PRINCIPLES *of* GENETICS

Sixth Edition

ROBERT H. TAMARIN

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of GENETICS

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University of Massachusetts Lowell

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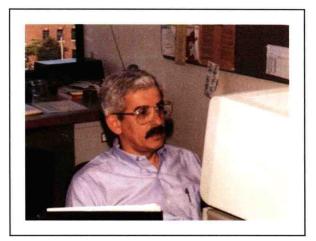
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For Ginger, David, and Bonnie

ABOUT THE AUTHOR

ROBERT H. TAMARIN is currently Professor of Biology and Dean of Sciences at the University of Massachusetts Lowell, a position he has held since September 1996. Before this he was Professor of Biology at Boston University where he began his teaching career and remained for twenty-five years. During his last six years at Boston University, Dr. Tamarin was also Chairman of the Biology Department. He received his B. S. degree from the City University of New York, Brooklyn College, and his Ph. D. from Indiana University.

Before beginning his teaching career, Professor Tamarin was a National Institutes of Health Postdoctoral Fellow in the Genetics Department at the University of Hawaii and a Ford Foundation Postdoctoral Fellow at Princeton University. His research interests have focused on the interaction of genetics and ecology, specifically the role of genetic factors in regulating animal population numbers. He has developed electrophoretic, radioisotope, and DNA fingerprinting techniques for use in small mammal studies in research funded by the National Institutes of Health, the National Science Foundation, the Atomic Energy Commission, and the American Philosophical Society.

Most recently he was the recipient of two educational grants from the Howard Hughes Medical Institute. Professor Tamarin is also a widely published and well-recognized author of many scientific articles. He is a regular contributor to *Science Year*, The World Book Annual Supplement, and a consultant for Microsoft's Encarta CD encyclopedia. He is listed in ten "Who's Who" listings, including Who's Who in the World and Who's Who in Frontiers of Science and Technology.

Professor Tamarin has taught Introductory Genetics to thousands of students at Boston University in a broad range of class sizes and settings. His other courses have included Population Genetics, Population Biology, Introductory Biology, Ecology, and topics ranging from critical thinking in biology to mathematical modeling of genetic and evolutionary processes. He most recently began teaching Evolutionary Biology at the University of Massachusetts Lowell. Professor Tamarin is keenly aware of the difficulties faced by students taking genetics, and responding to their needs is a crucial consideration in the development of each edition of *Principles of Genetics*.

PREFACE

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 be truly appreciated or understood without an understanding of genetics because genes control cellular processes, and thus determine the course of evolution. Genetics is an exciting basic science whose concepts provide the framework for the study of modern biology.

This text provides a balanced treatment of the major areas of genetics to prepare you for upper-level courses and to help you 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. However, for an understanding of the concepts in this text, 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. 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 and allow for flexibility in their presentation. A comprehensive glossary and index help maintain continuity if the order of the chapters is changed from the original.

An understanding of genetics is crucial to advancements in medicine, agriculture, and animal breeding. Genetic controversies—such as the potential harm of recombinant DNA, the pros and cons of the Human Genome Project, and cloning of mammals—have captured the interest of the general public. Throughout this text, the implications for human health and welfare of the research conducted in laboratories and universities around the world are pointed out. Digressions, in the form of boxed material, give insights into genetic techniques, controversies, and breakthroughs.

Because genetics is the first analytical biology course for many students, you 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 you 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 you have worked out the problems, you may want to refer to the answer section in Appendix A. We also provide solved problems at the end of each chapter for additional 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 by reading the appropriate text chapter before coming to lecture rather than after. In that way you 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 who wish to pursue particular topics, a reference section at 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 either a landmark paper, a comprehensive summary, or a paper with some valuable aspect to it. Some papers may contain an insightful photograph or diagram. Some magazines and journals are especially recommended for you 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 teacher with supplementary material or material from which concepts have been developed. Photographs of selected geneticists are also included. Perhaps the glimpse of a face from time to time will help add a human touch to this science.

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, we have added new sections on plant development and sex

determination in flowering plants, and factual and ethical issues of cloning and the human genome project. We have also added new boxed material on chromosomal painting and cloning the sheep, Dolly.

Ethics and Genetics

Genetic Variation

LEARNING AIDS FOR THE STUDENT

To help you learn genetics, as well as enjoy the material, we have made every effort to provide pedagogical aids for that purpose. These aids are designed to help you organize and understand the material.

Study Objectives   Each chapter begins with a set of clearly defined, page-referenced objectives. They have been written with an attempt to preview the chapter and highlight the most important concepts.

Study Outline   The chapter topics are provided in a list of major headings of the subject matter. 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 type, 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, out of the main body of the chapter. These boxes fall into eight categories that are designated by icons as follows:

Historical Accounts

Experimental Methods

Analytical Thinking

Biomedical Applications

Molecular Structure and Function

Genetic Discoveries and Hypotheses

These icons help you categorize and cross-reference material presented in these boxes. The material is designed to supplement the material in each chapter with entertaining, interesting, and relevant topics.

Full Color Art and Graphics   Many genetics concepts are made much clearer with full-color illustrations and the latest in molecular computer models to help you visualize and interpret difficult concepts.

Summary   Each chapter summary is presented with reference to the study objectives at the beginning of the chapter. Thus you can determine if you have gained an understanding of the material as presented in the study objectives and reinforced with the summary.

Solved Problems   From two to four problems are worked out at the end of each chapter to give you insights into the best way to solve the most basic problems presented by the material.

Exercises and Problems   At the end of the chapter are numerous problems to test your understanding of the material presented. New to this edition, these problems have been 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 in the Student Study Guide. With all of the answers available for use, you can be certain that you are gaining a complete understanding of the material.

Critical Thinking Questions   Two critical thinking questions have been added to each chapter in this edition. These questions have been designed to help you develop your ability to evaluate and solve problems. The answer to the first critical thinking question in each chapter can be found in Appendix A and the answer to the second question is given in the Student Study Guide.

Technology Links   The end-of-chapter exercises and problems are linked directly to the Explorations in Genetics CD-ROM. This technology link is designed to help you gain a better understanding of genetics and improve your problem-solving skills.

ANCILLARY MATERIALS

- *Student Study Guide in Genetics,* written by Deborah C. Clark of Middle Tennessee State University, is a valuable study tool for all students. Specific features include key concepts, problem-solving hints, and practice problems and general questions as well as the complete solutions for both. An important feature for students in this new Study Guide is the inclusion of detailed solutions to the even-numbered end-of-chapter problems found in *Principles of Genetics*. (ISBN: 0-697-35464-4)

- An *Instructor's Manual with Test Item File,* written by William Wellnitz of Augusta College, is available upon request to adopters. It contains important instructional hints and a test item file of thirty-five to fifty multiple-choice questions, five completion questions, and five true or false questions for each chapter.

- *Test Item File on MicroTest III Classroom Testing Software* is an easy-to-use computerized test generator also offered free upon request to adopters of this text. The software requires no programming experience. Using the software requires access to a personal computer (3.5-inch disk drive): Windows, or Macintosh Diskettes are available to instructors through a local McGraw-Hill sales representative.

- Instructors may also request a set of *125 full-color transparencies* and/or a *Visual Resource Library (VRL),* an electronic library of 300 images on a CD-ROM with PowerPoint presentation options.

- *Tamarin Web Site,* developed new for this edition, is a book-specific site that can be found through the WCB/McGraw-Hill Internet site: www.mhhe.com/wcbp/cellmicro. Designed as a resource for students and instructors, chapter specific links offer additional review questions with answers to qualified adopters, updates on latebreaking developments in genetics, and additional plant genetics material.

- *Explorations in Cell Biology and Genetics CD-ROM,* is an interactive multimedia program developed by George B. Johnson, Washington University–St. Louis, and WCB. It calls on users to manipulate genetic variables and examine how they impact the results as they explore such modules as Constructing a Genetic Map, DNA Fingerprinting: You Be the Judge, and Gene Regulation. The CD-ROM is compatible with both Windows and Macintosh systems. (ISBN: 0-697-37908-6)

- The new fourth edition of *Laboratory Manual of Genetics,* by A. M. Winchester and P. J. Wejksnora, University of Wisconsin–Milwaukee, is an up-to-date, practical manual. It features classical and molecular biology exercises that give students the opportunity to apply the scientific method to "real"—not simulated—lab investigations. (ISBN: 0-697-12287-5)

- *How Scientists Think,* by George B. Johnson, is a concise, illustrated book that presents discussions of twenty-one classic genetics and molecular biology experiments. It is an intriguing way to foster critical thinking and to reinforce the scientific method in a genetics course. (ISBN: 0-697-27875-1)

- *Genetics Problem-Solving Guide,* by William Wellnitz, is a companion guide that systematically walks students through the logical steps involved in solving genetics problems. (ISBN: 0-697-13739-2)

- *Compendium of Problems in Genetics,* by John Kuspira and Ramesh Bhambhani, University of Alberta, includes logical, illustrated exercises—including many based on actual experimental data from classic papers—for students at basic and advanced levels. (ISBN: 0-697-16734-8)

ACKNOWLEDGMENTS

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