

THE **CELL**
A MOLECULAR APPROACH

SECOND EDITION



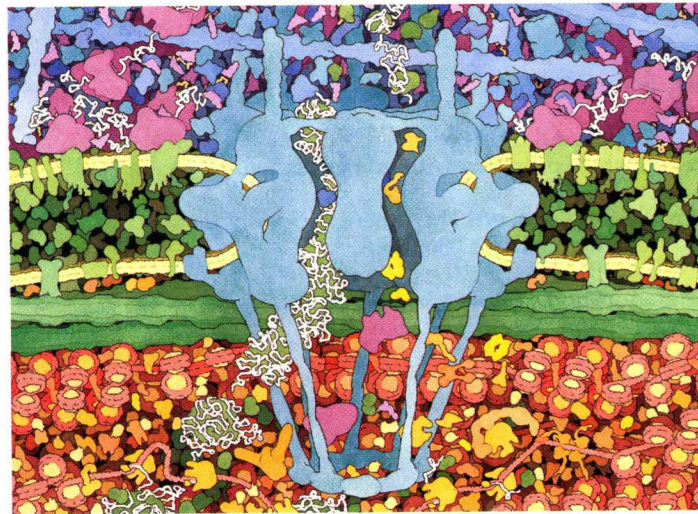
GEOFFREY M. COOPER

THE **CELL**
A MOLECULAR APPROACH

SECOND EDITION

Geoffrey M. Cooper

Boston University



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PRESS**



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Sunderland, Massachusetts

The Cover

A nuclear pore complex (center) is shown with the cytoplasm above and the nucleus below. The illustration includes all macromolecules, including ribosomes (purple) and actin filaments (blue) in the cytoplasm, and DNA double helices (red) being transcribed into messenger RNA (white) in the nucleus. Illustration by David S. Goodsell, The Scripps Research Institute.

Part One opener image

Confocal micrograph of mouse embryo cells.
(Courtesy of David Albertini, Tufts University School of Medicine)

Part Two opener image

Light micrograph of stained salivary gland polytene chromosomes in *Drosophila*.
(Peter J. Bryant/Biological Photo Service)

Part Three opener image

Micrograph of macrophages ingesting red blood cells.
(Courtesy of Joel Swanson)

Part Four opener image

Fluorescence micrograph of the telophase stage of mitosis in newt lung cells.
(Conly L. Rieder/Biological Photo Service)

The Cell: A Molecular Approach, Second Edition

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STUDENT CD-ROM

Adopters have the option of bundling *The Cell* with a special edition of the CD-ROM *Molecules, Cells, and Genes* (ISBN 0-87893-074-4).^{*} This invaluable resource is keyed to the textbook and combines the essential features of a Study Guide and a Problems book. The CD-ROM includes:

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^{*}Students who wish to order the CD-ROM directly can do so at the following web site: www.sinauer.com

THE CELL

A MOLECULAR APPROACH
SECOND EDITION

*This book is dedicated to
Howard M. Temin (1934–1994),
whom I was privileged to know as
a teacher, mentor, and friend.*

Preface

Cell and molecular biology is one of the most rapidly moving areas of the life sciences, and a number of substantial advances have been made since the first edition of *The Cell* was published in 1997. Particularly noteworthy progress has been made in the area of genome sequencing: We now know the complete sequences not only of yeast and bacterial genomes but also of *C. elegans* and *Drosophila melanogaster*, as well as much of the genomic sequence of the model plant *Arabidopsis thaliana*. Projects directed toward sequencing the human genome have also moved forward rapidly, and completion of the human genome sequence can be confidently anticipated in the near future. These advances in genome sequencing are opening whole new approaches to understanding the regulation and function of cells, and they will undoubtedly provide a new database upon which much of the future research in molecular and cell biology will be built.

There have been significant advances in the understanding of several aspects of the molecular biology of eukaryotic cells—the mechanisms that control the initiation of DNA replication have been elucidated, studies of histone acetylation have provided a clear link between chromatin structure and transcriptional regulation, and new mechanisms of translational regulation have been described. Substantial progress has similarly been made in understanding a variety of aspects of protein trafficking, including nuclear import and export, the pathways of protein import to the endoplasmic reticulum and transport to the Golgi apparatus, the molecular mechanisms of vesicular transport, and the mechanisms of protein import into mitochondria and chloroplasts. The exciting areas of cell signaling and cell cycle regulation have also continued to rapidly move forward, with particularly noteworthy progress being made in understanding the regulation of programmed cell death and the signaling pathways that control cell fate during embryonic development. These advances in basic science have been coupled with progress in medically-related areas, including the potential use of stem cells to replace damaged human tissue and the development of new anticancer drugs targeted against specific oncogene proteins.

The second edition of *The Cell* has been completely updated to include these exciting advances and to present the most current information available. The goals and distinguishing features of *The Cell*, however, remain unchanged from the first edition. *The Cell* continues to be a basic text that provides an accessible introduction for undergraduate or medical students who are taking a first course on cell and molecular biology. My principal goal has been to provide an accessible and readable book that can be approached and mastered by undergraduate students, while still being intellectually gratifying and conveying the excitement and challenges of research in contemporary molecular and cellular biology.

As in the first edition, *The Cell* is focused on the molecular biology of cells as a unifying theme, with specialized topics discussed throughout the book as examples of more general principles. Aspects of developmental biology, the immune system, the nervous system, and plant biology are thus discussed in their broader biological context in chapters covering areas such as genome structure, gene expression, DNA rearrangements, the plasma membrane, cell signaling, and the cell cycle. Relationships between cell biology and medicine are similarly discussed throughout the text, as well as being highlighted in the Molecular Medicine essays that are included as a special feature in each chapter. These discussions illustrate the striking impact of molecular and cellular biology on human health, and are intended to stimulate as well as inform those students interested in medicine.

Since *The Cell* deals with one of the most rapidly progressing areas of biology, it remains critical for students not only to have the most current information available, but also to understand the experimental nature of contemporary research in cell and molecular biology. With this goal in mind, representative experiments are discussed throughout the text to illustrate the kinds of approaches upon which our current understanding has been built. In addition, each chapter contains a Key Experiment essay that describes a seminal paper and its background in detail, with the intent of giving the reader a sense of "doing science." Finally, I have tried to point out the limits of our knowledge and to identify outstanding unanswered questions throughout the text. I hope that, together, these approaches give the student an appreciation of the ways in which progress in understanding the cell has been made, and convey the excitement and challenges of participating in this frontier of scientific exploration.

GEOFFREY M. COOPER
MAY 2000

ORGANIZATION AND FEATURES OF *The Cell*

The Cell has been designed to be an approachable and teachable text that can be covered in a single semester while allowing students to master the material in the entire book. It is assumed that most students will have had introductory biology and general chemistry courses, but will not have had previous courses in organic chemistry, biochemistry, or molecular biology. Several aspects of the organization and features of the book will help students to approach and understand its subject matter.

ORGANIZATION

The Cell is divided into four parts, each of which is self-contained, so that the order and emphasis of topics can be easily varied according to the needs of individual courses. In covering this vast subject matter, however, I developed an organizational overview of the book, as described below.

Part I of the book provides background chapters on the evolution of cells, methods for studying cells, the chemistry of cells, and the fundamentals of modern molecular biology. For those students who have a strong background from either a comprehensive introductory biology course or a previous course in molecular biology, various parts of these chapters can be skipped or used for review.

Part II focuses on the molecular biology of cells and contains chapters dealing with genome organization; DNA replication, repair, and recombination; transcription and RNA processing; and the synthesis, processing, and regulation of proteins. The order of chapters follows the flow of genetic information (DNA → RNA → protein) and provides a concise but up-to-date overview of these topics.

Part III contains the core block of chapters on cell structure and function, including chapters on the nucleus, cytoplasmic organelles, the cytoskeleton, and the cell surface. This part of the book starts with coverage of the nucleus, which puts the molecular biology of Part II within the context of the eukaryotic cell, and then works outward through cytoplasmic organelles and the cytoskeleton to the plasma membrane. These chapters

are relatively self-contained, however, and could be used in a different order should that be more appropriate for a particular course.

Finally, Part Four focuses on the exciting and fast-moving area of cell regulation, including coverage of topics such as cell signaling, the cell cycle, and programmed cell death. This part of the book concludes with a chapter on cancer, my own field of research, which synthesizes the consequences of defects in basic cell regulatory mechanisms.

FEATURES

Several pedagogical features have been incorporated into *The Cell* in order to help students master and integrate its contents. These features are reviewed below as a guide to students studying from this book.

Chapter organization. Each chapter is divided into four or five major sections, which are further divided into a similar number of subsections. An outline listing the major sections at the beginning of each chapter provides a brief overview of its contents.

Key Terms and Glossary. Key terms are identified as boldfaced words when they are introduced in each chapter. These key terms are reiterated in the chapter summary and defined in the glossary at the end of the book.

Illustrations and micrographs. An illustration program of full-color art and micrographs has been carefully developed to complement and visually reinforce the text.

Key Experiment and Molecular Medicine essays. Each chapter contains one Key Experiment and one Molecular Medicine feature. These essays are designed to provide the student with a sense of both the experimental basis of cell and molecular biology and its applications to modern medicine.

Chapter Summaries. Chapter summaries are organized in outline form corresponding to the major sections and subsections of each chapter. This section-by-section format is coupled with a list of the key terms introduced in each section, providing a succinct but comprehensive review of the material.

Questions and Answers. Questions at the end of each chapter (with answers in the back of the book) are designed to further facilitate review by calling for students to understand and integrate the material presented in the chapter and to use this material to predict or interpret experimental results.

References. Comprehensive lists of references at the end of each chapter provide access to both reviews and selected papers from the primary literature. In order to help the student identify articles of interest, the references are organized according to chapter sections. Review articles and primary papers are distinguished by [R] and [P] designations, respectively.

Acknowledgments

Many people made critical contributions to both the first and second editions of *The Cell*, and it is a pleasure to thank them for their efforts.

The project was initiated by Patrick Fitzgerald at ASM Press. His efforts were carried on for the second edition by Jeff Holtmeier, who provided a continued source of encouragement and support. The help of Karen Jones and Norma Davis in obtaining reviews of the second edition is also greatly appreciated.

Both the first and second editions of *The Cell* benefited greatly from the many scientists who gave generously of their time to read and critique the text. The reviewers of both editions are listed separately on the following pages, and I am deeply grateful for their efforts and advice. It is a special pleasure to acknowledge the help of Elaine Lai (Brandeis University), who read and critiqued the entire text of the second edition, providing extremely valuable advice from her perspective as both a scientist and a teacher of cell biology.

The production of the second edition of *The Cell* was again undertaken by Andy Sinauer and his colleagues at Sinauer Associates. I am delighted to thank Andy and Dean Scudder for their continued help and encouragement throughout all stages of the project. It is also a pleasure to acknowledge the superb efforts of Joyce Zymeck, who did a wonderful job editing the text, David McIntyre, who obtained the many new micrographs included in the book, and Christopher Small, who was responsible for production of the completed volume. The artwork is the product of Patrick Lane of the J/B Woolsey studio, who once again succeeded in turning my rough sketches into an outstanding art program. The cover illustration was created especially for the second edition of *The Cell* by David S. Goodsell of the Scripps Research Institute, and I am most grateful for his contribution.

Finally, it is a pleasure to acknowledge the careful and cheerful work of Sean Valles, who compiled and copied the many research papers I used as references to bring the second edition of *The Cell* up to date.

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- multiple-choice quiz modules for each chapter, with feedback provided for every possible response
- several problems with answers for each textbook chapter
- over 30 minicourses, keyed to text chapters and covering over 1,000 topics in basic cell biology, molecular biology, genetics, immunology, terminology, cancer, and more
- more than 100 animated sequences, with narration
- 800 original illustrations
- 17 video microscopy sequences
- over 125 micrographs
- an extensive library of spoken pronunciations
- an Index that allows the student to instantly locate every Key Term
- endless hypertext links that provide easy navigation throughout the program
- web links that guide the student to useful and effective web sites to further augment the learning process

World Wide Web Site [www.sinauer.com/cooper/]

This site provides links, for each chapter, to resources on the World Wide Web.

FOR THE INSTRUCTOR

Instructor's Resource CD-ROM (ISBN 0-87893-072-8)

This CD-ROM includes:

- all of the full-color figures and tables from the text
- video clips that include: cell signaling proteins localized in relation to cell behavior; interflagellar transport (GFP-labeled); Ca^{++} wave during frog egg fertilization; 4-cell-stage embryo; lysosomes and mitochondrial transport; lamellipodia and wound closure; actin nucleation and retrograde flow; epidermal migration; endoplasmic reticulum extension; stationary actin; and nucleation
- animations from the Student CD-ROM
- over 200 electron micrographs
- all problems and solutions from the Student CD-ROM
- the computerized test file
- PowerPoint® presentations
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Overhead Transparencies (ISBN 0-87893-104-X)

A set of 150 full-color figures from the textbook is available as overhead transparencies.

Test File (ISBN 0-87893-103-1)

A collection of over 500 multiple-choice and true/false questions is available in printed form, or in Windows or Macintosh computer formats (on the Instructor's Resource CD-ROM).

Other Media

The following videos and CD-ROMs are available to qualified adopters of the text:

- Sardet, Larssonneur, and Koch: *Voyage Inside the Cell* (ISBN 0-87893-763-3, NTSC Video)
- Pickett-Heaps and Pickett-Heaps: *Living Cells: Structure and Diversity* (ISBN 0-646-29291-9, NTSC Video)
- Pickett-Heaps and Pickett-Heaps: *From Egg to Tadpole: Early Morphogenesis in Xenopus* (ISBN 09586081-1-3, NTSC Video)
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- Fink: *CELLibration* (ISBN 0-87893-166-X, NTSC Video)
- Tyler, Schnetzer, and Tartaglia: *Fly Cycle: The Lives of a Fly, Drosophila melanogaster* (ISBN 0-87893-837-0, NTSC Video)
- Tyler, Kozlowski, and Iten: *FlyCycle* CD (ISBN 0-87893-839-7, CD-ROM)
- Tyler and Kozlowski: *Vade Mecum: An Interactive Guide to Developmental Biology* (ISBN 0-87893-842-7, CD-ROM)

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