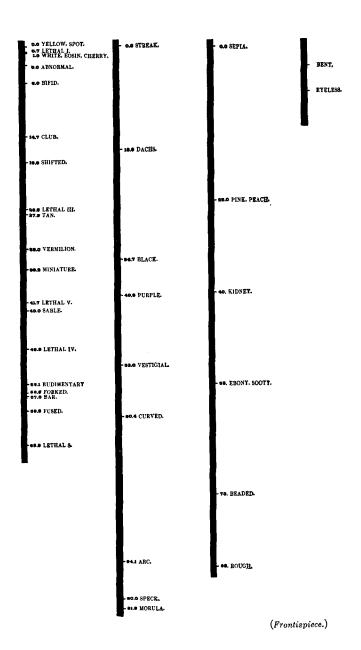
THE MECHANISM

OF

MENDELIAN HEREDITY



THE MECHANISM

 \mathbf{OF}

MENDELIAN HEREDITY

BY

T. H. MORGAN

PROFESSOR OF EXPERIMENTAL ZOOLOGY
COLUMBIA UNIVERSITY

A. H. STURTEVANT

CUTTING FELLOW, COLUMBIA UNIVERSITY

H. J. MULLER

ASSISTANT IN ZOOLOGY, COLUMBIA UNIVERSITY

C. B. BRIDGES

FELLOW IN ZOOLOGY, COLUMBIA UNIVERSITY



NEW YORK
HENRY HOLT AND COMPANY
1915

COPYRIGHT, 1915 BY HENRY HOLT AND COMPANY

THE MAPLE PRESS YORK PA

To EDMUND BEECHER WILSON

PREFACE

From ancient times heredity has been looked upon as one of the central problems of biological philoso-It is true that this interest was largely speculative rather than empirical. But since Mendel's discovery of the fundamental law of heredity in 1865, or rather since its re-discovery in 1900, a curious situation has begun to develop. The students of heredity calling themselves geneticists have begun to draw away from the traditional fields of zoology and botany, and have concentrated their attention on the study of Mendel's principles and their later developments. The results of these investigators appear largely in special journals. Their terminology is often regarded by other zoologists as something barbarous,—outside the ordinary routine of their pro-The tendency is to regard genetics as a subject for specialists instead of an all-important theme of zoology and botany. No doubt this is but a passing phase; for biologists can little afford to hand over to a special group of investigators a part of their field that is and always will be of vital import. It would be as unfortunate for all biologists to remain ignorant of the modern advances in the study of heredity as it would be for the geneticists to remain unconcerned viii PREFACE

as to the value for their own work of many special fields of boilogical inquiry. What is fundamental in zoology and botany is not so extensive, or so intrinsically difficult, that a man equipped for his profession should not be able to compass it.

In the following pages we have attempted to separate those questions that seem to us significant from that which is special or merely technical. We have, of course, put our own interpretation on the facts, and while this may not be agreed to on all sides, yet we believe that in what is essential we have not departed from the point of view that is held by many of our co-workers at the present time. Exception may perhaps be taken to the emphasis we have laid on the chromosomes as the material basis of inheritance. Whether we are right here, the future probably a very near future—will decide. But it should not pass unnoticed that even if the chromosome theory be denied, there is no result dealt with in the following pages that may not be treated independently of the chromosomes; for, we have made no assumption concerning heredity that cannot also be made abstractly without the chromosomes as bearers of the postulated hereditary factors. Why then, we are often asked, do you drag in the chromosomes? Our answer is that since the chromosomes furnish exactly the kind of mechanism that the Mendelian laws call for; and since there is an ever-increasing body of information that points clearly to the chromosomes as the bearers of the Mendelian factors, it would be folly to close one's eyes to so patent a relation. Moreover, as biologists, we are interested in heredity not primarily as a mathematical formulation but rather as a problem concerning the cell, the egg, and the sperm.

T. H. M.

CONTENTS

CHAPTER I

N	MENDELIAN.	SEGREGATION	AND THE	CHROMOSOMES

Introduction. The Groups of Linked Factors and the Chromosomes	18
CHAPTER II	
TYPES OF MENDELIAN HEREDITY	
Dominance and Recessiveness 27 Manifold Effects of Single Factors 35 Similar Effects Produced by Different Factors 36 Modification of the Effects of Factors 38 I. By Environmental Influences 38 II. By Developmental Influences 42 III. By the Influence of Other Factors 46 IV. Conclusion 46	3 3 3 5
CHAPTER III	
LINKAGE	
Examples Illustrating "Coupling". 48 Examples Illustrating "Repulsion" 51 Examples of Different Frequencies of Crossing Over 52 The Mechanism of Crossing Over 62 Double Crossing Over 62 The Principle of Interference 64 The Linear Arrangement of Factors shown by Linkage Relations 64 Linkage in Other Animals and in Plants 70 The Reduplication Hypothesis 74) } !
xi	

CONTENTS

CHAPTER IV

SEX	TN	TT	TOTO	TT	A	NICHT	3
SEX	111	ιн	н к	. 1 1	A	NUL	۲,

The Drosophila or XX-XY Type	
CHAPTER V	
THE CHROMOSOMES AS BEARERS OF HEREDITARY MATERIAL	
The Evidence from Embryology	
CHAPTER VI	
THE CORRESPONDENCE BETWEEN THE DISTRIBUTION OF THE CHROMOSOMES AND OF THE GENETIC FACTORS	
Parallelism between the Distribution of Chromosomes and of Factors 140 1. In Cases of Normal Distribution	
CHAPTER VII	
MULTIPLE ALLELOMORPHS	
Definition of Multiple Allelomorphs	

CONTENTS	xiii
CHAPTER VIII	
MULTIPLE FACTORS	PAGE
The Meaning of the term "Multiple Factors" Examples of Multiple Factors	. 172 . 172
CHAPTER IX	
THE FACTORIAL HYPOTHESIS	
On the Relation between Factors and Characters	. 211
Character	
3. So-called Contamination of Allelomorphs	
4. Fractionation	
5. The Presence and Absence Hypothesis	. 216
Weismann's Præformation Hypothesis and the Factorial Theory	. 223
APPENDIX	
Methods of Breeding Drosophila	. 229
Acknowledgments	
Bibliography	
Index	. 259