GENETICS
Second Edition

URSULA GOODENOUGH

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Harvard University

HOLT, RINEHART AND WINSTON

New York Chicago San Francisco Atlanta
Dallas Montreal Toronto London Sydney

cover photo: Histone-depleted metaphase chromosome from a human HeLa cell. A scaffold or core, having the shape characteristic of a metaphase chromosome, is surrounded by a halo of DNA. The halo consists of many loops of DNA, each anchored in the scaffold at its base; most of the DNA exists in loops at least 10–30 μm long. (From J. R. Paulson and U. K. Laemmli, *Cell* **12:**817–828, 1977, copyright © M.I.T.)

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Library of Congress Cataloging in Publication Data

Goodenough, Ursula.
Genetics.

Includes bibliographies.
1. Genetics. I. Title.
QH430.G66 1978 575.1 77-26245
ISBN 0-03-019716-3

Printed in the United States of America
8 9 0 1 032 9 8 7 6 5 4 3 2

PREFACE

Children are like pancakes, they say: you should throw away the first one. First children have their redeeming features, but the aphorism certainly applies to textbooks. The combination of rapid changes in the field of genetics and numerous suggestions from users of the first edition of this text has resulted in my writing an almost completely new book. Retained is a molecular/chromosomal approach to the subject and the use of human examples whenever feasible; retained also is an extensive use of illustrative materials. Major changes include the following:

1. Mitosis, meiosis, and Mendelism now follow the introductory chapter.
2. Topics such as recombination mechanisms, histocompatability genetics, and somatic cell genetics have been expanded considerably, and such new topics as environmental mutagenesis, recombinant DNA, and restriction mapping are presented in detail.
3. Strictly biochemical topics are found in Chapter 7, "Molecular Biology of Chromosomes," and the focus on genetics is sharpened throughout the text.
4. The two population genetics chapters, while still only an introduction to a very large field, have been expanded.
5. Chapter sections are numbered and extensively cross-referenced. Many new problems have been added, and "worked out" problems have been included for such topics as three-factor crosses and complementation tests.

There appear to be two extremes in textbook writing: some texts present little more than would be covered in a semester's worth of lectures, while others border on the encyclopedic. I have attempted to chart a middle course. Many more topics are included than would ordinarily be covered in a one-semester genetics course, allowing both instructors and students to pick and choose. Moreover, the topics are generally considered in more depth than would be possible in 30–40 hours of lecture. At the same time, I have tried to select my examples carefully and to focus on their important features. My goal has been to document and "flesh out" key genetic concepts in a clear and readable fashion; the reader who then desires additional facts on a particular subject can consult the detailed reference list at the end of each chapter.

Individual revised chapters were reviewed and carefully criticized by Drs. John Drake (National Institute of Environmental Health Sciences, Triangle Park, North Carolina), Nancy Martin (University of Minnesota), Howard Schneiderman (University of California, Irvine), and Peter Cherbas, David Dressler, Sarah Elgin, Argiris Efstratiadis, and Jan Pero (Harvard University); the entire book was reviewed by Julian Adams (University of

Michigan), Richard Siegel (UCLA), Edward Simon (Purdue University), and S. R. Snow (University of California, Davis). Extensive appraisals of the first edition were also received from many sources, particularly helpful being those of Sally Allen (University of Michigan), John Brumbaugh (University of Nebraska, Lincoln), A. Gib De Busk (Florida State University), Søren Nørby (University of Copenhagen), and Michael Freeling, James Fristrom, Leonard Kelly, and Philip Spieth (University of California, Berkeley). Errors that persist are, of course, of my own making. The skilled combination of patience and persistence practiced by Ken Getman and Peggy Middendorf at Holt, Rinehart and Winston cannot be overpraised, nor can I adequately express my gratitude to members of my laboratory, and to Jason and Mathea, for bearing with all too many months of "the book." The retirement from textbook writing of Paul Levine, my former co-author, did not allow him much escape from its pervasive tedium, since he has remained my husband, scientific colleague, and best friend.

A professional story writer remarked in a recent interview that yes, writing did give him pleasure, perhaps two minutes per day. Having just emerged from six months of galleys and page proof, the pleasures of researching and writing this text seem remote. When, however, it was a matter of reading, thinking, and writing about the structure and transmission of genes, there were many very pleasurable hours, for which I thank many hundreds of inspired geneticists.

March 1978 — Ursula Goodenough

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PREFACE TO THE FIRST EDITION

This book is intended to accompany a one-semester course in genetics for college or medical students who have a knowledge of introductory biology and chemistry. A certain amount of biochemistry is included in the text, but biochemical concepts and techniques are explained at the time they are introduced; no prior knowledge is assumed.

As anyone who has organized a course in genetics is aware, the field has come to play a central role in virtually all biological disciplines. To give full treatment to the many and diverse applications of genetics would result in a diffuse and thereby useless text, but to ignore these applications would produce a limited and sterile view of genetics. We have therefore made the necessary compromises. We give major attention and emphasis to the principles and methodology that are unique to genetics, but we also indicate how these genetic principles relate to such active research areas as biochemistry and molecular biology, embryology, and evolutionary biology.

The teaching of genetics has traditionally followed an historical approach: the experiments that have led to our present understanding of genetic systems are presented in their chronological order. This approach has an immediate strength, for the development of scientific ideas is classically illustrated by the history of genetics and the student can often come away with a deep appreciation of how scientific discoveries, combined with careful experimental observatión, can generate a complex science within a relatively short period of time. We do not avoid presenting genetic ideas in their historical context when this seems the clearest way to develop a particular concept, but neither do we adhere to a "Mendel first, phages later" formula. It is our experience that students enter a genetics course with a knowledge, however superficial, of DNA, RNA, and protein synthesis, and they are eager to learn how such subjects relate to genes. To delay discussion of these subjects becomes both confusing and somewhat artificial, whereas to master these subjects first and then apply them to the more classical genetic observations becomes fascinating.

We have therefore organized the material according to key topics in genetics. The sequence of topics progresses from more simple to more complex orders of genetic organization. Thus we first focus on the molecular properties of the genetic material: its ability to replicate, to recombine, to mutate, and to dictate RNA and protein synthesis. We then discuss the ordering of genes within chromosomes and the capacity of genes to segregate and assort. Finally, we discuss functional interactions between genes, genetic regulation, and genes in populations. Realizing that a different sequence of chapters may well suit individual instructors, we have tried to write each chapter with enough internal consistency and cross-referencing so that a different ordering of chapters can still be meaningful. We have also made our index as comprehensive as possible. We often found it necessary to deal separately with viruses, bacteria, and nucleate organisms, since each has evolved genetic systems that are often quite distinct. We try, however, to relate these systems to one another whenever possible so that the student can come away with a grasp of the common denominators of genetics rather than segregated information classed, for example, as "molecular genetics" or "animal genetics."

In writing this text we sought to present genetics in a readable fashion, avoiding the telescopic "dictionary style" of textbook writing. We also sought to convey that genetics is a way of thinking as well as a collection of important facts, and we have avoided detailed summaries of procedures and data in the belief that such catalogues offer a poor substitute for the reading of original research papers. It is our hope that the text will provide a sufficiently up-to-date and integrated view of genetics that students can explore the original literature in a meaningful way. To this end we have included an extensive bibliography with each chapter and have made special note of those papers that describe experiments cited in the chapter. Instructors may well choose to assign particular research papers and to focus lectures or class discussions directly on the papers themselves.

Each chapter concludes with questions and problems. For many of these we are indebted to the past and present instructors of Natural Sciences 5 and Biology 14 and 140 at Harvard University. To the best of our knowledge, all of the problems are original with us or with these instructors; if, however, any were in fact culled from published sources, we express our gratitude to their originators.

Several genetics textbooks have included photographs of distinguished geneticists, and we have continued this enjoyable tradition. In making our choice, we focused on those who had not happened to appear in other collections. The choices remained most difficult, however, and numerous persons of high distinction remain for future textbooks to include.

While we are responsible for any errors in this text, a number of persons read all or portions of various drafts of the manuscript and offered invaluable comments and criticisms. These include Drs. Jonathan Beckwith, Peter Carlson, John Drake, David Dressler, Maurice Fox, Martin Gorovsky, Guido Guidotti, Joel Huberman, Roger Milkman, Janice Pero, John Preer, Herbert Riley, Robert Stellwagen, Andrew Travers, Thomas Wegman, J. A. Weir, and Ms. Nancy Hinckley. We are also grateful to the many persons who sent us photographs and micrographs. We are indebted to the late Sir Ronald Fisher, Dr. Frank Yates, F.R.S., Rothamsted, and to Messrs. Oliver & Boyd Ltd., Edinburgh, for permission to reprint Table III from their book, *Statistical Tables for Biological, Agricultural, and Medical Research*.

The preparation of the manuscript and the final publication processes were aided enormously by the following persons: Ms. Susan F. Klinger who presided over endless drafts and bibliographies and almost never lost heart;

Mr. Donald Schumacher and Ms. Lyn Peters of Holt, Rinehart and Winston who guided us through the early stages of the project; the artists of Eric Hieber Associates who transformed our scribblings into intelligent and pleasing drawings; and Ms. Dorothy Crane of Holt, Rinehart and Winston whose expert editing and unfailing sense of humor permitted the final six months of the project to be almost pleasurable.

Ursula Goodenough
Robert Paul Levine

August 1973

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CHAPTER 1

DNA (and RNA) as the Genetic Material

INTRODUCTION

Today, when the terms **gene** or **genetics** are mentioned, most biologists immediately think of DNA. DNA, or deoxyribonucleic acid, is well known as the chemical bearer of genetic information; RNA (ribonucleic acid) serves this function in certain viruses.

In the history of genetics as a science DNA became the center of attention only relatively recently. Focus first centered on **heredity,** on the patterns of inheritance of a given trait (blue eyes, red flower color, short tail) from parent to offspring. It was postulated that these inherited traits were somehow dictated by genes and that genes were linearly aligned along the chromosomes of higher animals and plants. "Maps" of gene order on chromosomes were constructed, and many of the details of gene transmission from generation to generation were worked out well before much was known about what a gene is and how it acts.

As the science of genetics developed, increased attention was given to how genes function and more experimental use was made of microorganisms, notably bacteria and bacterial viruses. During this period it was proposed, with good evidence, that the function of most genes is to specify the formation of proteins. When it was eventually established that most genes are borne within molecules of DNA, primary attention was given to the chemical nature of the gene itself.

In beginning our text with DNA and RNA and in developing a molecular picture of genes and gene function at the same time as we establish patterns of heredity we are, in one sense, violating the sequence set by scientific history. In another sense, of course, we are more closely following evolutionary history, since genes almost certainly developed their fundamental properties well before the hereditary patterns exhibited by modern organisms were established.

THE REQUIREMENTS TO BE MET BY GENETIC MATERIAL

Certain requirements must be met by any molecules if they are to qualify as the substances that transmit genetic information. These requirements extend directly from what is known about the continuity of species and the process of evolutionary change.

1. The genetic material must contain biologically useful information that is maintained in a stable form.
2. The genetic information must be reproduced and transmitted faithfully from cell to cell or from generation to generation.
3. The genetic material must be able to express itself so that other biological molecules, and ultimately cells and organisms, will be produced

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