



Seventh Edition

Principles of Genetics

Robert H. Tamarin

PRINCIPLES

of GENETICS

PRINCIPLES

of GENETICS

Seventh Edition

ROBERT H. TAMARIN
University of Massachusetts Lowell



**Mc
Graw
Hill**

WCB
McGraw-Hill

Boston Burr Ridge, IL, Dubuque, IA WI New York, San Francisco

WCB/McGraw-Hill
A Division of The McGraw-Hill Companies

PRINCIPLES OF GENETICS, SIXTH EDITION

Copyright © 1999 by The McGraw-Hill Companies, Inc. All rights reserved. Previous edition © 1996 Times Mirror Higher Education Group, Inc. All rights reserved. Printed in the United States of America. Except as permitted under the United States Copyright Act of 1976, no part of this publication may be reproduced or distributed in any form or by any means, or stored in a data base or retrieval system, without the prior written permission of the publisher.

This book is printed on acid-free paper.

2 3 4 5 6 7 8 9 0 VNH/VNH 9 3 2 1 0 9

ISBN 0-697-35462-8

Vice president and editorial director: *Kevin T. Kane*
Publisher: *James M. Smith*
Developmental editor: *Kathleen M. Naylor*
Editorial assistant: *Michael Prater*
Marketing manager: *Martin J. Lange*
Senior project manager: *Gloria G. Schiesl*
Production supervisor: *Sandy Ludovissy*
Coordinator of freelance design: *Michelle D. Whitaker*
Senior photo research coordinator: *Carrie K. Burger*
Art editor: *Joyce Watters*
Supplement coordinator: *Tammy Juran*
Compositor: *Precision Graphics*
Typeface: *10/12 Garamond Book*
Printer: *Von Hoffmann Press, Inc.*

Freelance interior/cover designer: *Rebecca Lloyd Lemna*
Cover image: © *Alfred Pasieka/Science Photo Library; Photo Researchers, Inc.*

Library of Congress Cataloging-in-Publication Data

Tamarin, Robert H.
Principles of genetics / Robert H. Tamarin — 6th ed.
p. cm.
Includes bibliographical references and index.
ISBN 0-697-35462-8
I. Genetics. I. Title.
576.5—dc21

98-18181
CIP

INTERNATIONAL EDITION

Copyright © 1999. Exclusive rights by The McGraw-Hill Companies, Inc. for manufacture and distribution. This book cannot be re-exported from the country to which it is consigned by McGraw-Hill. The International Edition is not available in North America.

When ordering this title, use ISBN 0-07-115581-3.

PREFACE

The twentieth century began with the rediscovery of Mendel's rules of inheritance and ended with the complete sequence of the human genome, one of the most monumental scientific accomplishments of all time. What lies in the future? What will the twenty-first century, the century of genomics, bring? Will geneticists a hundred years from now speak of a complete cure for cancer, heart disease, and mental illness? Will we have a cure for autoimmune diseases such as diabetes and arthritis? Will aging be slowed or even prevented? Will we have a complete understanding of the process of development and a concurrent elimination of birth defects and developmental problems? Will genetics put an end to world hunger? How will we live, and what will be the quality of our lives? The students who now are taking genetics will learn the answers to these questions as time progresses. Some students will contribute to the answers.

The science of genetics includes the rules of inheritance in cells, individuals, and populations and the molecular mechanisms by which genes control the growth, development, and appearance of an organism. No area of biology can truly be appreciated or understood without an understanding of genetics because genes not only control cellular processes, they also determine the course of evolution. Genetic concepts provide the framework for the study of modern biology.

This text provides a **balanced treatment** of the major areas of genetics in order to prepare the student for upper-level courses and to help share in the excitement of research. Most readers of this text will have taken a general biology course and will have had some background in cell biology and organic chemistry. For an understanding of the concepts in this text, however, the motivated student will need to have completed only an introductory biology course and have had some chemistry and algebra in high school.

Genetics is commonly divided into three areas: classical, molecular, and population, although molecular advancements have blurred these distinctions. Many genetics teachers feel that a historical approach provides a sound introduction to the field and that a thorough grounding in Mendelian genetics is necessary for an understanding of molecular and population genetics—an approach this text follows. Other teachers, however, may prefer to begin with molecular genetics. For this reason, the chapters have been grouped as **units that allow for flexibility**

in their use. A comprehensive glossary and index will help maintain continuity if the instructor chooses to change the order of the chapters from the original.

An understanding of genetics is crucial to advancements in medicine, agriculture, and many industries. Genetic controversies—such as the pros and cons of the Human Genome Project, the potential ethical and medical risks of recombinant DNA and cloning of mammals, and human behavioral genetic issues such as the degree of inheritance of homosexuality, alcoholism, and intelligence—have captured the interest of the general public. Throughout this text, we examine the **implications for human health and welfare** of the research conducted in universities and research laboratories around the world; boxed material in the text gives insight into genetic techniques, controversies, and breakthroughs.

Because genetics is the first analytical biology course for many students, some may have difficulty with its quantitative aspects. There is no substitute for work with pad and pencil. This text provides a larger number of problems to help the student learn and retain the material. All problems within the body of the text and a selection at the end of the chapters should be worked through as they are encountered. After the student has worked out the problems, he or she can refer to the answer section in Appendix A. We provide solved problems at the end of each chapter to help.

In this text, we stress **critical thinking**, an approach that emphasizes understanding over memorization, experimental proof over the pronouncements of authorities, problem solving over passive reading, and active participation in lectures. The latter is best accomplished if the student reads the appropriate text chapter before coming to lecture rather than after. That way the student can use the lecture to gain insight into difficult material rather than spending the lecture hectically transcribing the lecturer's comments onto the notebook page.

For those students who wish to pursue particular topics, a **reference section** in the back of the text provides chapter-by-chapter listings of review articles and articles in the original literature. Although some of these articles might be difficult for the beginner to follow, each is a landmark paper, a comprehensive summary, or a paper with some valuable aspect. Some papers may contain an insightful photograph or diagram. Some magazines and journals are especially recommended for the student to look at periodically, including *Scientific American*,

Science, and *Nature*, because they contain nontechnical summaries as well as material at the cutting edge of genetics. Some articles are included to help the instructor find supplementary materials related to the concepts in this book. Photographs of selected geneticists also are included. Perhaps the glimpse of a face from time to time will help add a human touch to this science.

The World Wide Web also can provide a valuable resource. The textbook has its own website: www.mhhe.com/tamarin7. In addition, the student can find much material of a supplemental nature by “surfing” the web. Begin with a search engine such as: www.yahoo.com, or www.google.com and type in a key word. Follow the links from there. Remember that the material on the web is “as is”; it includes a lot of misinformation. Usually, content from academic, industrial, and organizational sources is relatively reliable; however, caveat emptor—buyer beware. Often in surfing for scientific key words, the student will end up at a scientific journal or book that does not have free access. Check with the university librarian to see if access might be offered to that journal or book. The amount of information that is accurate and free is enormous. Be sure to budget the amount of time spent on the Internet.

NEW TO THIS EDITION

Since the last edition of this text, many exciting discoveries have been made in genetics. All chapters have been updated to reflect those discoveries. In particular:

- The chapter on Recombinant DNA Technology has been revised to be a chapter on Genomics, Biotechnology, and Recombinant DNA (sixth edition chapter 12 has become chapter 13 in this edition). The chapter includes new material on the completion of the Human Genome Project, bioinformatics, proteomics, and the latest techniques in creating cDNA and knockout mice.
- The chapter on Control of Transcription in Eukaryotes (sixth edition chapter 15 has become chapter 16 in this edition) has been completely reorganized and rewritten to emphasize signal transduction, specific transcription factors, methylation, and chromatin remodeling in control of gene expression; as in the last edition, there are specific sections on *Drosophila* and plant development, cancer, and immunogenetics.
- For better continuity, the chapter on Mutation, Recombination, and DNA Repair has been moved to follow the chapters on Transcription and Translation (sixth edition chapter 16 has become chapter 12 in this edition).

- The material in chapter 3 on Genetic Control of the Cell Cycle has been upgraded to a chapter section on the Cell Cycle.
- Molecular material throughout the book has been completely updated to include such subjects as numerous DNA repair polymerases and their functioning; base-flipping; TRAP control of attenuation; and chromosomes.

LEARNING AIDS FOR THE STUDENT

To help the student learn genetics, as well as enjoy the material, we have made every effort to provide pedagogical aids. These aids are designed to help organize the material and make it understandable to students.

- **Study Objectives** Each chapter begins with a set of clearly defined, page-referenced objectives. These objectives preview the chapter and highlight the most important concepts.
- **Study Outline** The chapter topics are provided in an outline list. These headings consist of words or phrases that clearly define what the various sections of the chapter contain.
- **Boldface Terms** Throughout the chapter, all new terms are presented in boldface, indicating that each is defined in the glossary at the end of the book.
- **Boxed Material** In most chapters, short topics have been set aside in boxed readings, outside the main body of the chapter. These boxes fall into four categories: **Historical Perspectives**, **Experimental Methods**, **Biomedical Applications**, and **Ethics and Genetics**. The boxed material is designed to supplement each chapter with entertaining, interesting, and relevant topics.
- **Full Color Art and Graphics** Many genetic concepts are made much clearer with full-color illustrations and the latest in molecular computer models to help the student visualize and interpret difficult concepts. We've added thirty new photographs and over a hundred new and modified line drawings to this edition.
- **Summary** Each chapter summary recaps the study objectives at the beginning of the chapter. Thus, the student can determine if he or she has gained an understanding of the material presented in the study objectives and reinforce them with the summary.
- **Solved Problems** From two to four problems are worked out at the end of each chapter to give the student practice in solving and understanding basic problems related to the material.
- **Exercises and Problems** At the end of the chapter are numerous problems to test the student's

understanding of the material. These problems are grouped according to the sections of the chapter. Answers to the odd-numbered problems are presented in Appendix A, with the even-numbered problems answered only in the Student Study Guide so that the student and instructor can be certain that the student is gaining an understanding of the material.

- **Critical Thinking Questions** Two critical thinking questions at the end of each chapter are designed to help the student develop an ability to evaluate and solve problems. The answer to the first critical thinking question can be found in Appendix A, and the answer to the second question is in the Student Study Guide.

ANCILLARY MATERIALS

For the Instructor

- **Website.** Visit us at www.mhhe.com/tamarin7. Here instructors will find jpeg files of the line drawings and tables suitable for downloading into PowerPoint, quizzes for study support, and links to genetic sites. In addition, instructors will also find a link to our hugely successful **PageOut: The Course Website Development Center**, where instructors can create a professional-looking, customized course website. It's incredibly easy to use, and you need not know html coding.
- **Visual Resource Library (VRL).** This Windows- and Macintosh-compatible CD-ROM has all the line drawings and tables from the text suitable for PowerPoint presentations. (ISBN 0072334266)
- **Instructor's Manual with Test Item File.** Available on the website, the Instructor's Manual contains outlines, key words, summaries, instructional hints, and supplemental aids. The Test Item File contains 35 to 50 objective questions with answers for each chapter. (ISBN 0072334215)
- **Test Item File on MicroTest III Classroom Testing Software** is an easy-to-use CD-ROM test generator also offered free upon request to adopters of this text. The software requires no programming experience and is compatible with Windows or Macintosh systems. (ISBN 0072334231).

For the Student

- **Website.** Visit us at www.mhhe.com/tamarin7. Here the student will find quizzes for study support, web exercises and resources, and links to genetic sites.
- **Genetics: From Genes to Genomes CD-ROM**, by Ann E. Reynolds, University of Washington. Packaged free with every text, this CD-ROM covers the most chal-

lenging concepts in the course and makes them more understandable through the presentation of full-color, narrated animations and interactive exercises. The text indicates related topics on the CD with the following icon:



- **Student Study Guide.** This study guide features key concepts, problem-solving hints, practice problems, terms, study questions, and answers to even-numbered questions in the text. (ISBN 0072334207)
- **Laboratory Manual of Genetics 4/e**, by A. M. Winchester and P. J. Wejksnora, University of Wisconsin-Milwaukee. This manual for the genetics laboratory features classical and molecular biology exercises that give students the opportunity to apply the scientific method to “real”—not simulated—lab investigations. (ISBN 0697122875)
- **Case Workbook in Human Genetics, 2/e**, by Ricki Lewis, SUNY-Albany. The Workbook includes thought-provoking case studies in human genetics, with many examples gleaned from the author's experiences as a practicing genetic counselor. (ISBN 0072325305) Also included is the Answer Key. (ISBN 0072439009)

ACKNOWLEDGMENTS

I would like to thank many people for their encouragement and assistance in the production of this Seventh Edition. I especially thank Brian Loehr, my Developmental Editor, for continuous support, enthusiasm, and help in improving the usability of the text. It was also a pleasure to work with many other dedicated and creative people at McGraw-Hill during the production of this book, especially James M. Smith, Thomas Timp, Gloria Schiesl, David Hash, Sandy Ludovissy, Carrie Burger, and Jodi Banowetz. I wish to thank Dr. Michael Gaines of the University of Miami for many comments that helped me improve the textbook and Marion Muskiewicz, Reference Librarian at the University of Massachusetts Lowell, who was an enormous help in my efforts to use the university's electronic library. Many reviewers greatly helped improve the quality of this edition. I specifically wish to thank the following:

Reviewers of the Seventh Edition

John Belote

Syracuse University

Douglas Coulter

Saint Louis University

James M. Freed

Ohio Wesleyan University

Elliott S. Goldstein

Arizona State University

Keith Hartberg

Baylor University

Vincent Henrich

University of North Carolina at Greensboro

Mitrick A. Johns

Northern Illinois University

Philip Mathis

Middle Tennessee State University

Bruce McKee

University of Tennessee

Elbert Myles

Tennessee State University

John Osterman

University of Nebraska–Lincoln

Uwe Pott

University of Wisconsin–Green Bay

Ken Spitze

University of Miami

Randall G. Terry

University of Montana

Michael Wooten

Auburn University

John R. Ellison

Texas A&M University

Elliott S. Goldstein

Arizona State University

Keith Hartberg

Baylor University

David R. Hyde

University of Notre Dame

Pauline A. Lizotte

Northwest Missouri State University

James J. McGivern

Gannon University

Gregory J. Phillips

Iowa State University

Mark Sanders

University of California–Davis

Ken Spitze

University of Miami

Joan M. Stoler

Massachusetts General Hospital, Harvard Medical School

Robert J. Wiggers

Stephen F. Austin State University

Ronald B. Young

University of Alabama

Lastly, thanks are due to the many students, particularly those in my Introductory Genetics, Population Biology, Evolutionary Biology, and Graduate Seminar courses, who have helped clarify points, find errors, and discover new and interesting ways of looking at the many topics collectively called genetics.

ROBERT H. TAMARIN
Lowell, Massachusetts

Reviewers of the Sixth Edition

Edward Berger

Dartmouth

Deborah C. Clark

Middle Tennessee State University

Table of Contents

Part I Genetics and the Scientific Method

1 Introduction

Part II Mendelism and the Chromosomal Theory

2 Mendel's Principles

3 Mitosis and Meiosis

4 Probability and Statistics

5 Sex Determination, Sex Linkage, and Pedigree Analysis

6 Linkage and Mapping in Eukaryotes

7 Linkage and Mapping in Prokaryotes and Bacterial Viruses

8 Cytogenetics

Part III Molecular Genetics

9 Chemistry of the Gene

10 Gene Expression: Transcription

11 Gene Expression: Translation

12 DNA: Its Mutation, Repair and Recombination

13 Genomics, Biotechnology, and Recombinant DNA

14 Gene Expression: Control in Prokaryotes and Phages

15 The Eukaryotic Chromosome

16 Gene Expression: Control in Eukaryotes

17 Non-Mendelian Inheritance

Part IV Quantitative and Evolutionary Genetics

18 Quantitative Inheritance

19 Population Genetics: The Hardy-Weinberg Equilibrium and Mating Systems

20 Population Genetics: Processes That Change Allelic Frequencies

21 Evolution and Speciation

Appendixes

A. Brief Answers to Selected Exercises, Problems, and Critical Thinking Questions

B. Suggestions for Further Reading