and research have taken him on sabbatical leaves at Harvard University, Edinburgh University, the University of Indonesia, the University of Puerto Rico, Canterbury University in Christchurch, New Zealand, and the Chinese University of Hong Kong. His honors include a Guggenheim Fellowship, a Chancellor's Award For Distinguished Teaching, and a Visiting Scholar Award from the Royal Society of London.



Lewis J. Kleinsmith is a professor of biology at the University of Michigan, where he has served on the faculty since receiving his Ph.D. from Rockefeller University in 1968. His teaching experiences have involved courses in introductory biology, cell biology, and cancer biology, while his research interests have included studies of growth control in cancer cells, the role of protein phosphorylation in eukaryotic gene regulation, and the control of gene expression during development. Among his numerous publications, he is the author of *Principles of Cell and Molecular Biology,* first published in 1988, and several award-winning educational software programs. His honors include a Guggenheim Fellowship, the Henry Russel Award, a Michigan Distinguished Service Award, several citations for outstanding teaching from the Michigan Students Association, a Thurnau Professorship, and a Best Curriculum Innovation Award from the EDUCOM Higher Education Software Awards Competition.



Jeff Hardin received his Ph.D. in biophysics from the University of California, Berkeley, and pursued postdoctoral work at Duke University. In 1991 he joined the faculty of the Zoology Department at the University of Wisconsin, Madison, where he is currently an associate professor. His research interests center on how cells within embryos move and change the shape of the embryo. Dr. Hardin's teaching is enhanced by his extensive use of videomicroscopy and his Web-based teaching materials, which are used on many campuses in the United States and other countries. As part of his interest in teaching biology, Dr. Hardin has been involved in several teaching initiatives, including being a founding member of the University of Wisconsin Teaching Academy and cofounder of a University of Wisconsin system-wide instructional technology initiative known as BioWeb. His teaching awards include a Lily Teaching Fellowship and a National Science Foundation Young Investigator Award.

PREFACE

The past several decades have witnessed an explosive growth in our understanding of the properties and functions of living cells. As a consequence, the scientific literature is now growing so rapidly that it is almost a full-time job to keep abreast of the major developments relating to cellular organization and behavior. This enormous profusion of information presents a great challenge to authors as they confront the task of preparing an introductory textbook that is both modest in length and readily comprehensible to students encountering the field of cell and molecular biology for the first time. In rising to the challenge, we have been blessed by the happy circumstance of having the lead authors of two respected cell biology textbooks (Wayne Becker and Lewis Kleinsmith) join forces to update one of the texts, ably assisted by a third author (Jeff Hardin), whose research interests in developmental biology complement well the strengths and professional expertise of the other authors. Each of us has brought our own teaching and writing experience to the venture in ways that we have found mutually beneficial—a view that we hope our readers will share.

In preparing this fourth edition of *The World of the Cell,* we have focused on three central goals. As always, our primary goal is to introduce students to the fundamental principles that guide cellular organization and function. Second, we think it is important for students to understand some of the critical scientific evidence that has led to the formulation of these central concepts without getting bogged down in experimental details that run the risk of obscuring the overarching principles. And finally, we have sought to accomplish these goals in a book of manageable length that can be easily read and understood by a beginning cell biology student in the time allotted for a typical course—a quarter or semester, in most cases. To accomplish this third objective, we have necessarily been selective both in the types of examples chosen to illustrate key concepts and in the quantity of scientific evidence included. We have, in other words, attempted to remain faithful to the purpose of this text in each of its previous editions: To present the essential principles, processes, and methodology of cell biology as lucidly as possible.

Something Old and Something New

Like the proverbial bride, this edition has "something old and something new," in the sense that we have tried to retain the features of the first three editions that readers have identified as "user-friendly" while still reorganizing and updating the material. We have also added new features that we hope will make the text even more useful and accessible to introductory students.

Something Old ... Features that we have been careful to retain from prior editions include an organization of subject matter that is readily adaptable to a great variety of course plans; careful and selective use of micrographs, accompanied in most cases by size bars to indicate magnification; problem sets that are intended to encourage thoughtful application of information; and boxed essays to provide further insights into selected topics. In addition, we have continued to make frequent use of overview figures, which outline complicated structures or processes in broad strokes before the details are examined more closely in the text and figures that follow. Finally, we have as always paid careful attention to accuracy, consistency, vocabulary, and readability, hoping thereby to minimize confusion and maximize understanding for our readers.

... And Something New. New features that further enhance the usefulness of the text include the following:

- Reorganization of chapter sequence to cover electrical and chemical signaling (previously Chapters 22 and 23) at much earlier points in the text (now Chapters 9 and 10), right after discussion of membrane structure, function, and transport.
- Subdivision of each chapter into a series of conceptual sections, each introduced by a sentence heading that summarizes the concept to be described.
- Substantial updating of many figures, with more color added throughout the text to facilitate an understanding of complex topics by the color coding of atoms, molecules, structures, pathways, and organelles, as appropriate.

- Chapters on signal transduction and cell-surface receptors, nerve cell function, cell junctions and extracellular structures, and the cell cycle significantly updated to reflect recent progress in these rapidly growing fields of research.
- More emphasis on the experimental evidence that underlies our understanding of cell structure and function, thereby reminding readers that advances in cell biology, as in all branches of science, come not from lecturers in their classrooms or textbook authors in their offices but from researchers in their laboratories.
- Inclusion in the Problem Sets of several especially challenging problems, identified by red dots, that are intended to test the reasoning ability and problem-solving skills of especially able students.
- Updated list of Suggested Readings at the end of each chapter to reflect the most recent advances, often including references through 1998 or 1999.

Techniques and Methods

Throughout the text, we have tried to explain not only what we know about cells but also how we know what we know. Toward that end, we have included descriptions of experimental techniques and findings in every chapter, almost always in the context of the questions they address and in anticipation of the answers they provide. For example, polyacrylamide gel electrophoresis is introduced not in a chapter that describes a variety of methods for studying cells but in Chapter 7, where it becomes important to our understanding of how membrane proteins can be separated from one another. Similarly, equilibrium density centrifugation is described in Chapter 12, where it is essential to our understanding of how lysosomes were originally distinguished from mitochondria and subsequently from peroxisomes as well.

To help readers locate techniques out of context, an alphabetical *Guide to Techniques and Methods* appears on pages xiii–xv, with references to chapters, pages, tables, figures, and boxed essays, as appropriate. To enhance its usefulness, the Guide to Techniques and Methods includes references not just to laboratory techniques but also to mathematical determination of values such as ΔG (free energy change) and $\Delta E_0'$ (standard reduction potential) and even to clinical procedures such as the determination of blood types and the treatment of methanol poisoning.

The only exception to the introduction of techniques in context is microscopy. The techniques of light and electron microscopy are so pervasively relevant to so much of contemporary cell biology that they warrant special consideration as a self-contained unit. Accordingly, we include on pp. 817–845 an *Appendix* devoted exclusively to the principles and techniques of microscopy. Significantly updated for this edition, the Appendix is fully illustrated and is cross-referenced at numerous points in the text.

Pedagogical Features

To enhance the effectiveness of this text as a learning tool, each chapter includes the following basic features:

- **Boldface type** is used to highlight the most important terms in each chapter. *Italics* are employed to identify additional technical terms that are less important than boldfaced terms but significant in their own right. Occasionally, italics are also used to highlight important phrases or sentences.
- A list of *Key Terms* at the end of each chapter includes all of the boldfaced terms in the chapter and provides the page number of the location at which each term appears in boldface and is defined or described.
- A *Suggested Reading* list is also included at the end of each chapter, with an emphasis on review articles and carefully selected research publications that motivated users are likely to find understandable. We have tried to avoid overwhelming readers with lengthy bibliographies of the original literature but have referenced articles that are especially relevant to the topics of the chapter. In most chapters, we have included a few citations of especially important historical publications, which are marked with red dots to alert the reader to their historical significance.
- The inclusion of a *Problem Set* at the end of each chapter reflects our conviction that we learn science not just by reading or hearing about it, but by working with it. The problems are designed to emphasize understanding and application, rather than rote recall. Many of the problems are class-tested, having been selected from problem sets and exams we have used in our own courses. To maximize the usefulness of the problem sets, detailed answers for all problems appear in the *Solutions Manual* described below. At the discretion of the instructor, this manual can be made available to students through the local bookstore or used by the instructor as a resource for homework and exam questions.
- Each chapter contains one or more *Boxed Essays* to aid students in their understanding of particularly important or intriguing aspects of cell biology. Some of the essays provide interesting historical perspectives on how science is done—the discovery of the double-helical structure of DNA as described in Box 3A, for example. Other essays are intended to help readers understand potentially difficult principles, such as the essay that uses the analogy of monkeys shelling peanuts to explain enzyme kinetics (Box 6A). Still others provide insights into contemporary techniques used by cell biologists, as exemplified by the description of DNA fingerprinting in Box 16C. Yet another role of the boxed essays is to illustrate clinical applications of research findings in cell biology, as shown by the discussion of intermediate filaments and the diagnosis of tumors in Box 22C.

Supplementary Learning Aids

Supplementary materials that are available with this text include the following:

- A Solutions Manual containing detailed answers to all problems in the text, available as ISBN 0-8053-4493-4.
- A set of 175 transparencies corresponding to selected figures from the text but with enlarged labels to enhance their usefulness in the classroom, available as ISBN 0-8053-4495-0.
- An Instructor's Presentation CD-ROM contains animations of key concepts and most of the line art from the text. A presentation program enables instructors to design a customized slide show of images, edit labels, import illustrations and photos from other sources, and export figures into other presentation software programs, including Power Point. ISBN: 0-8053-4494-2.
- *The World of the Cell* Companion Website provides students with animations of key concepts, additional multiple choice questions, essay questions, and web links for each chapter. In addition, the site allows instructors to offer on-line quizzing, create syllabi, conduct threaded discussion groups, provide customizations of on-line content, and have access to art and table files from the text. **http://www.awlonline.com/becker**
- *BiologyLabs On-Line* allows students to learn biological principles by designing and conducting simulated experiments on line. Explore HemoglobinLab, MitrochondriaLab, EnzymeLab, and TraslationLab at **http://biologylab.awlonline.com.**

We Welcome Your Comments and Suggestions

The ultimate test of any textbook is how effectively it helps instructors teach and students learn. We welcome feedback and suggestions from readers and will try to acknowledge all correspondence. Please send your comments, criticisms, and suggestions to the appropriate authors, as follows:

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We want to acknowledge the contributions of the numerous people who have made this book possible. We are indebted especially to the many students whose words of encouragement catalyzed the writing of these chapters and whose thoughtful comments and criticisms have contributed much to whatever level of reader-friendliness the text may be judged to have. Each of us owes a special debt of gratitude to our colleagues, from whose insights and suggestions we have benefited greatly and borrowed freely. These include Bill Bement, Ann Burgess, Rick Eisenstein, Donata Oertel, and Millard Susman at the University of Wisconsin-Madison. We are especially grateful to John Raasch for his very skillful and thorough revision of Chapters 12 and 15. We also acknowledge those who have contributed to previous editions of our textbooks, including David Deamer, Martin Poenie, Jane Reece, and Valerie Kish, as well as Peter Armstrong, John Carson, Ed Clark, Joel Goodman, David Gunn, Jeanette Natzle, Mary Jane Niles, Timothy Ryan, Beth Schaefer, Lisa Smit, David Spiegel, Akif Uzman, and Karen Valentine. In addition, we want to express our appreciation to the many colleagues who graciously consented to contribute micrographs to this endeavor, as well as the authors and publishers who have kindly granted permission to reproduce copyrighted material.

The many reviewers listed below provided helpful criticisms and suggestions at various stages of manuscript development and revision. Their words of appraisal and counsel were gratefully received and greatly appreciated. Indeed, the extensive review process to which this and the prior editions of the book have been exposed should be considered a significant feature of the book. Nonetheless, the final responsibility for what you read here remains ours, and you may confidently attribute to us any errors of omission or commission encountered in these pages.

We are also deeply indebted to the many publishing professionals who made this venture a reality. Special recognition goes to Evelyn Dahlgren, Susan Weisberg, Patty O'Connell, and Kelly Murphy, whose consistent encouragement, hard work, and careful attention to detail contributed much to the clarity of both the text and the art.

Finally, we are grateful beyond measure to our wives, families, graduate students, and postdoctoral associates, without whose patience, understanding, and forbearance this book would never have been written.

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Guide to Techniques and Methods

The following techniques are important to cell biologists. Each technique is described in the text at the indicated location, in the context of its actual use by researchers. Page numbers refer to the page on which the description of a technique begins; in many cases, the description continues on subsequent pages.

Cancer

Oncogene transfection assay: Chapter 17 (p. 575; Figure 17-39)

Cell Cycle

Cell fusion: Chapter 17 (pp. 566–567; Figure 17-31)

Micropipetting: Chapter 17 (Figure 17-32, on p. 568, cytoplasm transfer); Chapter 21 (Box 21A on p. 717, nuclear transfer)

Cell Signaling

Calcium indicators (to measure cytosolic calcium concentrations): Chapter 10 (pp. 276–277; Figure 10-10)

Calcium ionophores (to induce ion movement): Chapter 10 (p. 276)

Dominant negative mutations (to study growth factor receptor function): Chapter 10 (p. 285; Figure 10-18)

Clinical Techniques

Administration of ethanol as an antidote for methanol poisoning: Chapter 13 (p. 402; Problem 13-7)

Determination of human blood types: Chapter 11 (Box 11A on p. 313)

Cytoskeleton

Drugs and mutations as tools for studying cytoskeletal function: Chapter 22 (pp. 754 for tubulin, and 768 for actin)

Intermediate filament typing: Chapter 22 (Box 22A on pp. 774–775)

Myosin S1 decoration to determine actin polarity: Chapter 22 (pp. 767–768; Figure 22-17)

Use of microscopy techniques in studying the cytoskeleton: Chapter 22 (Table 22-2 on p. 755)

Energetics

Calculation of ΔE (change in internal energy) and ΔH (change in enthalpy): Chapter 5 (p. 118)

Calculation of $\Delta G'$ (free energy change) and $\Delta G^{\circ\prime}$ (standard free energy change) for chemical reactions: Chapter 5 (pp. 126–127; Table 5-1 on p. 128)

Calculation of $\Delta G'$ (free energy change) for transport of charged and uncharged solutes across membranes: Chapter 8 (pp. 222–225; Table 8-4)

Calculation of E' (reduction potential) and $\Delta E_0'$ (change in reduction potential): Chapter 14 (pp. 429–430)

Calculation of pmf (proton motive force): Chapter 14 (p. 437)

Determination of standard reduction potentials ($\Delta G^{0\prime}$): Chapter 14 (p. 430; Figure 14-16)

Disruption and reconstitution of mitochondria (to demonstrate the presence of a mitochondrial ATP synthase): Chapter 14 (pp. 437–438; Figure 14-20)

Synthetic phospholipid vesicles with respiratory complexes (used to determine ATP yield and to demonstrate capacity to pump protons): Chapter 14 (p. 434)

Uncoupling agents (used to demonstrate coupling of electron transport to ATP generation): Chapter 14 (p. 434)

Enzyme Kinetics

Analysis of competitive and noncompetitive inhibition: Chapter 6 (p. 151; Figure 6-15)

Determination of K_m (Michaelis constant) and V_{max} (maximum velocity): Chapter 6 (pp. 149–150; Figures 6-13 and 6-14)

Experimental evidence in support of allosteric regulation: Chapter 6 (Box 6B on p. 155)

Genetics

Cis-trans test with partially diploid bacteria: Chapter 21 (pp. 706–707; Table 21-2)

Cotransductional mapping: Chapter 18 (p. 611)

Labeling and Staining

Membranes and Membrane Transport

Microscopy

Nucleic Acids and Recombinant DNA

Proteins

Scientific Method

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