


PRINCIPLES OF GENETICS

Fourth Edition



SNUSTAD • SIMMONS



Principles of Genetics



Fourth Edition

D. Peter Snustad

University of Minnesota

Michael J. Simmons

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About the cover:

The science of genetics began with Gregor Mendel's experiments with peas. Mendel analyzed the inheritance of traits such as flower color and plant height. The white pea flower on the front cover comes from one of the varieties of peas he studied. Today geneticists study many different kinds of organisms; however, their efforts are concentrated on a dozen or so species that are especially well suited to experimentation. The fruit fly, shown on the back cover, is one of these model organisms.

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Dedications

To Judy, my wife and best friend.
D.P.S.

To my family, especially to Benjamin John.
M.J.S.



About the Authors

D. Peter Snustad is a professor in the Department of Plant Biology at the University of Minnesota, Twin Cities. He received his B.S. degree in science specialization from the University of Minnesota and his M.S. and Ph.D. degrees in genetics from University of California, Davis. During his 40 years as a member of the faculty at Minnesota, he has taught courses at all levels from general biology to advanced biochemical genetics. For 20 years, his research focused on bacteriophage T4 morphogenesis and the interaction between T4 and its host, *Escherichia coli*. For the past 20 years, his research group has studied the genetic control of the cytoskeleton in *Arabidopsis thaliana* and the glutamine synthetase gene family in *Zea mays*. He has served on the National Institutes of Health Molecular Cytology Study Section and as the Program Chairperson for the Annual Meeting of the Genetics Society of America. His honors include the Morse-Amoco and Stanley Dagley Memorial teaching awards. A lifelong love of the Canadian wilderness has kept him in nearby Minnesota.

Michael J. Simmons is a Professor in the Department of Genetics, Cell Biology and Development at the University of Minnesota, Twin Cities. He received his B.A. degree in biology from St. Vincent College in Latrobe, Pennsylvania, and his M.S. and Ph.D. degrees in genetics from the University of Wisconsin, Madison. Dr. Simmons has taught courses in general biology, genetics, population biology, population genetics, and molecular biology. His research activities are focused on the genetic significance of transposable genetic elements, especially those present in the genome of *Drosophila melanogaster*. He has served on advisory committees at the National Institutes of Health and is currently a member of the Editorial Board of Genetics, published by the Genetics Society of America. In 1986, Dr. Simmons received the Morse-Amoco teaching award from the University of Minnesota in recognition of his contributions to undergraduate education. One of his favorite activities, figure skating, is especially compatible with the Minnesota climate.

Preface

In recent years the science of genetics has been undergoing a sea change. The DNA of genomes, even large ones, can now be analyzed in great detail; the functions of individual genes can be studied with an impressive array of new techniques; and organisms can be changed genetically by introducing alien or altered genes into their genomes. All of these developments have placed genetics in the center of a technological revolution that is affecting agriculture, medicine, and society. At a more basic level, genetics has become a key science—some would say *the* key science—in all of biology. Genetic information and genetic analysis are now crucial to research in almost every biological discipline. We have prepared the fourth edition of *Principles of Genetics* with these considerations in mind. Recent discoveries have been incorporated into the text, and the pedagogy has been enhanced. By building on the strengths of previous editions, we hope that *Principles of Genetics* will continue to serve students and teachers of genetics around the world.

GOALS

This edition of *Principles of Genetics* continues our efforts to create a book that balances new information with fundamental principles. As in previous editions, we have been guided by four overarching goals:

- **To focus on the basic principles of genetics** by presenting the important concepts of classical, molecular, and population genetics. The rapid growth in genetics is rooted in basic principles about gene replication, transmission, expression, and mutation. This textbook strives to develop these principles carefully and thoroughly. We believe that an understanding of current advances in genetics and an appreciation for their practical significance must be based on a strong foundation. Furthermore, we believe that the breadth and depth of coverage in the different areas of genetics—classical, molecular, and populational—must be balanced, and that the ever-growing mass of information in
- genetics must be organized by a sturdy—but flexible—framework of key concepts.
- **To focus on the scientific process** by showing how scientific concepts develop from observation and experimentation. Our book provides numerous examples to show how genetic principles have emerged from the work of different scientists. We emphasize that genetics is an ongoing process of observation, experimentation, and discovery. In this regard, we have incorporated a new feature called *A Milestone in Genetics* into each of the 27 chapters in the text. Each *Milestone* focuses on an important advance in genetics and discusses how that advance came about.
- **To focus on human genetics** by incorporating human examples and showing the relevance of genetics to societal issues. Experience has shown us that students are keenly interested in the genetics of their own species. Because of this interest, they find it easier to comprehend complex concepts when these concepts are illustrated with human examples. Consequently, we have used human examples to illustrate genetic principles wherever possible. We have also included discussions of the Human Genome Project, human gene mapping, genetic disorders, gene therapy, and genetic counseling throughout the text. Issues such as genetic screening, DNA fingerprinting, genetic engineering, cloning, and gene therapy have sparked vigorous debates about the social, legal, and ethical ramifications of genetics. We believe that it is important to involve students in discussions about these issues, and we hope that this textbook will provide students with the background to engage in such discussions thoughtfully.
- **To focus on developing critical thinking skills** by emphasizing the analysis of experimental data and problems. Genetics has always been a bit different from other disciplines in biology because of its heavy emphasis on problem-solving. In this text, we have fleshed out the analytical nature of genetics in many ways—in the development of principles in classical genetics, in the discussion of

experiments in molecular genetics, and in the presentation of calculations in population genetics. Throughout the book we have emphasized the integration of observational and experimental evidence with logical analysis in the development of key concepts. Each chapter has two sets of worked-out problems—the *Basic Exercises* section, which contains simple problems that illustrate basic genetic analysis, and the *Testing Your Knowledge* section, which contains more complex problems that integrate different concepts and techniques. Each chapter also has a set of *Questions and Problems* for students to enhance their understanding of the concepts in the chapter and to develop analytical skills.

CONTENT AND ORGANIZATION OF THE FOURTH EDITION

As in previous editions, we have tried to create a text that can be adapted to different course formats. Many instructors prefer to present the topics in much the same way as we have, starting with classical genetics, progressing into molecular genetics, and finishing with quantitative, population, and evolutionary genetics. However this text is constructed so that teachers can present topics in different orders. They may, for example, begin with basic molecular genetics (Chapters 9–14), then present classical genetics (Chapters 3–8), progress to more advanced topics in molecular genetics (Chapters 15–24), and finish the course with quantitative, population, and evolutionary genetics (Chapters 25–27). Alternatively, they may wish to insert quantitative and population genetics between classical and molecular genetics. In selecting material to be included in this edition of *Principles of Genetics*, we have tried to be comprehensive but not encyclopedic. To keep the length of the text reasonable, we had to make difficult decisions about what to include and exclude, and we had to streamline some of the older material to make room for emerging developments.

The text comprises 27 chapters and an epilogue. Chapters 1–2 introduce the science of genetics, basic features of cellular reproduction, and some of the model genetic organisms; Chapters 3–9 present the concepts of classical genetics and the basic procedures for the genetic analysis of microorganisms; Chapters 10–14 present the topics of molecular genetics, including DNA replication, transcription, translation, mutation, and definitions of the gene; Chapters 15–19 cover more advanced topics in molecular genetics and genomics; Chapters 20–24 deal with the regulation of gene expression and the genetic bases of development, immunity, and cancer; Chapters 25–27 present the concepts of quantitative, population, and evolutionary genetics. The Epilogue, by James F. Crow of the University of Wisconsin, Madison, provides a historical perspective on genetics and considers some prospects for the

future. We are especially grateful to Professor Crow for his willingness to continue contributing the epilogue to this book.

The organization of this edition of *Principles of Genetics* reflects the tremendous growth that has occurred in all aspects of genetics during the past few years. Much of this growth has come from the continued analysis of genes and genomes in model organisms. Accordingly, we introduce some of these organisms and their life cycles early in the book, along with basic information about cell division. Microorganisms (bacteria, viruses, and simple fungi) have played key roles in developing the concepts and techniques of molecular genetics. We now discuss the genetic analysis of these organisms in Chapter 8 in order to provide a better transition from classical genetics to molecular genetics. We have also reorganized the chapters that cover the more advanced topics in molecular genetics. The new format now integrates genomics more effectively into this material. The chapter on quantitative genetics has been moved to a position near the end of the book, and population and evolutionary genetics are now treated in separate chapters. This organization allows for a better discussion of evolution, especially the burgeoning topic of molecular evolution.

Several chapters in this edition (1, 2, 8, and 27) are new and others (7, 15, 16, 17, 21, 22, and 25) have been redesigned and extensively rewritten. New material has been incorporated in many places throughout the book. To make way for this material, we have rearranged and tightened the presentation of some topics. For example, linkage analysis in humans has been unified with linkage analysis in other eukaryotes in Chapter 7; the genetics of bacteria, bacteriophages, and simple fungi have been consolidated into one chapter (8); and the genetic analysis of complex human behavioral traits has been incorporated into the chapter on quantitative genetics (25).

Each chapter contains a new feature entitled *A Milestone in Genetics*. This feature focuses on a key development—usually an experiment or set of experiments—that has had a significant impact in genetics. The *Milestones* are opportunities to explore particular discoveries in depth, to investigate experimental strategies, and to analyze experimental data critically. They also provide the context to frame discussions of current issues in genetics. To this end, we have incorporated two open-ended *Questions for Discussion* into each of the *Milestones*.

Problem-solving is a standard feature of most genetics courses. In this edition we have added more worked-out problems in the *Basic Exercises* and *Testing Your Knowledge* sections. The answers to these problems are printed right below the questions so that students receive immediate feedback. More than 200 worked-out problems are now included in the book. In addition, there are over 800 exercises in another section, *Questions and Problems*, for students to work through; the answers to half of the questions and problems are provided at the end of the book, and the answers to all of them are provided in the *Student Companion Guide*, by H. James Price of Texas A & M University.

PEDAGOGY OF THE FOURTH EDITION

This text includes special features designed to emphasize the relevance of the topics discussed, to facilitate the comprehension of important concepts, and to assist students in evaluating their grasp of these concepts.

- **Chapter-Opening Vignette.** Each chapter opens with a vignette or brief story that highlights the significance of the topics discussed in the chapter.
- **Chapter Outline.** The main sections of each chapter are conveniently listed on the chapter's first page.
- **Section Summary.** The content of each major section of text is briefly summarized at the beginning of that section. These opening summaries serve to focus attention on the main ideas developed in a chapter.
- **Key Points.** These learning aids appear at the end of each major section in a chapter. They are designed to help students review for exams and to recapitulate the main ideas of the chapter.
- **Focus Boxes.** Throughout the text, special topics are presented in separate *Focus* boxes. The material in these boxes supports or develops concepts, techniques, or skills that have been introduced in the text of the chapter.
- **A Milestone in Genetics.** Each *Milestone* explores a key development in genetics—usually an experiment or a discovery. We cite the original papers that pertain to the subject of the *Milestone*, and we include two *Questions for Discussion* to provide students with an opportunity to investigate the current significance of the subject.
- **Basic Exercises.** At the end of each chapter we present several worked-out problems to reinforce each of the fundamental concepts developed in the chapter. These simple, one-step exercises are designed to illustrate basic genetic analysis or to emphasize important information.
- **Testing Your Knowledge.** Each chapter also has more complicated worked-out problems to help students hone their analytical and problem-solving skills. The problems in this section are designed to integrate different concepts and techniques. In the analysis of each problem, we walk the students through the solution step by step.
- **Questions and Problems.** Each chapter ends with a set of questions and problems of varying difficulty organized according to the sequence of topics in the chapter. The more difficult questions and problems have been marked with

black numbers. These sets of questions and problems provide students with the opportunity to enhance their understanding of the concepts covered in the chapter and to develop their analytical skills further.

- **Glossary.** This section of the book defines important terms. Students find it useful in clarifying topics and in preparing for exams.
- **Answers.** Answers to the odd-numbered questions and problems are given at the back of the text, and answers to all the questions and problems are included in the *Study Guide and Problems Workbook*, by H. James Price of Texas A & M University.

Supplements

Book Companion Website (www.wiley.com/college/snustad)

This text-specific web site provides students with additional resources and extends the chapters of the text to the resources of the World Wide Web.

Resources include:

- Animations illustrating key concepts.
- Web quizzes covering key concepts for each chapter of text.
- Instructor ancillaries are also available for download.

Student Companion Guide

Written by H. James Price of Texas A&M, the *Student Companion Guide* offers students a great way to review materials from the text and test their knowledge. The following tools have been included to help students master the material: Important Concepts, Important Terms, Important Names, Testing Your Knowledge Questions, Thought Challenging Exercises, Summary of Key Points, and Approaches to Problem-Solving.

Test Bank and Instructor's Manual

Available on both the instructor companion site and the Instructor's Resource CD-ROM, the Test Bank and Instructor's Manual contains sample syllabi, lecture outlines, key concepts, teaching strategies, and approximately 40 test questions per chapter. The complete set of answers to problems in the text is included here as well. A computerized test bank is also available to simplify your test creation.

Instructor's Resource CD-ROM

This dual platform CD-ROM contains every illustration, photograph, and table from the text. Animations from the student

website are also included in addition to PowerPoints, the Test Bank, and the Instructor's Manual.

Animations



Illustrating various concepts from the text these animations aid students in grasping some of the most difficult concepts in genetics. Fully integrated with the text, students may access these animations on the student companion website while instructors may access them on the instructor companion website or on the Instructor's Resource CD-ROM.

Take Note!

An art notebook that contains noteworthy figures from the text, allowing students to take notes directly on the page during class or lecture. This is a perfect student companion to presentations using PowerPoint slides or Transparencies.

Transparencies on Demand

A link on the instructor's book companion website that offers instructors the ability to build their own custom transparency set.

Encyclopedia of Life Sciences

Context-sensitive links from the Book Companion Website and the Wiley *PLUS* version of the textbook to Wiley's renowned Encyclopedia of Life Sciences provide students with free access to further reading materials written by world-class scientists.

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As with previous editions, this edition of *Principles of Genetics* has been influenced by the genetics courses we teach. We thank our students for their constructive feedback on both content and pedagogy, and we thank our colleagues at the University of Minnesota for sharing their knowledge and expertise on a host of topics. Professor John Lim at the University of Wisconsin, Eau Claire, and Dr. Jeremy Stuart at Harvard University commented on portions of the text, and genetics professors at other institutions provided many helpful suggestions. We appreciate all the advice we have received for improving this book. In particular, we acknowledge the help of the following reviewers:

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