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基因 XI

LEWIN'S GENES XI

JOCELYN E. KREBS

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高等教育出版社

LEWIN'S GENES XI

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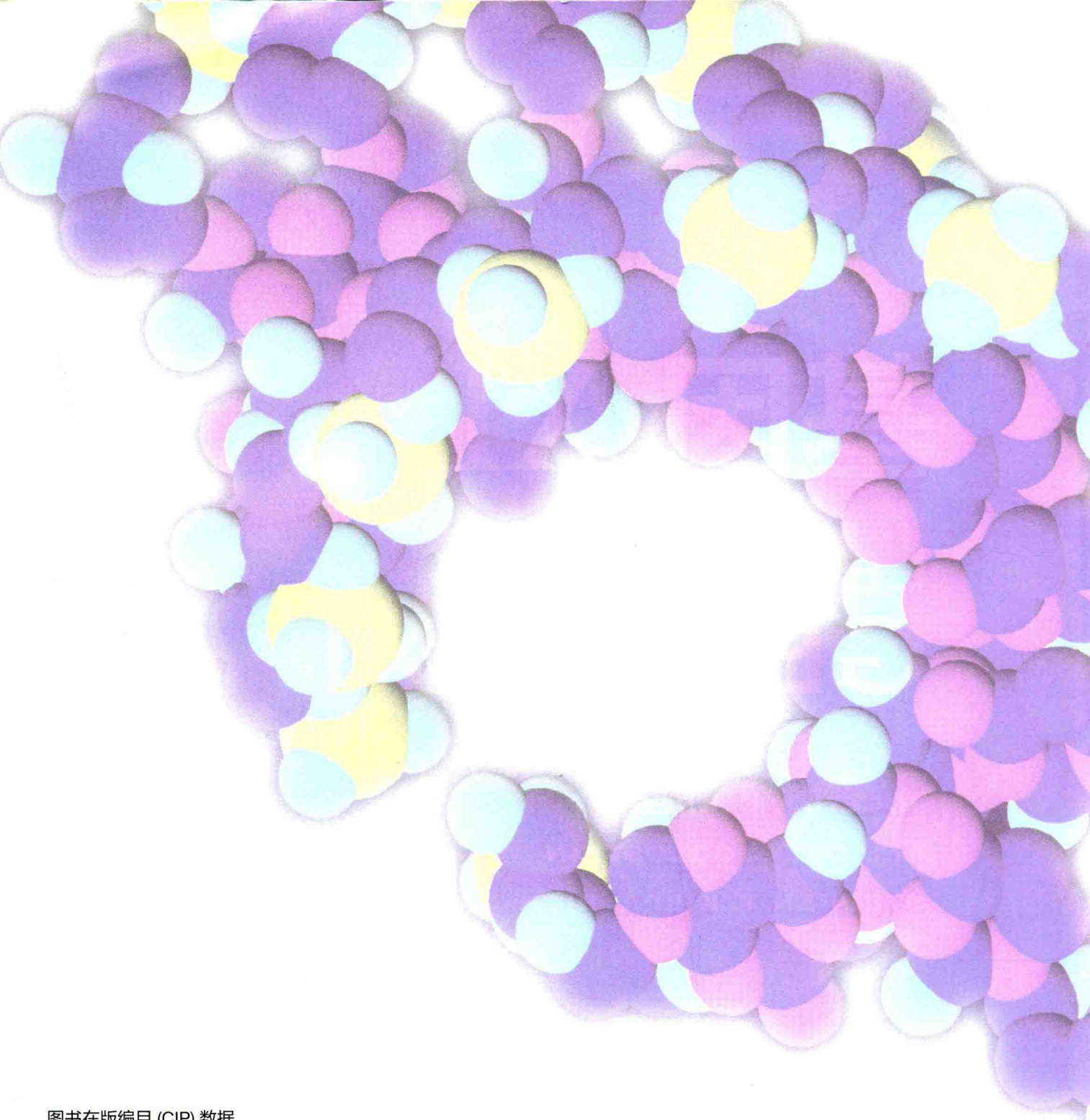
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Dedication

To Benjamin Lewin, for setting the bar high.

To my mother, Ellen Baker, for raising me with a love of science; to the memory of my stepfather, Barry Kiefer, for convincing me science would stay fun; to my partner, Susannah Morgan, for always pretending my biology jokes are funny; and to my sons, Rhys and Frey, who have each gestated during the writing of two editions of this book. Finally, I would like to dedicate this edition to the memory of my PhD mentor, Dr. Marietta Dunaway, a great inspiration who set my feet on the exciting path of chromatin biology.

Jocelyn Krebs

To my family: my wife, Suzanne, whose patience, understanding, and confidence in me are amazing; my children, Andy, Hyla, and Gary, who have taught me so much about using the computer; and my grandchildren, Seth and Elena, whose smiles and giggles inspire me. And to the memory of my mentor and dear friend, Lee A. Snyder, whose professionalism, guidance, and insight demonstrated the skills necessary to be a scientist and teacher. I have tried to live up to his expectations. This is for you, Doc.

Elliott Goldstein

To my wife, Lori, for our many years of love, support, and sometimes tolerance; to my daughter, Jennifer, who will actually read this book; to my son, Andrew, who continually renews my faith in humanity; and to my daughter, Sarah, who brings me joy daily.

Stephen Kilpatrick

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Preface

Of the diverse ways to study the living world, molecular biology has been most remarkable in the speed and breadth of its expansion. New data are acquired daily, and new insights into well-studied processes come on a scale measured in weeks or months rather than years. It's difficult to believe that the first complete organismal genome sequence was obtained less than 20 years ago. The structure and function of genes and genomes and their associated cellular processes are sometimes elegantly and deceptively simple but frequently amazingly complex, and no single book can do justice to the realities and diversities of natural genetic systems.

This book is aimed at advanced students in molecular genetics and molecular biology. In order to provide the most current understanding of the rapidly changing subjects in molecular biology, we have enlisted 21 scientists to provide revisions and content updates in their individual fields of expertise. Their expert knowledge has been incorporated throughout the text. Much of the revision and reorganization of this edition follows that of the third edition of *Lewin's Essential GENES*, but there are many updates and features that are new to this book. This edition follows a logical flow of topics; in particular, discussion of chromatin organization and nucleosome structure precedes the discussion of eukaryotic transcription, because chromosome organization is critical to all DNA transactions in the cell, and current research in the field of transcriptional regulation is heavily biased toward the study of the role of chromatin in this process. Many new figures are included in this book, some reflecting new developments in the field, particularly in the topics of chromatin structure and function, epigenetics, and regulation by noncoding and microRNAs in eukaryotes.

This book is organized into four parts. **Part 1 (Genes and Chromosomes)** comprises Chapters 1 through 10. Chapters 1 and 2 serve as an introduction to the structure and function of DNA and contain basic coverage of DNA replication and gene expression. Chapter 3 provides information on molecular laboratory techniques. Chapter 4 introduces the interrupted structures of eukaryotic genes, and Chapters 5 through 8 discuss

genome structure and evolution. Chapters 9 and 10 discuss the structure of eukaryotic chromosomes.

Part 2 (DNA Replication and Recombination) comprises Chapters 11 through 18. Chapters 11 to 14 provide detailed discussions of DNA replication in plasmids, viruses, and prokaryotic and eukaryotic cells. Chapters 15 through 18 cover recombination and its roles in DNA repair and the human immune system, with Chapter 16 discussing DNA repair pathways in detail and Chapter 17 focusing on different types of transposable elements.

Part 3 (Transcription and Posttranscriptional Mechanisms) includes Chapters 19 through 25. Chapters 19 and 20 provide more in-depth coverage of bacterial and eukaryotic transcription. Chapters 21 through 23 are concerned with RNA, discussing messenger RNA, RNA stability and localization, RNA processing, and the catalytic roles of RNA. Chapters 24 and 25 discuss translation and the genetic code.

Part 4 (Gene Regulation) comprises Chapters 26 through 30. In Chapter 26, the regulation of bacterial gene expression via operons is discussed. Chapter 27 covers the regulation of expression of genes during phage development as they infect bacterial cells. Chapters 28 and 29 cover eukaryotic gene regulation, including epigenetic modifications. Finally, Chapter 30 covers RNA-based control of gene expression in prokaryotes and eukaryotes.

For instructors who prefer to order topics with the essentials of DNA replication and gene expression followed by more advanced topics, the following chapter sequence is suggested:

Introduction: Chapters 1–2

Gene and Genome Structure: Chapters 5–7

DNA Replication: Chapters 11–14

Transcription: Chapters 19–22

Translation: Chapters 24–25

Regulation of Gene Expression: Chapters 9–10 and 26–30

Other chapters can be covered at the instructor's discretion.

Pedagogical Features

This edition contains several features to help students learn as they read. Each chapter begins with a *Chapter Outline*, and each section is summarized with a bulleted list of *Key Concepts*. *Key Terms* are highlighted in bold type in the text and compiled in the *Glossary* at the end of the book. Finally, each chapter concludes with an expanded and updated list of *References*, which provides both primary literature and current reviews to supplement and reinforce the chapter content. Additional instructional tools are available online and on the Instructor's Media CD.

Ancillaries

Jones & Bartlett Learning offers an impressive array of traditional and interactive multimedia supplements to assist instructors and aid students in mastering molecular biology. Additional information and review copies of any of the following items are available through your Jones & Bartlett sales representative or by visiting <http://www.jblearning.com/science/molecular/>.

For the Student

Interactive Student Study Guide

Jones & Bartlett Learning has developed an interactive, electronic study guide dedicated exclusively to this title. Students will find a variety of study aids and resources at <http://biology.jbpub.com/lewin/genesxi/>, all designed to explore the concepts of molecular biology in more depth and to help students master the material in the book. A variety of activities are available to help students review class material, such as chapter summaries, Web-based learning exercises, study quizzes, a searchable glossary, and links to animations, videos, and podcasts, all to help students master important terms and concepts.

For Instructors

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The *Instructor's Media CD* provides the instructor with the following resources:

- The **PowerPoint® Image Bank** provides all of the illustrations, photographs, and tables (to which Jones & Bartlett Learning holds the copyright or has permission to reprint digi-

tally) inserted into PowerPoint slides. With the Microsoft® PowerPoint program, you can quickly and easily copy individual image slides into your existing lecture slides.

- The **PowerPoint Lecture Outline** presentation package developed by author Stephen Kilpatrick, of the University of Pittsburgh at Johnstown, provides outline summaries and relevant images for each chapter of *Lewin's GENES XI*. A PowerPoint viewer is provided on the CD, and instructors with the Microsoft PowerPoint software can customize the outlines, figures, and order of presentation.

Online Instructor Resources

The **Test Bank**, updated and expanded by author Stephen Kilpatrick, is provided as a text file with 750 questions in a variety of formats. The Test Bank is easily compatible with most course management software.

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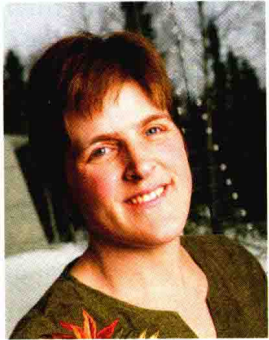
The authors would like to thank the following individuals for their assistance in the preparation of this book: The editorial, production, marketing, and sales teams at Jones & Bartlett have been exemplary in all aspects of this project. Cathy Sether, Erin O'Connor, Rachel Isaacs, Lauren Miller, Leah Corrigan, and Wendy Swanson deserve special mention. Cathy brought us together on this project and in doing so launched an efficient and amiable partnership. She has provided able leadership and has been an excellent resource as we ventured into new territories. Rachel, Wendy, and Leah have handled the daily responsibilities of the writing and production phases with friendly professionalism and helpful guidance. Lauren has made the process of choosing and revising figures very smooth.

We thank the editors of individual chapters, whose expertise, enthusiasm, and careful judgment brought the manuscript up to date in many critical areas.

Jocelyn E. Krebs
Elliott S. Goldstein
Stephen T. Kilpatrick

About the Authors

Benjamin Lewin founded the journal *Cell* in 1974 and was Editor until 1999. He founded the Cell Press journals *Neuron*, *Immunity*, and *Molecular Cell*. In 2000, he founded Virtual Text, which was acquired by Jones and Bartlett Publishers in 2005. He is also the author of *Essential GENES* and *CELLS*.



Jocelyn E. Krebs received a B.A. in Biology from Bard College, Annandale-on-Hudson, NY, and a Ph.D. in Molecular and Cell Biology from the University of California, Berkeley. For her Ph.D. thesis, she studied the roles of DNA topology and insulator elements in transcriptional regulation.

She performed her postdoctoral training as an American Cancer Society Fellow at the University of Massachusetts Medical School in the laboratory of Dr. Craig Peterson, where she focused on the roles of histone acetylation and chromatin remodeling in transcription. In 2000, Dr. Krebs joined the faculty in the Department of Biological Sciences at the University of Alaska, Anchorage, where she is now an Associate Professor. She directs a research group studying chromatin structure and function in transcription and DNA repair in the yeast *Saccharomyces cerevisiae* and the role of chromatin remodeling in embryonic development in the frog *Xenopus*. She teaches courses in molecular biology for undergraduates, graduate students, and first-year medical students. She also teaches a Molecular Biology of Cancer course and has taught Genetics and Introductory Biology. She lives in Eagle River, AK, with her partner and son, and a house full of dogs and cats. Her non-work passions include hiking, camping, and snowshoeing.



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Stephen T. Kilpatrick received a B.S. in Biology from Eastern College (now Eastern University) in St. Davids, PA, and a Ph.D. from the Program in Ecology and Evolutionary Biology at Brown University. His thesis research was an investigation of the population genetics

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He has participated in the development and authoring of ancillary materials for several introductory biology, genetics, and molecular genetics texts as well as writing articles for educational reference publications. For his classes at Pitt-Johnstown, Dr. Kilpatrick has developed many active learning exercises in introductory biology, genetics, and evolution. Dr. Kilpatrick resides in Johnstown, PA, with his wife and three children. Outside of scientific interests, he enjoys music, literature, and theater and occasionally performs in local community theater groups.

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Hank W. Bass is an Associate Professor of Biological Science at Florida State University. His laboratory works on the structure and function of meiotic chromosomes and telomeres in maize using molecular cytology and genetics.

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Chapter Opener Credits and Captions

Part 1

Photo courtesy of S. V. Flores, A. Mena, and B. F. McAllister. Used with permission of Bryant McAllister, Department of Biology, University of Iowa.

Chapter 1

A strand of DNA in blue and red. DNA is the genetic material of eukaryotic cells, bacteria, and many viruses. © Artsilensecome/Shutterstock, Inc.

Chapter 2

A visual representation of gene expression analysis that allows researchers to see patterns in a network of expressed genes. Each dot represents a gene, and links between the dots occur where there are similar patterns of expression between the genes. © Anton Enright, The Sanger Institute/Wellcome Images.

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DNA fragments separated by gel electrophoresis. © Nicemonkey/Dreamstime.com.

Chapter 4

A self-splicing intron in an rRNA of the large ribosomal subunit. © Kenneth Eward/Photo Researchers, Inc.

Chapter 5

Scanning electron micrograph (SEM) of human X and Y chromosomes in metaphase (35,000×). Most of the content of the genome is found in chromosomal DNA, though some organelles contain their own genomes. © Biophoto Associates/Photo Researchers, Inc.

Chapter 6

Mouse and human chromosomes. Both species' genomes have undergone chromosomal rearrangements from the genome of their most recent common ancestor. The colors and corresponding numbers on the mouse chromosomes indicate the human chromosomes containing homologous segments. Photo courtesy of U.S. Department of Energy. Used with permission of Lisa J. Stubbs, University of Illinois at Urbana-Champaign.

Chapter 7

Scanning electron micrograph (SEM) of red blood cells. Genes that encode the protein subunits of hemoglobin, the oxygen-carrying complex found in red blood cells, are members of a large gene family that have evolved by duplication and divergence. © Sebastian Kaulitzki/Shutterstock, Inc.

Chapter 8

A circular genome map showing shared (syntenic) regions between humans (outer ring) and (from inner ring outward) chimpanzee, mouse, rat, dog, chicken, and zebrafish genomes. Similar colors among rings show synteny. © Martin Krzywinski/Photo Researchers, Inc.

Chapter 9

Microphotograph of living cells undergoing mitosis. Individual chromosomes lined up at the metaphase plate or separating are visible in several cells. © Dimarion/Shutterstock, Inc.

Chapter 10

A three-dimensional model of chromatin showing one possible arrangement for the nucleosomes in the 30-nm fiber. Photo courtesy of Thomas Bishop, Tulane University, using VDNA plug-in for VMD (<http://www.ks.uiuc.edu/research/vmd/plugins/vdna/>).

Part 2

Image courtesy of Teresa Larsen, The Foundation for Scientific Literacy.

Chapter 11

A transmission electron micrograph of an *E. coli* bacterium in the mid to late stages of binary fission, the process by which the bacterium divides. The hair-like appendages around the bacterium are pili, structures used for bacterial conjugation (magnification: 17,500×). © CNRI/Photo Researchers, Inc.

Chapter 12

Computer model of DNA polymerase replicating a strand of DNA (across center). The secondary structure of the DNA polymerase and the primary structure of the DNA molecule are shown. DNA polymerases are enzymes that synthesize strands of DNA from a complementary template strand during DNA replication. This molecule is in the Y family of DNA polymerases, which are translesion synthesis polymerases, that is, they are able to replicate damaged areas of DNA that stall other DNA polymerases. The replication is not always accurate and can lead to mutagenesis or cancer. © Laguna Design/Photo Researchers, Inc.

Chapter 13

A type II topoisomerase acting on a knotted or supercoiled DNA substrate. The cleaved DNA is shown in green. The DNA that is being passed through the break is viewed end-on. Photo courtesy of James Berger, University of California, Berkeley.

Chapter 14

Plasmids. © Deco Images II/Almay Images.

Chapter 15

A model demonstrating the interaction of a RuvA tetramer with a DNA Holliday junction, an intermediate of recombination. Reproduced with permission from J. B. Rafferty et al., *Science* 274 (1996): 415–421. © 1996 AAAS. Photo courtesy of David W. Rice and John B. Rafferty, University of Sheffield.

Chapter 16

The XPD helicase, involved in both transcription and nucleotide excision repair, is shown unwinding DNA. Colors indicate different domains of XPD; the helicase domain is green. Photo courtesy of M. Pique, Li Fan, Jill Fuss, and John Tainer, The Scripps Research Institute and Lawrence Berkeley National Laboratory. More information available at L. Fan et al., *Cell* 133 (2008): 789–800.

Chapter 17

Artist's rendering of an electron micrograph showing retroviruses. © MedicalRF/Photo Researchers, Inc.

Chapter 18

Human Ig autoantibody binding double-strand DNA. Rendered by UCSF Chimera, P. Casali & E.J. Pone, 2012.

Part 3

Photo courtesy of Jie Ren and Jun Ma, University of Cincinnati College of Medicine and Cincinnati Children's Hospital.

Chapter 19

Transcription factor and DNA molecules. Molecular model showing the secondary structure (helices) of the transcription factor Brachyury (purple) binding to a molecule of DNA (deoxyribonucleic acid, running horizontally from left to right). Brachyury, also known as T, is a protein that controls the transcription of DNA to RNA (ribonucleic acid) by the enzyme RNA polymerase. RNA is the intermediate product in the formation of a protein from its gene. Brachyury binds to a specific sequence of bases in the DNA called a T-box. Brachyury has been found to be crucial in embryonic development in animals. It is necessary to form the mesoderm, the precursor tissue that eventually develops into the internal organs and bones. © Phantatomix/Photo Researchers, Inc.

Chapter 20

Biomedical illustration of transcription showing RNA polymerase at work. A DNA sequence is copied by RNA polymerase to produce a complementary nucleotide RNA strand, called messenger RNA (mRNA). © Carol & Mike Werner/Visuals Unlimited.

Chapter 21

A three-dimensional structure of the mammalian spliceosomal C complex. Spliceosome structure courtesy of Nikolaus Grigorieff, Brandeis University. Background photo © Bella D/Shutterstock, Inc.

Chapter 22

Computer artwork of aconitase (blue), in complex with ferritin mRNA (red). Aconitase is involved in the citric acid cycle, but here it is performing a secondary function as an iron regulatory protein (IRP). It does this by binding to ferritin mRNA, which prevents translation into the protein product (ferritin). Ferritin acts like a sponge and helps to protect cells from the toxic effects of excess iron. © Equinox Graphics/Photo Researchers, Inc.

Chapter 23

The figure shows the RNA/protein architecture of the large ribosomal subunit with the active site highlighted. The background shows a schematic diagram of the peptidyl transferase active site of the ribosome. Photo courtesy of Nenad Ban, Institute for Molecular Biology & Biophysics, Zurich.

Chapter 24

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