教育部高等教育司推荐
国外优秀生命科学教学用书

遗传学基础

（第8版）（影印版）

ESSENTIALS OF GENETICS

(Eighth Edition)

William S. Klug
Michael R. Cummings
Charlotte A. Spencer
Michael A. Palladino

Pearson

高等教育出版社

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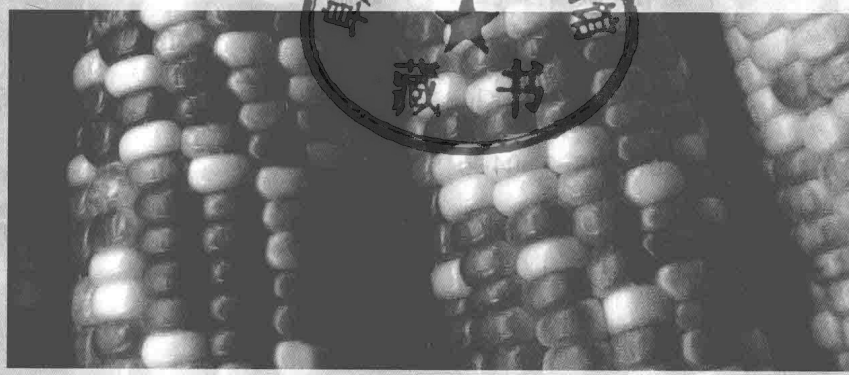

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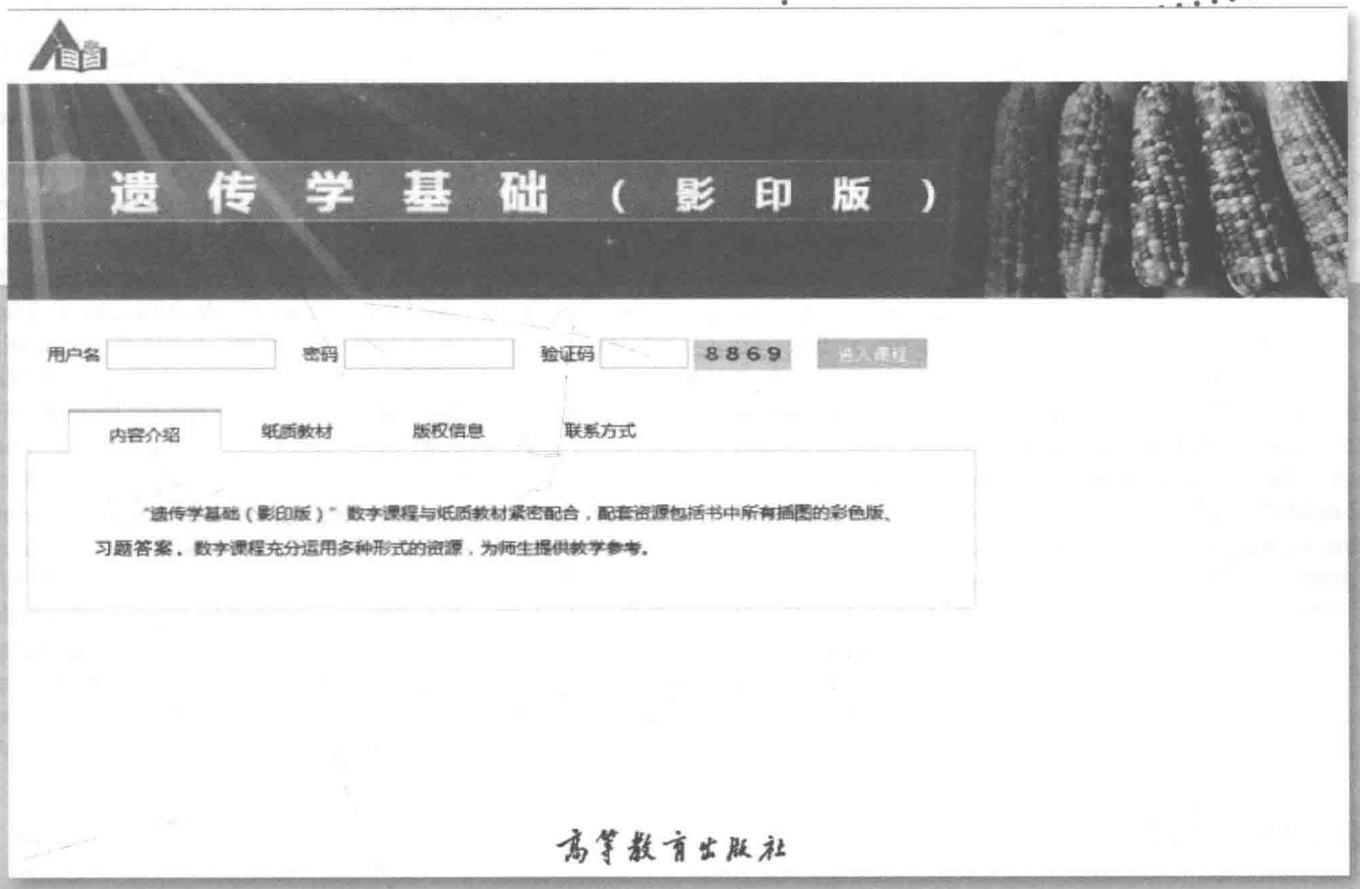

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About the Authors

William S. Klug recently retired as Professor of Biology at The College of New Jersey (formerly Trenton State College) in Ewing, New Jersey. He served as Chair of the Biology Department for 17 years, a position to which he was first elected in 1974. He received his B.A. degree in Biology from Wabash College in Crawfordsville, Indiana, and his Ph.D. from Northwestern University in Evanston, Illinois. Prior to coming to The College of New Jersey, he was on the faculty of Wabash College as an Assistant Professor. His research interests have involved ultrastructural and molecular genetic studies of oogenesis in *Drosophila*. He taught the genetics course as well as the senior capstone seminar course in human and molecular genetics to undergraduate biology majors for 38 years. In 2002, he was the recipient of the initial teaching award given at the College of New Jersey granted to the faculty member who most challenges students to achieve high standards. He also received the 2004 Outstanding Professor Award from the Sigma Pi International, and in the same year, he was nominated as the Educator of the Year, an award given by the Research and Development Council of New Jersey.

Michael R. Cummings is Research Professor in the Department of Biological, Chemical, and Physical Sciences at Illinois Institute of Technology, Chicago, Illinois. For more than 25 years, he was a faculty member in the Department of Biological Sciences and in the Department of Molecular Genetics at the University of Illinois at Chicago. He has also served on the faculties of Northwestern University and Florida State University. He received his B.A. from St. Mary's College in Winona, Minnesota, and his M.S. and Ph.D. from Northwestern University in Evanston, Illinois. In addition to this text and its companion volumes, he has also written textbooks in human genetics and general biology for nonmajors. His research interests center on the molecular organization and physical mapping of the heterochromatic regions of human acrocentric chromosomes. At the undergraduate level, he teaches courses in Mendelian and molecular genetics, human genetics, and general biology, and has received numerous awards for teaching excellence given by university faculty, student organizations, and graduating seniors.

Charlotte A. Spencer is a retired Associate Professor from the Department of Oncology at the University of Alberta in Edmonton, Alberta, Canada. She has also served as a faculty member in the Department of Biochemistry at the University of Alberta. She received her B.Sc. in Microbiology from the University of British Columbia and her Ph.D. in Genetics from the University of Alberta, followed by postdoctoral training at the Fred Hutchinson Cancer Research Center in Seattle, Washington. Her research interests involve the regulation of RNA polymerase II transcription in cancer cells, cells infected with DNA viruses, and cells traversing the mitotic phase of the cell cycle. She has taught courses in biochemistry, genetics, molecular biology, and oncology, at both undergraduate and graduate levels. In addition, she has written booklets in the Prentice Hall Exploring Biology series, which are aimed at the undergraduate nonmajor level.

Michael A. Palladino is Dean of the School of Science and Associate Professor in the Department of Biology at Monmouth University in West Long Branch, New Jersey. He received his B.S. degree in Biology from Trenton State College (now known as The College of New Jersey) and his Ph.D. in Anatomy and Cell Biology from the University of Virginia. He directs an active laboratory of undergraduate student researchers studying molecular mechanisms involved in innate immunity of mammalian male reproductive organs and genes involved in oxygen homeostasis and ischemic injury of the testis. He has taught a wide range of courses for both majors and nonmajors and currently teaches genetics, biotechnology, endocrinology, and laboratory in cell and molecular biology. He has received several awards for research and teaching, including the New Investigator Award of the American Society of Andrology, the 2005 Distinguished Teacher Award from Monmouth University, and the 2005 Caring Heart Award from the New Jersey Association for Biomedical Research. He is co-author of the undergraduate textbook *Introduction to Biotechnology,* Series Editor for the Benjamin Cummings *Special Topics in Biology* booklet series, and author of the first booklet in the series, *Understanding the Human Genome Project.*

Dedication

There are only a few chances to publicly recognize contributions that people have made to one's professional achievements, and to express appreciation for the positive role they have played in long-standing personal interactions, which is an added bonus.

I wish to dedicate this edition, the 19th in this text series, to my editors, of all kinds, past and present, in recognition of their contributions to the success and longevity of these books: Kerry Baruch, Bob Lakemacher, Bob Rogers, Sheri Snavely, Gary Carlson, Michael Gillespie, and Dusty Friedman. Over the past three decades, your insights and support have been indispensable; you are all hall-of-famers in your professions.

And with deep appreciation of their direct input to these books, I also dedicate this edition to my coauthors, Charlotte Spencer, Mike Cummings, Mike Palladino, and Harry Nickla—my four steadfast compatriots, who for decades have always been confident that we collectively could arrive at the most accurate formula to impart to students the ideal blend of the critical history, analytical thinking, and modern findings in Genetics.

To all — you have been voices of reason as well as sources of great inspiration and heartwarming friendship. It has been my good fortune that you have been a part of my life.

WSK

Preface

Essentials of Genetics is written for courses requiring a text that is briefer and less detailed than its more comprehensive companion, *Concepts of Genetics*. While coverage is thorough and modern, *Essentials* is written to be more accessible to biology majors early in their undergraduate careers, as well as to students majoring in a number of other disciplines, including agriculture, animal husbandry, chemistry, engineering, forestry, psychology, and wildlife management. Because *Essentials of Genetics* is shorter than many other texts, it is also more manageable in one-quarter and trimester courses.

Goals

In this and the previous edition of *Essentials of Genetics*, the two most important goals have been to devise modern pedagogic innovations that enhance learning, and to combine these with updated, highly accessible coverage of genetic topics of both historical and modern significance. As described below, this edition is no exception to achieving these goals, as we introduce: 1) a new set of chapters called Special Topics in Modern Genetics; and 2) MasteringGenetics, a powerful online learning and assessment system that helps students develop and practice problem-solving skills.

Beyond these new features, our overarching goals have remained the same as for previous editions. Specifically, we seek to

- Emphasize concepts rather than excessive detail.
- Write clearly and directly to students in order to provide understandable explanations of complex analytical topics.
- Emphasize problem solving, thereby guiding students to think analytically and to apply and extend their knowledge of genetics.
- Provide the most modern and up-to-date coverage of this exciting field.
- Propagate the rich history of genetics that so beautifully elucidates how information is acquired as the discipline develops and grows.
- Create inviting, engaging, and pedagogically useful figures enhanced by meaningful photographs to support student understanding.
- Provide outstanding interactive media support to guide students in understanding important concepts through animations, tutorial exercises, and assessment tools.

The above goals serve as the cornerstone of *Essentials of Genetics*. This pedagogic foundation allows the book to accommodate courses with many different approaches and lecture formats. While the book presents a coherent table of contents that represents one approach to offering a course in genetics, chapters are nevertheless written to be independent of one another, allowing instructors to utilize them in various sequences.

New to This Edition

We are excited to make available to users of this edition two pedagogic innovations that will expand our coverage of emerging topics and enhance students' learning. At the same time, the book has undergone a thorough streamlining to help instructors and students focus on the truly essential information.

- **Special Topics in Modern Genetics**—As new research topics in genetics gain stature and evolve, either they gradually find their way into textbooks as a short section in one chapter (when they are very specific), or they are mentioned briefly in many chapters (when either they are of more general impact). In either case, the topics are difficult for students and adopters of the text to locate among all of the other coverage, and sometimes they are barely covered at all. To provide greater prominence to such topics, new to this edition is a feature that we call **Special Topics in Modern Genetics**—a series of shorter, more specialized chapters about half the length of traditional chapters that provide concise, cohesive coverage of emerging genetics topics of great interest to students and instructors. Our goal is to facilitate the delivery of a lecture on each topic as well as to provide support for students who have heard such a lecture. And should the topics not be a formal part of the class, we are confident that they are of sufficient general interest that students may wish to read them on their own. For this edition, we have selected four important topics that are valuable, unique additions to the text, providing modern in-depth coverage that would otherwise not be present:

  1. Epigenetics
  2. DNA Forensics
  3. Genomics and Personalized Medicine

  Special Topics chapters, identified by colored margin tabs, fall at the end of the book, but they can be utilized at any time during the course. The strong supporting figures that accompany each Special Topics chapter are available in PowerPoint to facilitate their use in classroom presentations.

- **MasteringGenetics™**—This powerful online homework and assessment program helps students to understand key topics and concepts and to build effective problem-solving skills. In-depth tutorials coach students to correct answers with hints and feedback specific to their misconceptions. Assignments are auto-graded to save time for instructors,

and the gradebook makes it easy to identify specific students who are struggling and topics that the whole class is finding difficult.

Updated Topics

In addition to introducing the new Special Topics mini chapters, we have revised each chapter in the text to present the most current findings in genetics. Below is a list of some of the most significant additions and updates that were incorporated.

Ch. 1: Introduction to Genetics • Revised section on the Dawn of Modern Biology • Section on DNA and RNA rewritten • Expanded discussion of gene expression • Updated coverage of biotechnology • New coverage of genomics and proteomics

Ch. 2: Mitosis and Meiosis • New coverage and a new figure involving the role of cohesin and shugoshin during mitosis and meiosis

Ch. 3: Mendelian Genetics • New section—Correlation between Independent Assortment and Meiosis

Ch. 4: Modification of Mendelian Ratios • Several new problems added

Ch. 5: Sex Determination and Sex Chromosomes • New information regarding sex determination in chickens • Updated coverage of mammalian sex determination • Updated coverage of the human Y chromosome • Updated coverage of the mechanism of X chromosome inactivation

Ch. 6: Chromosome Mutations: Variation in Number and Arrangement • Noninvasive prenatal genetic diagnosis (NIPGD) introduced

Ch. 7: Linkage and Chromosome Mapping in Eukaryotes • New information involving chromosome mapping using DNA markers and annotated databases

Ch. 8: Genetic Analysis and Mapping in Bacteria and Bacteriophages • Revised figures involving conjugation • Introduction to horizontal versus vertical gene transfer • New information on the history of multiple resistant bacteria

Ch. 9: DNA Structure and Analysis • Continued classical coverage of DNA structure and analysis

Ch. 10: DNA Replication and Recombination • New figures depicting DNA replication

Ch. 11: Chromosome Structure and DNA Sequence Organization • Introduction to the role of chromatin remodeling in epigenetic modifications • New section on telomeric DNA sequences and TERRA (telomere repeat-containing RNA) • New coverage on chromosome banding

Ch. 12: The Genetic Code and Transcription • New figure and updated coverage depicting the action of RNA polymerase during prokaryotic transcription • Updated coverage on RNA splicing

Ch. 13: Translation and Proteins • New coverage on the dynamic role of the ribosome during translation

Ch. 14: Gene Mutation, DNA Repair, and Transposition • New Section—Alkylating, Intercalation, and Adduct-Forming Agents • New Section—Single-Gene Mutations Cause a Wide Range of Human Diseases—describes the types of human disorders caused by the various types of single-gene mutations

Ch. 15: Regulation of Gene Expression • New coverage, including a new figure, to encompass attenuation and riboswitches as metabolite-sensing RNAs • New and updated material on core promoters, focused and dispersed promoters, and promoter elements, along with two new figures

Ch. 16: The Genetics of Cancer • New section on the cancer stem cell hypothesis

Ch. 17: Recombinant DNA Technology • Major revision and reorganization of recombinant DNA techniques • Added emphasis on radioactive labeling techniques to indicate more widespread current usage of nonradioactive detection and labeling methods (e.g., probe-labeling, sequencing) • Addition of RT-PCR and quantitative real-time PCR (qPCR) techniques • New material on FISH and spectral karyotyping • Major revision of DNA sequencing technologies to include capillary electrophoresis-based computer automated sequencing and next generation sequencing technologies • Major revision of Problems and Discussion Questions section

Ch. 18: Genomics and Proteomics • New section on "10 years after the HGP," including a new section on the Human Microbiome Project • Updated content on the human genome, including new information about copy number variations (CNVs) • Expanded content on "stone age" genomics and new data on the Neanderthal genome • Expanded content on comparative genomics to include comparisons of model organism genomes and the human genome • New section on personal genomes and sequencing of individual diploid genomes • New section on Genome 10K • Updated content on systems biology, including new figure comparing human disease gene interaction network

Ch. 19: Applications and Ethics of Genetic Engineering and Biotechnology • New section on synthetic genomes • New and updated content on direct to consumer genetic testing (DTC) and patenting genetic

information • New section and figure on genome wide association studies for studying genetic diseases • Updated discussions on synthetic genomes, direct to consumer genetic testing (DTC), and patenting genetic information

Ch. 20: Developmental Genetics • Refined discussion on evolutionary conservation of developmental mechanisms and model organisms • Clarified section on genetic analysis of embryogenesis

Ch. 21: Quantitative Genetics and Multifactorial Traits • Revised coverage of twin studies • Updated coverage of quantitative trait loci (QTLs)

Ch. 22: Population and Evolutionary Genetics • Section on macroevolution and speciation rewritten with new examples and two new figures • Expanded coverage of phylogenetic analysis including a new figure • Rewritten section on molecular clocks including a new figure • Updated coverage on comparative genomics of Neanderthals and modern humans

This list reflects the rapid growth of information in genetics.

Emphasis on Concepts

Essentials of Genetics focuses on conceptual issues in genetics and uses problem solving to develop a deep understanding of them. We consider a concept to be a cognitive unit of meaning that encompasses a related set of scientifically derived findings and ideas. As such, a concept provides broad mental imagery, which we believe is a very effective way to teach science, in this case, genetics. Details that might be memorized, but soon forgotten, are instead subsumed within a conceptual framework that is easily retained. Such a framework may be expanded in content as new information is acquired and may interface with other concepts, providing a useful mechanism to integrate and better understand related processes and ideas. An extensive set of concepts may be devised and conveyed to eventually encompass and represent an entire discipline—and this is our goal in this genetics textbook.

To aid students in identifying the conceptual aspects of a major topic, each chapter begins with a section called ***Chapter Concepts,*** which identifies the most important ideas about to be presented. Then, throughout each chapter, *Essential Points* are provided that establish the key issues that have been discussed. And in the ***How Do We Know?*** question that starts each chapter's problem set, students are asked to identify the experimental basis of important genetic findings presented in the chapter. As an extension of the learning approach in biology called "Science as a Way of Knowing," this feature enhances students' understanding of many key concepts covered in each chapter.

Collectively, these features help to ensure that students easily become aware of and understand the major conceptual issues as they confront the extensive vocabulary and the many important details of genetics. Carefully designed figures also support this approach throughout the book.

Emphasis on Problem Solving

Helping students develop effective problem-solving skills is one of the greatest challenges of a genetics course. The feature called ***Now Solve This,*** integrated throughout each chapter, asks students to link conceptual understanding in a more immediate way to problem solving. Each entry provides a problem for the student to solve that is closely related to the current text discussion. A pedagogic hint is then provided to aid in arriving at the correct solution. All chapters conclude with ***Insights and Solutions,*** a popular and highly useful section that provides sample problems and solutions that demonstrate approaches useful in genetic analysis. These help students develop analytical thinking and experimental reasoning skills. Digesting the information in *Insights and Solutions* primes students as they move on to the lengthier *Problems and Discussion Questions* section that concludes each chapter. Here, we present questions that review topics in the chapter and problems that ask students to think in an analytical and applied way about genetic concepts. Problems are of graduated difficulty, with the most demanding near the end of each section. The addition of MasteringGenetics extends our focus on problem solving online, and it allows students to get help and guidance while practicing how to solve problems.

Continuing Features

The Eighth Edition has maintained a number of popular features that are pedagogically useful for students as they study genetics. Collectively, these create a platform that seeks to challenge students to think more deeply about, and thus understand more comprehensively, the information he or she has just finished studying.

- **Exploring Genomics** Appearing in 10 chapters, this feature illustrates the pervasiveness of genomics in the current study of genetics. Each entry asks students to access one or more genomics-related Web sites that collectively are among the best publicly available resources and databases. Students work through interactive exercises that ensure their familiarity with the type of genomic or proteomic information available. Exercises instruct students on how to explore specific topics and how to access significant data. Questions guide student exploration and challenge them to further explore the sites on their own. Importantly, *Exploring Genomics* integrates genomics information throughout the text, as this emerging field is linked to chapter content. This feature provides the basis for individual or group assignments in or out of the classroom.
- **Genetics, Technology, and Society Essays** Appearing in 12 chapters, this feature provides a synopsis of a topic related to a current finding in genetics that impacts directly on our current society. After each essay, a section entitled

"Your Turn" appears in which questions are posed to students along with various resources to help answer them. This innovation provides yet another format to enhance classroom interactions.

- **Case Study** This feature appears at the end of each chapter and provides the basis for enhanced classroom interactions. In each entry, a short scenario related to one of the chapter topics is presented, followed by several questions. These ask students to apply their newly acquired knowledge to real-life issues that may be explored in small-group discussions or serve as individual assignments.

Acknowledgments

Reviewers

All comprehensive texts are dependent on the valuable input provided by many colleagues. The following individuals provided valuable advice, constructive criticism, and/or suggestions regarding the content of the Eighth Edition:

Althea K. Alton, *Western Illinois University;* Thomas H. Alton, *Western Illinois University;* Brian Ashburner, *University of Toledo;* George Bates, *Florida State University;* Mark Brick, *Colorado State University;* Jill Buettner, *Richland College;* Susan Capasso, *St. Vincent's College;* Aaron Cassill, *University of Texas – San Antonio;* Steve Denison, *Eckerd College;* John P. Doucet, *Nicholls State University;* Kurt Elliott, *Northwest Vista College;* Lehman L. Ellis, *Our Lady of Holy Cross College;* Victor Fet, *Marshall University;* Clarence E. Fouche, *Virginia Intermont College;* Gail Fraizer, *Kent State University;* Alexandros Georgakilas, *East Carolina University;* Edward F. Golenberg, *Wayne State University;* John Gray, *University of Toledo;* Danielle Hamill, *Ohio Wesleyan University;* David Kass, *Eastern Michigan University;* Mary Kimble, *Northeastern Illinois University;* Joan Kuh, *University of Hawaii;* Jospeh Kulkosky, *Chestnut Hill College;* Alan C. Leonard, *Florida Institute of Technology;* Janet Lewis, *Michigan State University;* Jeannette M. Loutsch, *University of Science and Arts of Oklahoma;* Roy B. Mason, *Mt. San Jacinto College;* Philip McClean, *North Dakota State University;* Shawn Meagher, *Western Illinois University;* Sudhir Nayak, *The College of New Jersey;* Harry Nickla, *Creighton University;* Phillip A. Ortiz, *Empire State College;* Terrence Puryear, *Northeastern Illinois University;* Thomas F. Savage, *Oregon State University;* Brian W. Schwartz, *Columbus State University;* Allan Showalter, *Ohio University;* Thomas Smith, *Southern Arkansas University;* Tatiana Tatum, *Saint Xavier University;* Pattie Thompson, *University of Texas – San Antonio;* Paul Wilson, *Trent University;* Michael Zarowitz, *California Polytechnic University – San Luis Obispo*

While we take full responsibility for any errors in this book, we gratefully acknowledge the help and input provided by the above individuals.

Contributors

We offer a special acknowledgment to those who have provided direct input during many revisions of this text. We thank Sarah Ward at Colorado State University for her contribution of the conservation genetics chapter; Sudhir Nayak from The College of New Jersey for his input into all things genomic; David Kass at Eastern Michigan University, Katherine Uyhazi at Yale Medical School, and Tamara Mans at North Hennepin Community College for their numerous contributions to the Genetics, Technology, and Society essays; Elliott Goldstein from Arizona State University for his perpetual input into molecular genetics coverage, and Mike Guidry of LightCone Interactive and Karen Hughes of the University of Tennessee for their original contributions to the media program. We thank Jutta Heller at University of Washington—Tacoma, John Osterman at the University of Nebraska—Lincoln, Virginia McDonough at Hope College, and Kiran Misra at Edinboro University of Pennsylvania for their work on the media program. We also offer special thanks to Harry Nickla, recently retired from Creighton University. In his role as author of the *Student Handbook,* he has written many new problems and authored the Selected Answers section that appear in Appendix A. We are grateful to all of the above contributors not only for sharing their genetic expertise, but for their dedication to this project as well as the pleasant interactions they provided.

Editorial and Production Input

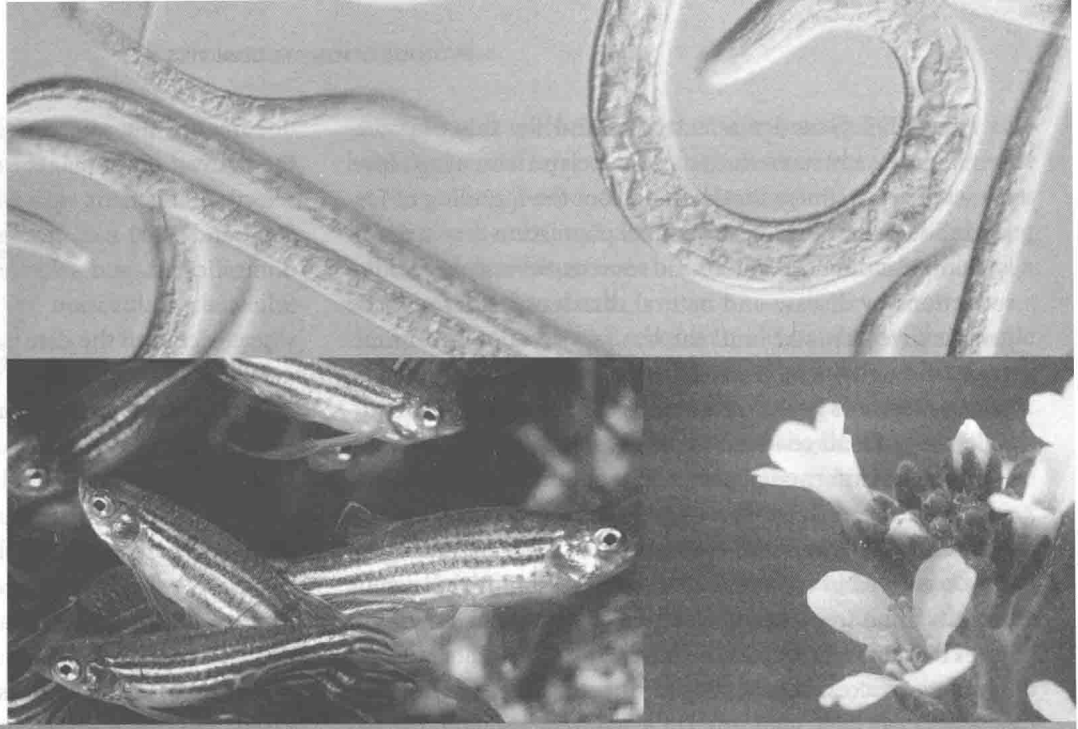
At Pearson, we express appreciation and high praise for the editorial guidance of Michael Gillespie, whose ideas and efforts have helped to shape and refine the features of this edition of the text. Dusty Friedman, our Project Editor, has worked tirelessly to keep the project on schedule and to maintain our standards of high quality. In addition, our editorial staff—Deborah Gale, Executive Director of Development, Laura Tommasi, Senior Media Producer, Daniel Ross, Associate Media Producer, Caroline Ross, Assistant Media Producer, Juliana Tringali, Project Editor, Zane Coleman, Content Specialist, and Tania Mlawer, Director of Editorial Content for Mastering Genetics—has provided valuable input into the current edition. They have worked creatively to ensure that the pedagogy and design of the book and media package are at the cutting edge of a rapidly changing discipline. Sudhir Nayak of The College of New Jersey provided outstanding work for the new MasteringGenetics program, and his input regarding genomics was appreciated. Camille Herrera supervised all of the production intricacies with great attention to detail and perseverance. Outstanding copyediting was performed by Betty Pessagno, for which we are most grateful. Lauren Harp has professionally and enthusiastically managed the marketing of the text. Finally, the beauty and consistent presentation of the art work is the product of Imagineering of Toronto. Without the work ethic and dedication of the above individuals, the text would never have come to fruition.

Proofreading a manuscript of a 600-page text deserves more thanks than words can offer. Our utmost appreciation is extended to the individuals who confronted this task with patience and diligence, including Virginia McDonough, Ford Lux, Matthew Gilg, and Brian Flynn, a recent graduate of The College of New Jersey.

As these many acknowledgments make clear, a text such as this is a collective enterprise. All of the above individuals deserve to share in any success this text enjoys. We want them to know that our gratitude is equaled only by the extreme dedication evident in their efforts.

Brief Contents

Contents



Newer model organisms in genetics include the roundworm *C. elegans*, the zebrafish, *D. rerio*, and the mustard plant *A. thaliana*.

1 Introduction to Genetics

CHAPTER CONCEPTS

- Genetics in the twenty-first century is built on a rich tradition of discovery and experimentation stretching from the ancient world through the nineteenth century to the present day.
- Transmission genetics is the general process by which traits controlled by genes are transmitted through gametes from generation to generation.
- Mutant strains can be used in genetic crosses to map the location and distance between genes on chromosomes.
- The Watson-Crick model of DNA structure explains how genetic information is stored and expressed. This discovery is the foundation of molecular genetics.
- Recombinant DNA technology revolutionized genetics, was the foundation for the Human Genome Project, and has generated new fields that combine genetics with information technology.
- Biotechnology provides genetically modified organisms and their products that are used across a wide range of fields including agriculture, medicine, and industry.
- Model organisms used in genetics research are now utilized in combination with recombinant DNA technology and genomics to study human diseases.
- Genetic technology is developing faster than the policies, laws, and conventions that govern its use.

In December 1998, the Icelandic Parliament passed a law granting a biotechnology company, deCODE Genetics, a license to create and operate a database drawn from medical records of all of Iceland's 270,000 residents. The records in this Icelandic Health Sector Database (or HSD) were encoded to ensure anonymity. The new law also allowed deCODE Genetics to cross-reference the medical information from the HSD with a comprehensive genealogical database from the National Archives and to correlate information in these two databases with results from the analysis of deoxyribonucleic acid (DNA) samples collected from Icelandic donors. This combination of medical, genealogical, and genetic information forms a powerful resource available exclusively to deCODE Genetics for marketing to researchers and companies for a period of 12 years, ending in 2012.

This is not a science fiction scenario from a movie such as *Gattaca* but a real example of the increasingly complex interaction of genetics and society in the first decades of the twenty-first century. The development and use of these databases in Iceland have generated similar large-scale projects in Great Britain, Estonia, Latvia, the Kingdom of Tonga, and other countries. In the United States, smaller-scale programs, involving tens of thousands of individuals, are underway. All these databases will be used to search for susceptibility genes that control complex human diseases.