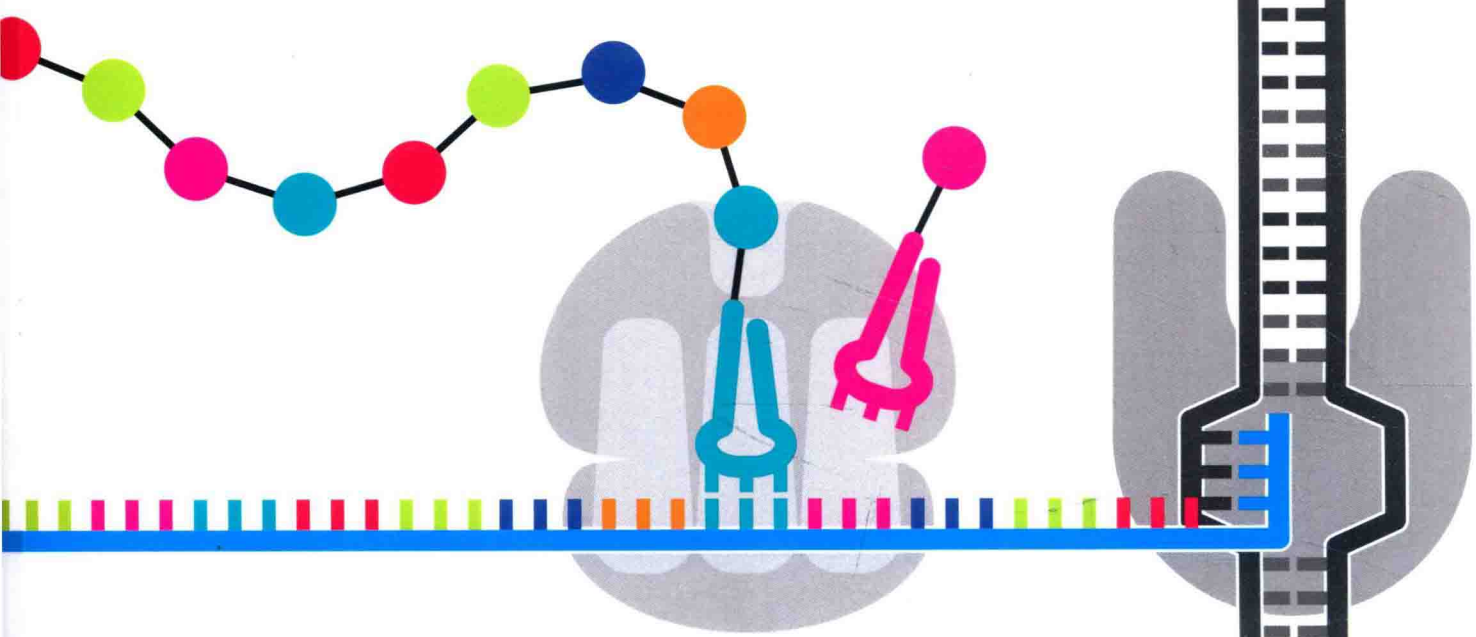
OXFORD

Molecular Biology

Principles of Genome Function

SECOND EDITION



Nancy L. Craig • Orna Cohen-Fix
Rachel Green • Carol Greider
Gisela Storz • Cynthia Wolberger

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With end of chapter questions by Deborah Zies and Claire Burns

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MOLECULAR BIOLOGY

Organism	Gene name	Example	Mutant allele	Example	Protein name	Example
Bacteria	Three lowercase letters, followed by upper case letter, all italicized	*recA*	Same as gene name, followed by allele number (can have non-integer allele designations such as 'am' or 'ts' for amber- and temperature-sensitive mutants, respectively)	*recA11*	Same as gene name except first letter is upper case and gene name is not italicized	RecA
Saccharomyces cerevisiae	Letters (all uppercase if dominant, all lowercase if recessive) followed by an Arabic number, all italicized	*URA3*	Same as gene name followed by a hyphen and an Arabic number (can have additional information about how mutant was generated)	*ura3-52*	Uppercase first letter, followed by lowercase letters and number, not italicized	Ura3
Schizosaccharomyces pombe	Three lowercase letters followed by a number and superscript +, all italicized	*cdc2*$^{+}$	Same as gene name, followed by allele number (but no superscript +)	*cdc2-5*	Same as gene name except first letter is uppercase and gene name is not italicized and there is no superscript +	Cdc2
Caenorhabditis elegans	Three to four lowercase letters, followed by a hyphen and a number, all italicized	*dpy-5*	Same as gene name, followed by an allele name (one or two letters followed by a number) in parentheses	*dpy-5(e61)*	Same as gene name except all uppercase letters and gene name is not italicized	DPY-5
Drosophila melanogaster	Can be any word lowercase italicized (most genes also have a shorter unique symbol)	*dacapo* (*dap*)	Same as gene name followed by a superscript number(s) or letter(s) (for dominant mutants, the gene name is followed by a superscript D)	*dacapo*^{4}, *dacapo*^{D}	Same as gene name except first letter is uppercase and gene name is not italicized	Dacapo
Mus musculus	Usually three to five letters and Arabic numbers (maximum ten characters) begin with an uppercase letter (not a number), followed by lowercase letters and numbers, all italicized	*Grid2*	Same as the gene with the original mutant symbol added as a superscript to the gene symbol	*Grid2*^{ho}	Same as gene name except all uppercase letters and gene name is not italicized	GRID2
Homo sapiens	Maximum six characters: all uppercase letters or by a combination of uppercase letters and Arabic numbers, all italicized	*ATM*	Sequence variants are described by the specific sequence change in the DNA with sequence change, insertion, and deletions having specific nomenclature	c.1636C4G (p.Leu546-Val) (this example corresponds to a C to G change at position 1636 of the *ATM* coding sequence	Same as gene name except not italicized	ATM

Nomenclature table. Note that the names of some genes and proteins that have become accepted in the literature, such as the human Rb and p53 proteins, do not follow the conventions listed in this table.

To our teachers

ABOUT THE AUTHORS OF MOLECULAR BIOLOGY

Nancy L Craig received an A.B. in Biology and Chemistry from Bryn Mawr College in 1973 and a Ph.D. in Biochemistry in 1980 at Cornell University in Ithaca, New York, where she worked on DNA repair with Jeff Roberts. She then worked on phage lambda recombination as a postdoctoral fellow with Howard Nash at the National Institutes of Health. She joined the faculty of Department of Microbiology and Immunology at the University of California, San Francisco in 1984 and began her work on transposable elements. She joined the Department of Molecular Biology and Genetics at the Johns Hopkins University School of Medicine in 1991, where she is currently a Professor and a Howard Hughes Medical Institute Investigator, as well as the recipient of the Johns Hopkins University Alumni Association Excellence in Teaching Award. Nancy Craig is a Fellow of the American Academy of Microbiology, the American Academy of Arts and Sciences and the American Association for the Advancement of Science, and was elected to the National Academy of Sciences.

Orna Cohen-Fix received a B.A. from the Tel Aviv University in 1987 and a Ph.D. in Biochemistry with Zvi Livneh at the Weizmann Institute of Science in 1994. She did a post-doctoral fellowship with Doug Koshland at the Carnegie Institution of Washington in Baltimore, studying the regulation of chromosome segregation. In 1998, she moved to the National Institute of Diabetes and Digestive and Kidney Diseases in Bethesda, where she is now a Senior Investigator. Her research focuses on cell cycle regulation and nuclear architecture, using budding yeast and *C. elegans* as model organisms. She is also an Adjunct Professor at Johns Hopkins University and the Co-Director of the NIH/Johns Hopkins University Graduate Partnership Program. She is a recipient of a Presidential Early Career Award for Scientists and Engineers, and an Association of Women in Science Mentoring Award for her work on promoting the retention of women in science.

Rachel Green received a B.S. in chemistry from the University of Michigan in 1986 and a Ph.D. in Biological Chemistry from Harvard University in 1992, where she worked with Jack Szostak studying catalytic RNA. She then did postdoctoral work in the laboratory of Harry Noller at the University of California, Santa Cruz, studying the role played by the ribosomal RNAs in the function of the ribosome. She is currently a Professor in the Department of Molecular Biology and Genetics at The Johns Hopkins University School of Medicine, an Investigator of the Howard Hughes Medical Institute, and a member of the National Academy of Sciences. Her work continues to focus on the mechanism and regulation of translation in bacteria and eukaryotes. She is the recipient of a Johns Hopkins University School of Medicine Graduate Teaching Award.

Carol Greider received a B.A. from the University of California at Santa Barbara in 1983. In 1987, she received her Ph.D. from the University of California at Berkeley, where she and her advisor, Elizabeth Blackburn, discovered telomerase, the enzyme that maintains telomere length. In 1988, she went to Cold Spring Harbor Laboratory as an independent Fellow and remained as a Staff Scientist until 1997, when she moved to The Johns Hopkins University School of Medicine. She is currently a Professor and Director of the Department of Molecular Biology and Genetics, and her work focuses on telomerase and the role of telomeres in cell senescence, age-related disease, and cancer. She is a member of the National Academy of Sciences and is the recipient of numerous awards, including the Gairdner Foundation International Award, the Louisa Gross Horwitz Prize, and the Lasker Award for Basic Medical Research. In 2009, she was awarded the Nobel Prize in Physiology or Medicine together with Elizabeth Blackburn and Jack Szostak for the discovery of telomerase.

Gisela Storz graduated from the University of Colorado at Boulder in 1984 with a B.A. in Biochemistry and received a Ph.D. in Biochemistry in 1988 from the University of California at Berkeley, where she worked for Bruce Ames. After postdoctoral fellowships with Sankar Adhya at the National Cancer Institute and Fred Ausubel at Harvard Medical School, she moved to the National Institute of Child Health and Human Development in Bethesda, where she is now a Senior Investigator. Her research is focused on understanding gene regulation in response to environmental stress as well as elucidating the functions of small regulatory RNAs and very small proteins. She is a Fellow of the American Academy of Microbiology, American Academy of Arts and Sciences, and National Academy of Sciences, and received the American Society for Microbiology Eli Lilly Award.

Cynthia Wolberger received her A.B. in Physics from Cornell University in 1979 and a Ph.D. in Biophysics from Harvard University in 1987, where she worked with Stephen Harrison and Mark Ptashne on the structure of a phage repressor bound to DNA. She did postdoctoral work on eukaryotic protein–DNA complexes in the laboratory of Robert Stroud and the University of California, San Francisco and then in the laboratory of Carl Pabo at The Johns Hopkins University School of Medicine. She joined the faculty of the Department of Biophysics and Biophysical Chemistry in 1991, where she is now a Professor. Her research focuses on the structural and biochemical mechanisms underlying transcriptional regulation and ubiquitin-mediated signaling. She is a Fellow of the American Association for the Advancement of Science and a recipient of the Dorothy Crowfoot Hodgkin Award of the Protein Society.

Molecular Biologists of Fells Point, Baltimore: (L–R) Rachel Green, Gisela (Gigi) Storz, Orna Cohen-Fix, Nancy Craig, Cynthia Wolberger and Carol Greider. The photo-digital illustration was created by Robert McClintock, a Fells Point artist.

PREFACE

A contemporary perspective on molecular biology

Molecular Biology: Principles of Genome Function offers a distinctive approach to the teaching of molecular biology. It is an approach that reflects the challenge of teaching a subject that is in many ways unrecognizable from the molecular biology of the twentieth century – a discipline in which our understanding has advanced immeasurably, but about which many intriguing questions remain to be answered. Among the students being taught today are the molecular biologists of tomorrow; these individuals will be in a position to ask fascinating questions about fields whose complexity and sophistication become more apparent with each year that passes.

We have written the book with several guiding themes in mind, all of which focus on providing a faithful depiction of the key themes and challenges that surround molecular biology in the twenty-first century, and on communicating this reality to students in a way that will engage and motivate, rather than overwhelm and intimidate.

A focus on the underlying principles

Arguably one of the biggest challenges facing instructors and students of molecular biology today is the vast amount of information encapsulated by the field. It is impossible for an instructor to convey every last detail (and equally impossible for students to absorb everything that there is to know). Indeed, we believe that it is not necessary to delve into every fine detail in order to understand the main concepts. Therefore, our approach focuses on communicating the *principles* of the subject.

We believe it is better for students to truly understand the foundational principles rather than simply learn a series of facts. To this end, we do not try to be exhaustive in our coverage. In the digital age in which we live, it is easier than ever before for students to gather a vast amount of information on a particular topic of interest. This information is of little value, however, if the student lacks a conceptual framework within which to make sense of all the information to which they are exposed.

By focusing on key principles, we seek to equip students with a conceptual framework, which we believe will be invaluable to them during their later careers.

An emphasis on commonalities

Until relatively recently, much more was known about the molecular components and processes of bacterial systems than of their archaeal and eukaryotic counterparts. In recent years, however, our understanding of archaeal and eukaryotic systems has increased enormously. With this increased understanding has come the realization that bacterial, archaeal, and eukaryotic systems exhibit many commonalities – commonalities that point to the common ancestry of the three kingdoms of life.

Throughout this book, therefore, our emphasis is on the *common features* of bacterial, archaeal, and eukaryotic systems. Differences do exist, of course – an inevitable outcome of evolutionary processes generating biological diversity. However, we have strived where possible to present a single view of key topics based

on conserved processes and components. We have then discussed key differences between bacterial processes and their archaeal and eukaryotic counterparts where they exist, and where they have helped to further our understanding.

We recognize that some may feel that the processes occurring in bacteria, and in eukaryotes and archaea, are best taught separately. However, our focus on principles – and on constructing an overarching conceptual framework – leads us strongly to believe that an emphasis on commonalities is a valuable educational approach.

Integration of key themes and concepts

One of the most startling realizations of recent years has been the widespread importance of certain molecular phenomena, such as chromatin modification, and regulatory RNAs, which have impacts on genome function in ways far more diverse than had previously been recognized. Rather than examining each of these phenomena in isolation, our approach reflects their diverse impacts by presenting them in the various contexts in which they function. We believe this overall approach reflects the reality of molecular biology, and helps students to appreciate molecular biology as a unified discipline, with many components and phenomena acting in concert, rather than as a series of isolated topics.

A demonstration of how we know what we know

At heart, molecular biology is an experimental science. Our understanding of the field is increased through the accumulation of experimental evidence, which leads to the gradual emergence of key ideas and paradigms. Therefore, a central element to the understanding of molecular biology is an appreciation of the approaches taken to yield the information from which concepts and principles are deduced.

However, as instructors, we face a potential conflict: a mass of experimental evidence can often be overwhelming for students, and can make it more challenging for them to grasp the central ideas and paradigms that the experimental evidence has allowed us to elucidate. On the other hand, ignoring the experimental evidence deprives students from fully understanding the fundamental aspects of molecular biology (and, indeed, of science in general). In response to this seeming conflict, our approach has been for the main body of the text to focus on the communication of key concepts, free from the layer of complexity that experimental evidence might introduce.

We have then complemented our coverage of key concepts in the main body of the text with separate 'Experimental approach' panels, which branch off from the text in a clearly signposted way. These panels describe pieces of research that have been undertaken and which have been particularly valuable in elucidating difference aspects of molecular biology.

Importantly, experimental research represents an ongoing journey of discovery, where the experimental approaches adopted develop as much as our understanding of the field. Uniquely, therefore, the experimental approach panels present, wherever possible, two approaches – one 'classic' and one 'contemporary'. Although all approaches have revealed valuable insights, regardless of whether they could be considered classic or contemporary, we believe that coupling the approaches in this way has additional educational value in terms of showing how both experimentation and the knowledge gained from such experimentation can evolve with time.

In addition to the experimental approach panels, further support for encouraging students to engage with experimental evidence is provided by an online Journal

Club, as described more fully in the description of the Online Resource Center, which follows.

The methods used in molecular biology

Many of the experimental approach panels (and the research work featured in the Journal Club papers) draw on particular laboratory techniques that are used in different contexts throughout molecular biology research. The final chapter of this book, 'Tools and techniques in molecular biology', provides an overview of the basic techniques that are exploited during the course of much experimental work in molecular biology. Rather than describing general methods in detail within the experimental approach panels, we have directed the reader to appropriate coverage in Chapter 19, where they can learn more about the methodological tools that are at a molecular biologist's disposal, how these tools work, and what they can tell us.

New for this edition

The preparation of this second edition has given us a welcome opportunity to refine a number of aspects of the text, particularly in the light of valuable feedback from those who have taught from the first edition. Beyond updating all topics in line with current research findings, the most notable changes are:

A new chapter on regulatory RNAs. We now include a broad survey of an area of molecular biology whose centrality to fully understanding genome function has come to the fore in recent years.

Individual chapters on the regulation of transcription and translation. Whereas the previous edition devoted one chapter each to transcription and translation, each of these topics is now covered in two chapters: one devoted to the core processes and another exploring how those processes are regulated.

New questions at the end of each chapter. Each chapter now includes a range of end-of-chapter questions, provided by Deborah Zies, University of Mary Washington, and Claire Burns, Washington and Jefferson College.

Additional Experimental approach panels. We have prepared a number of new Experimental approach panels, bringing the total throughout the book to 44. The format of these panels has also been refined, with new sub-headings to guide the reader, and links to explanations of relevant techniques in Chapter 19, 'Tools and techniques in molecular biology'.

Video animations. We have worked with the winner of OUP's Student Animation Award, Connor Hendrich of Colorado State University, to develop sixteen animations that illustrate some of the central processes in molecular biology, including those that are particularly challenging to visualize.

NLC
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CW
Baltimore, Maryland, July 2013

LEARNING FROM THIS BOOK

Molecular Biology: Principles of Genome Function features a number of learning features to help students get the most out of their study of the subject.

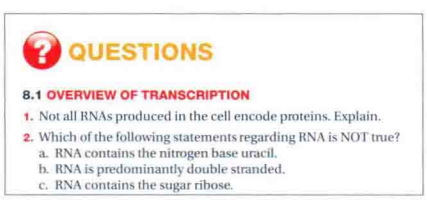
The Experimental approach panels

As noted previously, molecular biology is an experimental science. To help you gain an understanding of how some of the key molecular processes and components described in this book were characterized, without overburdening the main text with a lot of experimental detail, many chapters feature 'Experimental approach' panels. These panels describe pieces of research that have been particularly valuable in elucidating different aspects of molecular biology. 'Related techniques' at the end of each panel direct you to relevant sections in Chapter 19, 'Tools and techniques in molecular biology', where you can learn more about the specific techniques mentioned in the panels.


6.2 EXPERIMENTAL APP
Discovery of the origin reco
Biochemistry and footprinting lead to the discovery of the eukaryotic replication initiation protein
While DNA sequences that function as origins of replication

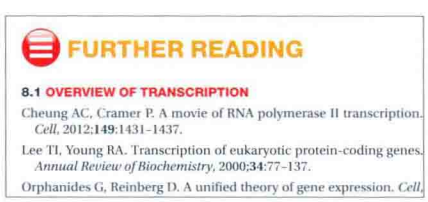
End of chapter questions

A set of questions is presented at the end of each chapter, grouped by section to help instructors to assign questions according to specific topics taught. Included in these questions are *Challenge questions*, which are designed to stimulate students' thinking, and often encourage the use of data analysis skills. Some questions also relate to Experimental approach panels, to encourage students to engage more closely with the research explored in those panels.


QUESTIONS
8.1 OVERVIEW OF TRANSCRIPTION
1. Not all RNAs produced in the cell encode proteins. Explain.
2. Which of the following statements regarding RNA is NOT true?
a. RNA contains the nitrogen base uracil.
b. RNA is predominantly double stranded.
c. RNA contains the sugar ribose.

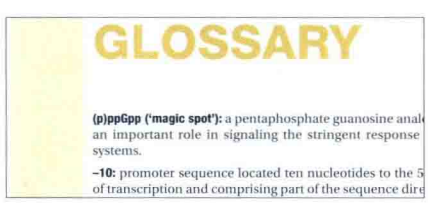
Further reading

Each chapter ends with a list of further reading materials, typically review articles that we feel would make a good next step in exploring the topics covered in the book in more detail. Each further reading list is divided into chapter sections to help you pinpoint articles that are relevant to the particular topic you are interested in.


FURTHER READING
8.1 OVERVIEW OF TRANSCRIPTION
Cheung AC, Cramer P. A movie of RNA polymerase II transcription. *Cell*, 2012;**149**:1431–1437.
Lee TI, Young RA. Transcription of eukaryotic protein-coding genes. *Annual Review of Biochemistry*, 2000;**34**:77–137.
Orphanides G, Reinberg D. A unified theory of gene expression. *Cell*,

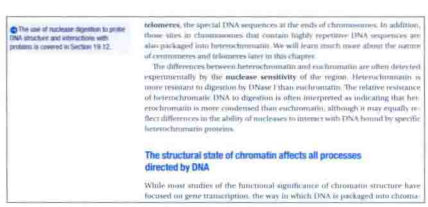
Glossary

Molecular biology, like many scientific disciplines, has its own particular vocabulary, and descriptions of molecular processes and procedures feature terms that may at first glance be unfamiliar. We have compiled an extensive glossary of all of the key terms featured in the book, which will be of value as you master the language of the subject.


GLOSSARY
(p)ppGpp ('magic spot'): a pentaphosphate guanosine anal
an important role in signaling the stringent response
systems.
–10: promoter sequence located ten nucleotides to the 5
of transcription and comprising part of the sequence dire

Cross-references

As we note previously, molecular biology comprises a range of interconnected topics, not a series of discrete, isolated ones. To help you make the connections between the topics presented in the book, and see how these topics come together to give a rounded picture of molecular biology, each chapter features numerous cross-references to other chapters in the book.


The use of nuclease digestion to probe DNA structure and interactions with proteins is covered in Section 19.12.
telomeres, the special DNA sequences at the ends of chromosomes. In addition, those sites in chromosomes that contain highly repetitive DNA sequences are also packaged into heterochromatin. We will learn much more about the nature of centromeres and telomeres later in this chapter.
The differences between heterochromatin and euchromatin are often detected experimentally by the **nuclease sensitivity** of the region. Heterochromatin is more resistant to digestion by DNase I than euchromatin. The relative resistance of heterochromatic DNA to digestion is often interpreted as indicating that heterochromatin is more condensed than euchromatin; although it may equally reflect differences in the ability of nucleases to interact with DNA bound by specific heterochromatin proteins.
The structural state of chromatin affects all processes directed by DNA
While most studies of the functional significance of chromatin structure have focused on gene transcription, the way in which DNA is packaged into chroma

Scan here to watch a video animation explaining more about transcription initiation, elongation and termination, or find it via the Online Resource Center at www.oxfordtextbooks.co.uk/orc/craig2e/.

Links to video animations

The functioning of the genome involves a number of intricate processes operating in three dimensions. To help you visualize some of the key processes, a series of video animations are available for you to watch on YouTube. When you see a QR code image in the text, simply scan it with your phone or tablet camera to be taken directly to the animation that relates to the topic you are reading about.

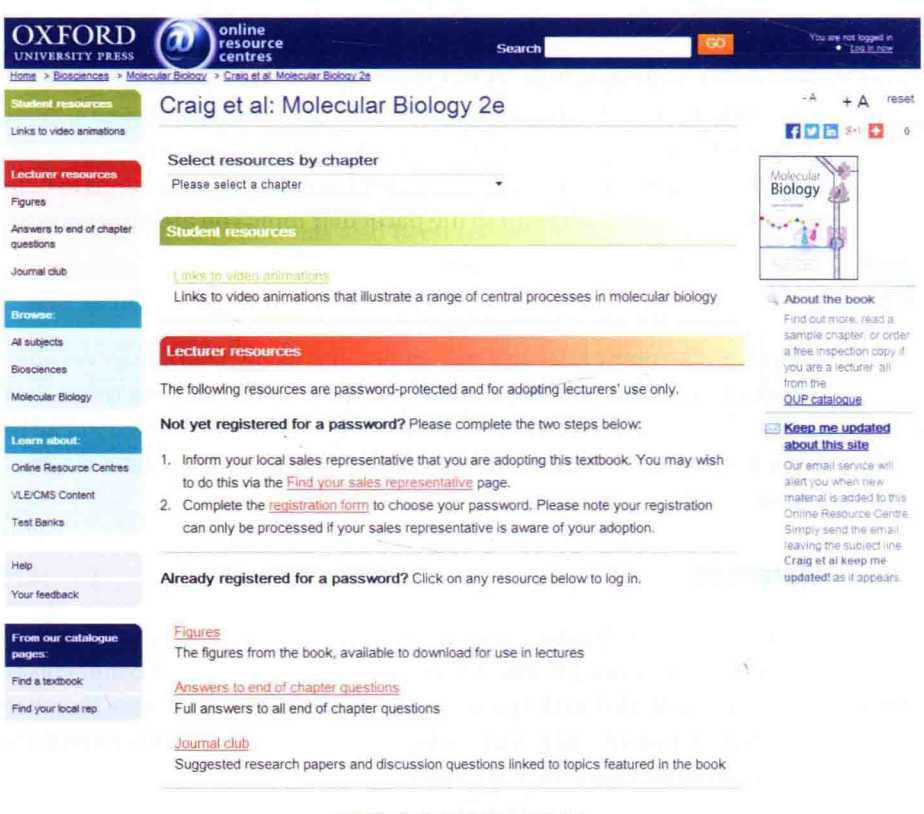
PDB codes

Many of the molecular structures that appear throughout this book have been generated from data deposited in the Protein Data Bank (PDB). Each entry in the PDB is assigned a unique code; this code can be used to retrieve the data related to the entry in question, which often includes crystallographic data, and onscreen renderings of molecular structures in three dimensions. The PDB codes relating to many of the molecular structures in the book are given in the relevant figure captions. Visit the PDB website (http://www.rcsb.org/pdb/home/home.do) and enter the PDB codes related to molecules of interest to retrieve data related to those molecules.

Online Resource Center

Molecular Biology: Principles of Genome Function does not end with this printed book. Instead, additional resources for both instructors and their students are available in the book's Online Resource Center.

Go to http://www.oxfordtextbooks.co.uk/orc/craig2e/



For instructors

Electronic artwork

Figures from the book are available to download, for use in lectures.

Answers to end of chapter questions

Full answers to all end of chapter questions are provided to help with the grading of your students.

Journal Club

Most chapters in the book are accompanied by an online Journal Club, which features suggested research papers and discussion questions linked to topics featured in the chapters. Understanding the details presented in primary literature articles can often be challenging; the purpose of the Journal Club is to guide students through some selected papers in a structured way, to build their confidence in reading and critically evaluating the work of others.

For students

Links to video animations

As an alternative to using the QR code images featured in the book, simply follow the links to view a series of video animations on YouTube, produced specifically to accompany the book.

ACKNOWLEDGMENTS

Many people made this textbook possible thanks to their advice and support.

We were fortunate to have worked under the guidance of two gifted individuals. The project was begun with Miranda Robertson at New Science Press, who convinced us that we could write a new textbook and helped show us the way. We benefited from her tremendous vision, advice, and insistence on clarity, as well as from her many visits to work with us in Baltimore and Washington. It was Jonathan Crowe at Oxford University Press who ushered us across the finish line by providing superb editorial advice, while teaching us how to work ever more effectively. He made outstanding contributions to the writing and organization of this book, and we are grateful for his efforts in helping us bring this project to completion as well as seeing us through the production of the second edition.

Our work was supported by many others, particularly Matthew McClements, who is responsible for the beautiful illustrations. At Oxford University Press, Joanne Hardern guided the book through the production process, while Elizabeth Farrell did an excellent job of copy editing. Our administrative assistants, particularly Patti Kodeck, helped to organize our meetings and carve out time for us to work on the book.

Our colleagues at Johns Hopkins and at the National Institutes of Health were generous, answering innumerable questions and providing comments on the text and figures. We are also grateful to the scientists outside our respective institutions for responding to our many emails and phone calls asking for information and clarifications. We owe special thanks to our students, postdoctoral fellows and laboratory staff, who gladly provided us with input while being patient when the writing took us away from the laboratory.

We extend our most profound thanks to our families for their support and encouragement throughout this project, which took far more time and work than any of us had imagined. We are grateful to our children, Rachel and Joshua Adams, Charles and Gwendolyn Comfort, Eric, Toby and Noel Cormack, Tal and Jonathan Fix, and Ella, Toby, and Felix Wu for their forbearance. We especially thank our spouses, Jeffrey Adams, Brendan Cormack, Alan Fix, Helen Lee McComas, and Carl Wu, for cheering us on while picking up the slack at home.

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Michael Lichten, Center for Cancer Research
Lasse Lindahl, University of Maryland

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John Lis, Cornell University
Bob Lloyd, University of Nottingham
John Lorsch, Johns Hopkins University School of Medicine
Sue Lovett, Brandeis University
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Peter B. Moore, Yale University
Margaret Olney, Saint Martin's University
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Anthony Ouellette, Jacksonville University
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Tanya Paull, University of Texas at Austin
Stephen Pelsue, University of Southern Maine
Eric Phizicky, IBM Life Sciences Discovery Center, University of Rochester
Marie Pizzorno-Simpson, Bucknell University
Anna Marie Pyle, Yale University
Venki Ramakrishnan, MRC Laboratory of Molecular Biology
John Rebers, Northern Michigan University
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Don Rio, University of California, Berkeley
Jeff Roberts, Cornell University
Peter Sarnow, Stanford University
Paul Schimmel, The Scripps Research Institute
Rey Sia, The College at Brockport, SUNY
Erik Sontheimer, Northwestern University
Forrest Spencer, Johns Hopkins University School of Medicine
Stephen Spiro, University of Texas at Dallas
Kevin Sullivan, National University of Ireland, Galway
Ben Szaro, State University of New York, Albany
Song Tan, Pennsylvania State University
David Tollervey, University of Edinburgh
Deborly Wade, Central Baptist College
Gabriel Waksman, University College London
Tracy Ware, Salem State College
Jon Warner, Albert Einstein College of Medicine, Yeshiva University
Alan Weiner, Washington University
Stephen West, London Research Institute
Jamie Williamson, The Scripps Research Institute
John Wilson, Michigan State University
Fred Winston, Harvard Medical School
Kate Leslie Wright, Rochester Institute of Technology
Stephen Wright, Carson–Newman College
Ramakrishna Wusirika, Michigan Tech University
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Ana Zimmerman, College of Charleston