A HISTORY OF GENETICS

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WITH AN INTRODUCTION BY EDWARD B. LEWIS

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NOTE FROM THE PUBLISHERS

This book is special in several rather diverse ways. First published by Alfred Sturtevant in 1965, it is one of the very few accounts of the early days of genetics by one who was there—the truths of a reporter rather than an historian. Sturtevant was one of an accomplished trio of Thomas Hunt Morgan's students, and although his name may resonate less with today's scientists than the names of his colleagues Bridges and Muller, his keen intelligence and broad scientific interests gave his book a scope of unusual breadth and interest. Yet it did not endure. A second printing appeared in 1967. Three years later Sturtevant was dead, and increasingly rare copies of his book were consigned to library shelves and second-hand shops as the concepts and techniques of molecular biology swept to dominance in the field of genetics.

This reprinted edition has its origins in two independent initiatives. Prompted by colleagues on the scientific staff, Cold Spring Harbor Laboratory Press has in recent years republished two long-out-of-print books with both historical interest and continued contemporary relevance: *The Biology of* Drosophila by Milislav Demerec and *The Structure and Reproduction of Corn* by Theodore Kiesselbach. The response to these volumes was warm and encouraging, so when the idea of reviving Sturtevant's classic was suggested, we were enthusiastic, particularly when it was pointed out that Sturtevant's student and recent Nobel Prize winner, Edward Lewis, might be persuaded to write a new introduction to the book. Dr. Lewis kindly agreed to the task and did his part quickly and well. However, the currently rapid rate of growth and expansion within the Press meant that momentum on the project slowed, since the project lacked the urgency of books with the latest research results that are our typical output.

Independently, Robert Robbins, a biologist turned information scientist with a long-standing interest in both the history of science and the technology of publishing, had become interested in seeing the book return to print. Intrigued by the possibilities of networked information, he had established the Electronic Scholarly Publishing Project, a web-based repository of historically interesting books and papers displayed in a way that leveraged the unique advantages of online delivery—full text-based searching, links to other electronic information sources, and personal annotation of the stored document. The ESP Project places a special emphasis on works related to the foundations of classical genetics.

Robbins' desire to add the Sturtevant book to this repository led him first to the Sturtevant family, then to Ed Lewis, then to Cold Spring Harbor Laboratory itself, with the result that the Electronic Scholarly Publishing Project and the Cold Spring Harbor Laboratory Press agreed to produce the

book jointly, with an online and a print version to appear simultaneously.

The outcome is the book you hold in your hands. Along with the physical book, we have also produced a website associated with the project. At that site, readers may obtain full-text electronic versions of many of the key papers discussed by Sturtevant, including Sturtevant's own "The linear arrangement of six sex-linked factors in Drosophila, as shown by their mode of association," which contained the world's first genetic map. The book's website can be seen at http://www.esp.org/books/sturt/history.

The partnership of Cold Spring Harbor Laboratory Press with the Electronic Scholarly Publishing Project is an experiment, one of many being conducted in this era of new publishing paradigms. It is our hope that for the reader, this print–online combination will deliver the best of both media, as a vehicle of an exceptional work of scholarship that deserves fresh recognition by a new generation of scientists.

We are pleased that this book appears in the year 2000—a year with special significance for genetics and for the study of *Drosophila melanogaster*. This is the 100th anniversary of the founding of modern genetics with the rediscovery of Mendel's work, and it is the year in which the full DNA sequence of the Drosophila genome was obtained. The fruit fly is still at the center of genetic research, just as it was when Sturtevant first began his work in the "Fly Room" at Columbia University.

JOHN R. INGLIS
Cold Spring Harbor Laboratory Press

ROBERT J. ROBBINS
Electronic Scholarly Publishing Project

INTRODUCTION

The reprinting of this classic book provides students with one of the few authoritative, analytical works dealing with the early history of genetics. Those of us who had the privilege of knowing and working with Sturtevant benefited greatly from hearing first-hand his accounts of that history as he knew it and, in many instances, experienced it. Fortunately, Sturtevant put it all together in this book.

In his preface to the book, Sturtevant lists the persons that he knew personally and who were major players in the field, in addition to those who occupied the famous fly room (Chapter 7) at Columbia University. As a result, much of the history is based on first-hand contacts as well as on a scholarly and critical review of the literature of genetics and cytology.

Sturtevant was clearly present at the creation of modern genetics, if dated from 1910 when Morgan commenced work on Drosophila. Of Morgan's three students—Sturtevant, Bridges, and Muller—Sturtevant was ideally suited to write the history because of his remarkable memory, his knowledge of almost all aspects of biology, and a keen analytical ability that extended not only to his experimental work, but also to tracing the history of the underlying ideas.

Sturtevant was a gifted writer and also an authority on many of the subjects he covers. While he was a sophomore in college, he deduced the linear order of the genes. Later, he postulated the existence of inversions and duplications before they were verified cytologically. Sturtevant was especially interested in how genes produce their effects and, consequently, was the father of a field now called developmental genetics. In this area, his style was to analyze exceptions to the rule. In so doing, he identified the phenomenon of position effect, in which the position of a gene (that of the Bar, and double-Bar, eye mutations) can be shown to affect its function. He identified the first clear case of a non-autonomously expressed gene, vermilion, mutants of which produce a vermilion, instead of the normal red, eye color. This was an important exception to the rule that sex-linked mutants behaved autonomously in gynandromorphs. How this led to the field of biochemical genetics is explained in Chapter 16.

In the tradition of such biologists as Darwin, Galton, and Bateson and of many of the early Mendelians, Sturtevant was an ardent evolutionist. He had a seemingly inexhaustible knowledge of embryology, anatomy, morphology, and taxonomy that served him well in treating evolutionary concepts historically, as described in Chapter 17. It is a wide-ranging chapter that covers many topics, including the development of population genetics, the role of

gene mutations in evolution, and, prophetically, the conservation of biochemical pathways in major groups from bacteria to vertebrates. His own experimental work, typically only briefly referred to, included his work on interracial and interspecific hybrids in the genus Drosophila, and the demonstration that the genetic content of different species of that genus is remarkably conserved, whether it be in the X chromosome or in each of the specific autosomal arms. Sturtevant always had a healthy skepticism, surely one of the most important qualities of a successful scientist. This is shown by his doubt of the value of many laboratory experiments in population genetics, on the basis that they cannot faithfully duplicate what really goes on in the great out-of-doors.

It may come as a surprise to many students to realize how much opposition there was in some quarters to the early discoveries of the Morgan school. Sturtevant's account of such controversies is a recurrent theme of this book, as it should be in a historical treatise.

Science has often been advanced by scientists who questioned existing dogma and found it flawed. Or, conversely, such dogma has probably in some cases slowed progress for years. Would advances in genetics have been more rapid had there not been the virtually universal belief that genes were proteins, or that development of an organism involved cytoplasmic rather than nuclear heredity? Sturtevant does not waste space speculating about such issues, but he does discuss several cases in which progress was held back because of failure to develop a satisfactory terminology and symbolism.

Sturtevant had a strong social consciousness that comes forth in Chapter 20. There he treats the history of human genetics, stressing the difficulties and pitfalls that plague studies in this field. He devotes considerable space to an objective and critical analysis of the so-called "nature vs. nurture" question.

In the last chapter, Sturtevant discusses how discoveries in science and particularly genetics tend to come about. He addresses in his typically analytical way the often-cited dictum: The time has to be ripe for a discovery to be made and that when that time comes someone is bound to make the discovery. He concludes that this attitude greatly oversimplifies what generally happens in science.

I believe Sturtevant's writing of this book after his retirement was one more intellectual exercise to stave off boredom. He had reduced his experimental work to an hour or so each day, and it must have been more difficult to keep up with the expanding literature of the field. His book is clearly a labor of love and his personality shines through every page.

July 2000 E. B. Lewis
Pasadena, California

AUTHOR'S PREFACE

The publication of Mendel's paper of 1866 is the outstanding event in the history of genetics; but, as is well known, the paper was overlooked until 1900, when it was found. Its importance was then at once widely recognized. These facts make the selection of topics for the early chapters of this book almost automatic. What was the state of knowledge about heredity in Mendel's day; what sort of man was Mendel, and how did he come to make his discovery; what happened between 1866 and 1900 to account for the different reaction to his results; how did his paper come to be found, and just what was the immediate reaction?

These questions are discussed in the first four chapters. From that point on, it has seemed more logical to treat the various topics separately rather than to follow a more nearly chronological order. The attempt has been, in each case, to trace the beginnings of a subject and to bring it down to the work currently being done—but not to discuss presently active fields of work, since these are adequately covered in current books and reviews. There is no definite terminal date, but work later than about 1950 is generally omitted or is referred to only briefly. In other fields the cutoff date is even earlier than this.

For Chapters 1 and 3 I have relied largely on secondary sources such as Sachs (1875), Zirkle (1935), Roberts (1929), and Wilson (1925). For the period after 1900 I have read or reread much of the original literature and, for general background, have been fortunate enough to have had some direct personal contact with many of the people discussed—including, among the early workers, de Vries, Bateson, Johannsen, Wilson, Morgan, McClung, East, Shull, Castle, Emerson, Davenport, Punnett, Nilsson-Ehle, Goldschmidt, and others. (I have seen Cuénot, Baur, Sutton, and Saunders but never really knew them.)

I am indebted to numerous colleagues who have read part or all of the manuscript and have made constructive suggestions. Especially to be named are Drs. N. H. Horowitz, E. B. Lewis, H. L. Roman, C. Stern, G. Hardin, and C. Fulton. Much of the material has been presented in a series of lectures at the California Institute of Technology and at the Universities of Washington, Texas, and Wisconsin; numerous discussions with colleagues at these institutions have been very helpful.

August 1965 A. H. STURTEVANT
Pasadena, California

History of Genetics. In the 19th century, it was known that offspring resemble their parents â€“ but almost nothing was known about why this happened. Why did some children â€œtake afterâ€ one parent, but not the other.Â The image below shows a Punnett square of Mendelâ€™s pea plants. The Punnett square was developed by English geneticist Reginald Punnett to visually represent how dominant and recessive traits were passed to offspring. The math yielded by the Punnett square matched the results Mendel found in his hands-on studies of pea plants. The history of genetics started with the work of the Augustinian friar Gregor Johann Mendel. His work on pea plants, published in 1866, described what came to be known as Mendelian Inheritance. In the centuries beforeâ€”and for several decades afterâ€”Mendel's work,wide variety of theories of heredity proliferated.Â With the basic patterns of genetic inheritance established, many biologists turned to investigations of the physical nature of the molecular genetics. In the following years, chemists developed techniques for sequencing both nucleic acids and proteins, while others worked out the relationship between the two forms of biological molecules: the genetic code. Developing Genetic Tools. Observing, identifying, and understanding the molecular processes that govern genetics was only the first part of humanityâ€™s gene-journey. People wanted to do something, and that required tools. Scientists began to study genetic processes in a new way.Â As the science of genetics progresses, one of the most exciting developments is gene therapy. Old-fashioned human curiosity may have been a driver of genetic research, but a stronger driver was the desire to better understand and cure human disease. In gene therapy, normal genes are transplanted into a sick patient to give their cellular machinery a non-diseased version of the gene that is making them sick.