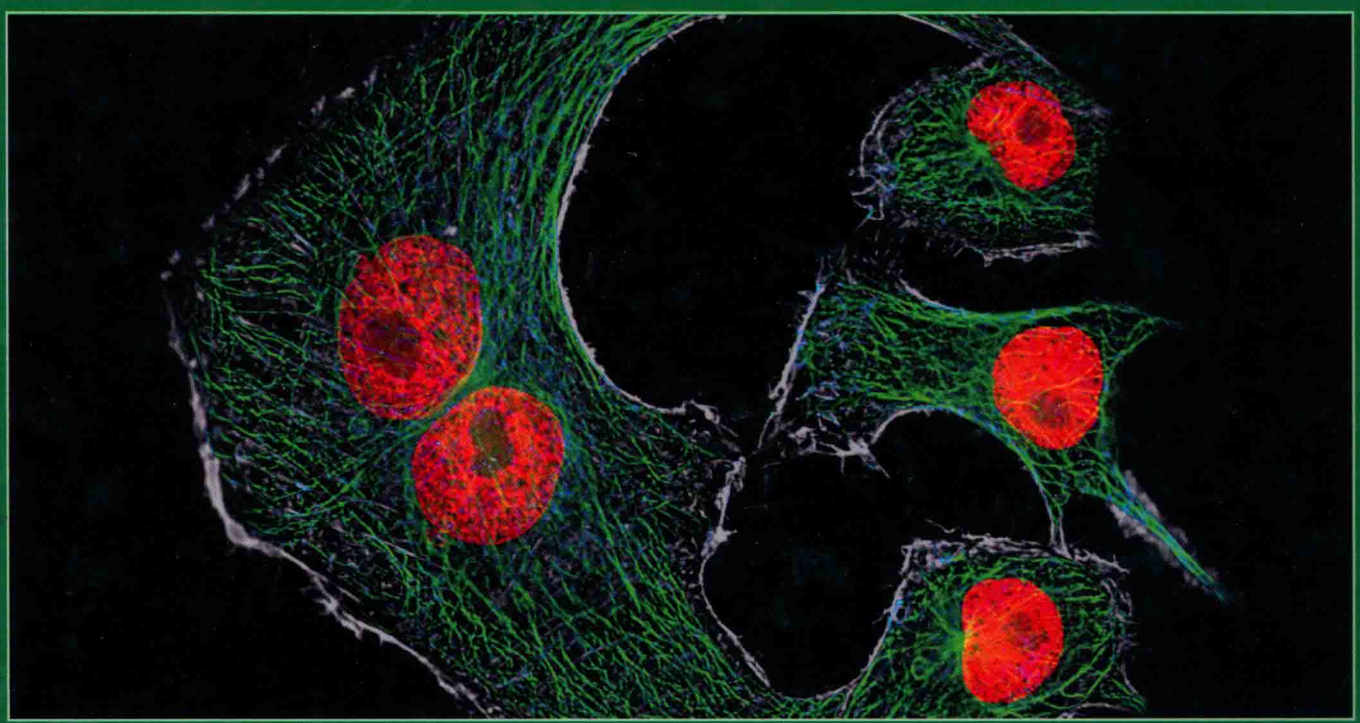
LEWIN'S CELLS

SECOND EDITION



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About the cover: *Xenopus* (frog) XLK2 cells. For each cell, a portion of the cell's internal skeleton is shown in green and the nucleus in red.

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Preface

Eighty years ago, the cellular world opened up. The electron microscope granted us, for the first time, a detailed perspective of basic cellular structures, and the ultracentrifuge allowed us to biochemically isolate and characterize fractions of cytoplasmic and nuclear material. Geneticists could investigate the relationship between the ever-shifting chromosomal structure and the molecular mechanisms of genetic inheritance—an effort that culminated with the triumphant revelation of the structures of DNA and RNA and a translation of the genetic code.

But we have come a long way from there. We have perfected our understanding of genes themselves, adjusting our definition from "determinants of a genetic phenotype," to "protein-encoding segments of DNA," and now, more precisely, "units of genomic information required for the transcription of functional messenger RNA or noncoding RNA." And we are still learning about the proteins these mRNAs produce. The RSCB Protein Data Bank (PDB) was established in 1971 as an international repository for structural data, but it did not truly begin to grow until the early 1990s. Now, in 2010, it holds more than 60,000 structures and is expanding at the rate of about 7,000 structures per year. For now, X-ray crystallography and nuclear magnetic resonance are the only techniques available for the determination of macromolecular structures at high resolution. Important advances in other methods, however—including visualization of fluorescently tagged proteins in living cells and new types of electron microscopy—are describing cellular structures and processes in ever-increasing detail.

What this all means is that the scope of biological questions that can be asked has been fundamentally changed. The new field of structural genomics has enabled us to relate increased structural resolution to functional changes, providing powerful insights at deeper levels of understanding. With our growing ability to process huge data sets, complete characterizations of cellular structures such as the nuclear pore complex and the centrosome, which are constructed from hundreds of proteins, may soon be attainable.

Perhaps most exciting is the combination of structural and mechanistic information with developments in genetics, biochemistry, and physiology—the primary vision of the emerging field of systems biology. Most cell biologists today recognize that only a comprehensive approach to research, from the nuclear pore complex to the extracellular matrix, will begin to lift the veil from the cellular processes underlying cystic fibrosis, epilepsy, and cancer.

Any cell biology textbook must provide a current perspective of the structure, function, and regulation of biological systems, but in today's world it is imperative that we also present the subject in the context of biochemistry and molecular biology, genomics, histology and pathology, and physiology. Thoroughly revised and updated, *Lewin's CELLS, Second Edition,* turns a new and sharper lens on the fundamental units of life.

Audience

This second edition, expanded and updated from Benjamin Lewin's *CELLS*, is geared for advanced undergraduate and graduate students taking a first course in cell biology. A key objective in developing this book was to present the concepts and mechanisms underlying cell structure and function, gleaned from decades of research, in a format that provides students with the information necessary for a solid foundation in cell biology, without overwhelming them with too much detail. The major goal of the team of lead editors and 26 expert authors has been to incorporate the current research in the field, thoroughly cover each topic, and provide ample illustrations of cellular processes at the molecular level—but without being unwieldy.

New and Key Features

Lewin's CELLS, Second Edition, covers the structure, organization, growth, regulation, movement, and interactions of cells, with an emphasis on those in the eukaryotic domain. These topics are presented in 21 chapters grouped into seven parts, beginning with the definition of a cell, providing background on basic cellular processes, continuing on to the components of cells and the regulation of cell functions, and ending with cell diversity. Plant cells and prokaryotic cells are covered in separate chapters to emphasize their diversity while highlighting the properties shared by all cells.

Areas of New Coverage

Chapters from the first edition were thoroughly updated and revised by their original authors, 26 experts in diverse areas of cell and molecular biology and biochemistry.

This second edition also includes several entirely new chapters:

Chapter 2, Bioenergetics and Cellular Metabolism
Chapter 3, DNA Replication, Repair, and Recombination
Chapter 4, Gene Expression and Regulation
Chapter 5, Protein Structure and Function

The following list highlights some other areas of key content updates:

- Chapter 9, Nuclear Structure and Transport, discusses the dramatic increase in our understanding of nuclear pore complex structure, organization, and biogenesis, and the nature of the molecular environment found in the central channel of the NPC, which ensures selectivity in transport. Also updated substantially is the discussion of RNA export, focusing on recent advances in our understanding of export of mRNA, tRNA, ribosomal subunits, and microRNAs.
- Chapter 10, Chromatin and Chromosomes, now contains an extensive discussion of histone variants and the roles they play in chromosome segregation, transcription, and DNA repair.
- Chapter 13, Intermediate Filaments, shows how mutations in keratin genes have been linked to skin blistering diseases.
- Chapter 14, Mitosis, explains how errors in chromosome attachment to the mitotic spindle are detected and corrected. It also discusses mitosis as a pharmacological target for development of anticancer drugs.
- Chapter 15, Cell Cycle Regulation, explains the mechanisms responsible for cell proliferation and the way these mechanisms are controlled to prevent chromosome damage.
- Chapter 16, Apoptosis, includes an expanded discussion of the inflammasome, a structure that senses danger signals and responds to them.
- Chapter 18, Principles of Cell Signaling, features a discussion of Abl and the development of inhibitors and resistance in the treatment of chronic myelogenous leukemia. The authors have also added improved protein structures that illustrate important regulatory principles.
- Chapter 19, The Extracellular Matrix and Cell Adhesion, discusses the role of the extracellular matrix during the evolution of multicellularity. It also contains an expanded discussion of various integrin-based complexes in vivo.
- Chapter 21, Plant Cell Biology, covers newly discovered proteins that predict the plane of cell division. It also includes advances showing that microtubules provide tracks for the movement of cellulose-synthesizing enzymes.

Design

The design of *Lewin's CELLS, Second Edition,* is specifically intended to enhance pedagogy. Chapters are divided into sections with declarative titles that emphasize the main points. Each section begins with a set of **Key Concepts** that enable readers to grasp the important ideas at the outset. To stimulate students' interest in future work, chapters include a section called **What's Next**? that describes some of the interesting questions that researchers are tackling. Key review articles have been listed for students interested in the experiments that led to the current understanding of each topic, and additional references to original research papers and reviews are available on this book's Student Companion Web Site. Each chapter in *Lewin's CELLS, Second Edition,* now includes several **Concept and Reasoning Checks**, allowing students to test their understanding of the material just presented. Pedagogy has also been enhanced by adding special feature boxes to highlight **Medical Applications**, **Historical Perspectives**, and **Methods and Techniques** used to study cell processes (for a list of these features, see page xvii).

The artists, in collaboration with the authors and editors, have developed the illustrations to be as self-explanatory as possible, with such features as text boxes that lead the reader through a figure. Liberal use of well-labeled micrographs and molecular structures helps students to recognize cellular components and understand relationships between structure and function. Whenever possible, the schematic figures take into account the relative sizes of molecules. Colors and molecular shapes, the latter based on atomic structures where known, are used in a consistent manner throughout the book.

Supplements to the text

Jones and Bartlett Publishers offers an impressive array of ancillaries to assist instructors and students in teaching and mastering the concepts in this text. Additional information and review copies of any of the following items are available through your Jones and Bartlett Publishers sales representative or by going to www.jbpub.com/biology.

For the student

The **Student Companion Web Site** we developed exclusively for the second edition of this text, http://biology.jbpub.com/lewin/cells, offers a variety of resources to enhance understanding of cell biology. Students will find chapter summaries and study quizzes that help them to review the key concepts,

as well as an interactive glossary, flashcards, and crosswords to aid with memorization of key terms. The site also contains a selection of interactive figures, animations, and videos, visual aids that are essential to understanding the dynamic nature of cells. These online images are indicated by the symbol  to the left of figure legends in this book. The interactive figures include diagrams and micrographs with labels that can be turned on and off as well as short videos with labels showing the progression of key processes. For those students who wish to explore topics in cell biology in greater depth, a list of important research papers and reviews is also provided for every chapter in the book, along with links to related sites on the Web.

For the instructor

Compatible with Windows® and Macintosh® platforms, the *Instructor's Media CD-ROM* provides instructors with the following traditional ancillaries:

- The **PowerPoint® Image Bank** provides the illustrations, photographs, and tables (to which Jones and Bartlett Publishers holds the copyright or has permission to reproduce digitally) inserted into PowerPoint slides. Instructors can quickly and easily copy individual images or tables into their existing lecture slides.
- The **PowerPoint Lecture Outline Slides** presentation package provides lecture notes and images for each chapter of *Lewin's CELLS, Second Edition*. Instructors with the Microsoft® PowerPoint software can customize the outlines, art, and order of presentation.
- The Instructor's Media CD also contains more than 350 interactive **figures, animations, and videos**.

A *Test Bank* (prepared by Esther Siegfried at Pennsylvania State University, Altoona) is also available through your Jones and Bartlett Publisher's representative. The questions are presented in straight text files that are compatible with most course management software.

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Abbreviations

A	Adenine or adenosine
ADP	Adenosine diphosphate
AMP	Adenosine monophosphate
cAMP	Cyclic AMP
ATP	Adenosine triphosphate
ATPase	Adenosine triphosphatase
bp	Base pair(s)
C	Cytidine or cytosine
cDNA	Complementary DNA
CDP	Cytidine diphosphate
CMP	Cytidine monophosphate
CTP	Cytidine triphosphate
DNA	Deoxyribonucleic acid
DNAase	Deoxyribonuclease
G	Guanine or guanosine
GDP	Guanosine diphosphate
GlcNAc	*N*-Acetyl-D-glucosamine
GMP	Guanosine monophosphate
GTP	Guanosine triphosphate
ΔG	Free energy change
kb	Kilobases or kilobase pairs
Mb	Megabases or megabase pairs
mRNA	Messenger RNA
MW	Molecular weight
Pi	Inorganic phosphate
PPi	Inorganic pyrophosphate
RNA	Ribonucleic acid
RNAase	Ribonuclease
rRNA	Ribosomal RNA
tRNA	Transfer RNA
T	Thymine or thymidine
U	Uracil
UDP	Uridine diphosphate
UMP	Uridine monophosphate
UTP	Uridine triphosphate

Prefix (Abbreviation)	**Multiple**
mega (M)	10^{6}
kilo (k)	10^{3}
deci (d)	10^{-1}
centi (c)	10^{-2}
milli (m)	10^{-3}
micro (μ)	10^{-6}
nano (n)	10^{-9}
pico (p)	10^{-12}

Units	
Å	Angstrom
D or Da	Dalton
g	Gram
h or hr	Hour
M	Molar concentration
m	Meter
m or min	Minute
N	Newton
S	Svedberg unit
s or sec	Second
v	Volt

Amino acids		
A	Ala	Alanine
C	Cys	Cysteine
D	Asp	Aspartic acid
E	Glu	Glutamic acid
F	Phe	Phenylalanine
G	Gly	Glycine
H	His	Histidine
I	Ile	Isoleucine
K	Lys	Lysine
L	Leu	Leucine
M	Met	Methionine
N	Asn	Asparagine
P	Pro	Proline
Q	Gln	Glutamine
R	Arg	Arginine
S	Ser	Serine
T	Thr	Threonine
V	Val	Valine
W	Trp	Tryptophan
Y	Tyr	Tyrosine

Brief contents

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