PRINCIPLES OF GENETICS

A Textbook, with Problems

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PREFACE

Owing to the rapid progress of genetics during the past few years the first edition of this book has ceased to be an adequate treatment of the subject. The chief purpose of the authors in preparing the present revised edition has been to incorporate in it those results of recent investigation which have led to important new ideas. Among the topics treated inadequately or not at all in the first edition may be mentioned the induction of mutations by radiation and other means; the recent extensive analysis of chromosome changes; the discovery of segmental interchange between chromosomes; the cytological demonstration of crossing over; the mapping of genes in chromosomes by cytological methods; the extension of the balance theory of sex and the establishment of the idea of balance in other fields; and the beginnings of a physiological interpretation of the facts of heredity.

An adequate discussion of these new ideas would have unduly increased the size of the new book, had we not restricted the scope of it to principles only. We have therefore eliminated the chapters on the application of genetics to plant and animal breeding and to human inheritance and eugenics. This was done the more readily since many good books are available in these applied fields. Much of the material in these chapters, however, in so far as it dealt with matters of theory rather than practice, has been distributed elsewhere in the book under various topics. The treatment of biometric methods has also been removed from the body of the text and placed in an appendix. It has been entirely rewritten by Mr. Donald R. Charles to serve as an introduction to statistics as applied in genetics and as a reference guide to biometric methods.

Two new chapters have been added. In Chapter XII the important contributions of genetics to evolutionary theory are discussed, but with emphasis on facts rather than speculation. The inclusion of Chapter XIII is a recognition of the growing interest in the relation between genetics and the problems of development. Its chief function will perhaps be to serve as a stimulant, since the experience of teachers of genetics indicates that many students want to look behind the statistical and mechanical ideas of genetics and to inquire how the genes produce their effects.

Many topics of importance omitted in the text itself are called to the attention of the student in a series of Reference Problems at the end of each chapter. The other Problems, with which have been incorporated the former Questions for Thought and Discussion, are an integral and essential part of the text, as in the first edition, but for the sake of convenience are now placed together at the end of the book. Many new ones have been added, and a number of old ones revised or eliminated.

To all those who have provided the new illustrative material the authors wish to extend sincere thanks. An acknowledgment has been made in each case in the legends or in the text.

The authors also wish to express their indebtedness to Mr. D. R. Charles for help with the manuscript and for numerous suggestions; to Dr. Walter Landauer for information and for criticism of our discussion of the "creeper" fowl; and to Miss Helen Houghtaling, who has assisted in the preparation of the problems.

Mrs. G. W. Little has prepared several new illustrations (Figs. 65, 66, 94–96, 130, 132, 150) and to her and to Miss Ilse Michaelis and Miss Margaret Hanson we extend our thanks for help with the manuscript.

THE AUTHORS.

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FOREWORD

There is a common feeling that a textbook is a full and final exposition of the subject which it treats, and that by virtue of "knowing the book" one acquires all the knowledge of the subject which it is necessary to have. Such beliefs have little to justify them. No text is or can be complete or final; nor, if it were, would an understanding of the subject be gained by committing the whole book to memory. Knowledge is not acquired in this way, but grows in the minds of those who discover for themselves new facts and relationships.

The principles of genetics have developed out of the arduous study of scores of investigators, and an understanding of them can best be gained by the student through a process which is somewhat similar to that employed in their original discovery. This process begins with and is continually stimulated by curiosity as to the methods and the mechanism of inheritance; it proceeds by the collection and study of facts, and by a critical discrimination between those which are true and relevant and those which are untrue or irrelevant; and finally it involves a considerable practice of the reasoning faculty by which deductions are made, and applied or tested on many similar cases. It is only in this way that the process of inheritance can be *understood*. The learning of facts alone cannot accomplish this.

As an aid to such a comprehension of the science of genetics, this book includes problems of three types, which form an integral part of the subject matter. These are designed to stimulate curiosity, to provide opportunity for practicing and extending the methods and applying the theories outlined in the text, and to point the way to other related facts not specifically treated in this book. They are not designed as memory tests, although the continual use of facts in solving problems is at once the best method of committing these facts to memory as well as of understanding them.

One of these aids consists of questions for thought and discussion. Answers to these are not to be found in the text itself, but may be reached by a process of reasoning for which only the premises are given. Familiarity with the subject matter of the text will provide the raw material, while the synthesis resulting in a correct answer or intelligent discussion must take place in the student's mind.

Other problems are designed to provide more extended practice in reasoning from principles. Nearly all of this type require some computation and may be most profitably studied as laboratory exercises under the guidance of an instructor. It is desirable to use labor-saving or "short-cut" methods (such as the checkerboard method described on page 62) wherever possible, in order that the mechanical work involved in calculation may not be regarded as the chief benefit to be derived from them. Sufficient information for solving all of them is contained in the text or in the supplementary notes in the problems.

The Reference Problems all require study of additional sources, such as the list of books and papers contained in the bibliographies. They are intended to convince the student that the subject as a whole is not contained in the text but is growing by the continual accretion of reports of experiments, all of which do not yield results in entire consonance with the few points of view which it is possible to present in a brief textbook. Many of the references will lead to new material not mentioned in the text, which must be reconciled with the fundamental principles of genetics, while others may serve to make the connections between the student's knowledge of genetics and his experience in other directions.

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PRINCIPLES OF GENETICS

CHAPTER I

THE SCIENCE OF GENETICS

Between those things which are *alive*—plants, animals, and man—and those things which are lifeless there exists a great gap, which science has not yet bridged. All living things are endowed with certain characteristic properties of structure and of behavior which in the aggregate have been named *life*, but as to what calls forth this remarkable phenomenon out of lifeless matter we are still essentially ignorant.

There is, however, general agreement concerning the chief peculiarities of living things. Life is always associated with a characteristic substance known as *protoplasm*, which is defined not merely by the materials of which it is composed but by the complex manner in which these materials are integrated into a living system. Protoplasm is not a continuous and homogeneous mass throughout the organism but is divided into definite though minute functional and structural units, the *cells*. Within each cell is a denser body—the *nucleus*—which exerts a governing influence over the activities of the cell. The cells are organized into animal and plant bodies each with a definite shape and structure and with peculiarities of behavior characteristic of the species of which it is a member. In the various cells of this body complex chemical and physical changes take place whereby growth, repair, and reproduction are effected and the necessary energy for the vital activities of the organism is released. These various characteristics of living things can be readily observed and described, but thus far there has been less success in explaining and understanding them. Many of the major problems of biology, which deal with the fundamental peculiarities of life, are still to be solved, and it is the province of genetics to elucidate the laws by which some of the aspects of life may be understood.

The Continuity of Life.—Living organisms are characterized not merely by the specific peculiarities of form and function which we have just mentioned; their origin is also remarkable. The conclusions reached by all thorough study of the life histories of animals and plants clearly show that every living individual must always arise from some pre-existing living individual and never directly from lifeless matter itself. The work of Spallanzani and of Pasteur gave the death blow to the old belief in the "spontaneous generation" of living things out of dead material and proved that even among the most minute organisms the spark of life can be kindled only by life itself. Every animal and plant is therefore to be looked upon as the latest member of a long and uninterrupted succession of living beings, extending back, generation after generation, to the dawn of life. This is the essential teaching of the theory of evolution. The actual origin of life itself is lost in the mists of antiquity, but the pageant of the evolutionary history of living things which unfolds itself in the fossil record of ancient times makes it clear beyond any reasonable doubt that the animals and plants of today are direct lineal descendants of earlier and more primitive types. Continuity is of the essence of life.

Reproduction.—Since individual living things grow old and die, however, this continuity must be maintained by the transmission of life from one individual to a succession of new ones, its offspring. This process is known as *reproduction* and may take place in various ways.

In the simplest methods, commonly called *asexual* or *vegetative* reproduction, the body of the parent becomes divided into two or more parts, each of which grows into a new individual. With animals this method is uncommon except in the simplest types, but among plants the fact that a small portion of the body, when removed and placed under favorable conditions, will often restore the missing parts and establish itself as a new individual makes multiplication of this type easy and effective both in nature and through the various arts of plant propagation.

Far commoner and more important than this asexual or vegetative method of reproduction, however, is that called *sexual*. An essential feature here is that the function of forming the new individual is delegated to *single cells*, which are set apart for this purpose. Sexual reproduction consists of the *union of two specialized sexual cells or gametes to form one cell*, the fertilized egg or *zygote*, from which develops a new individual. To insure the successful consummation of this process is the function of a great variety of structures throughout the animal and the plant kingdoms. In all except the lowest forms the gametes themselves are of two different types: small, usually motile, male gametes and relatively large, non-motile female ones. Among animals the male gametes are known as *sperms* and are produced in a testis, and the female gametes as *eggs* or *ova*, produced in an ovary. At fertilization a sperm and an egg come together and unite, the nucleus of one fusing completely with that of the other. The single cell resulting from this union begins to divide, forming a group of cells which develops into an embryo and finally into an adult organism. Among lower plants conditions are essentially like those in animals, although the sexual organs are extremely varied in character. In the higher plants, however, a series of complicated reproductive structures—the flower, fruit, and seed—have been evolved. The male gametes are here produced within the minute *pollen grains*, and the female gametes within the *ovules* or potential seeds. The fertilized egg develops into the embryo of the seed.

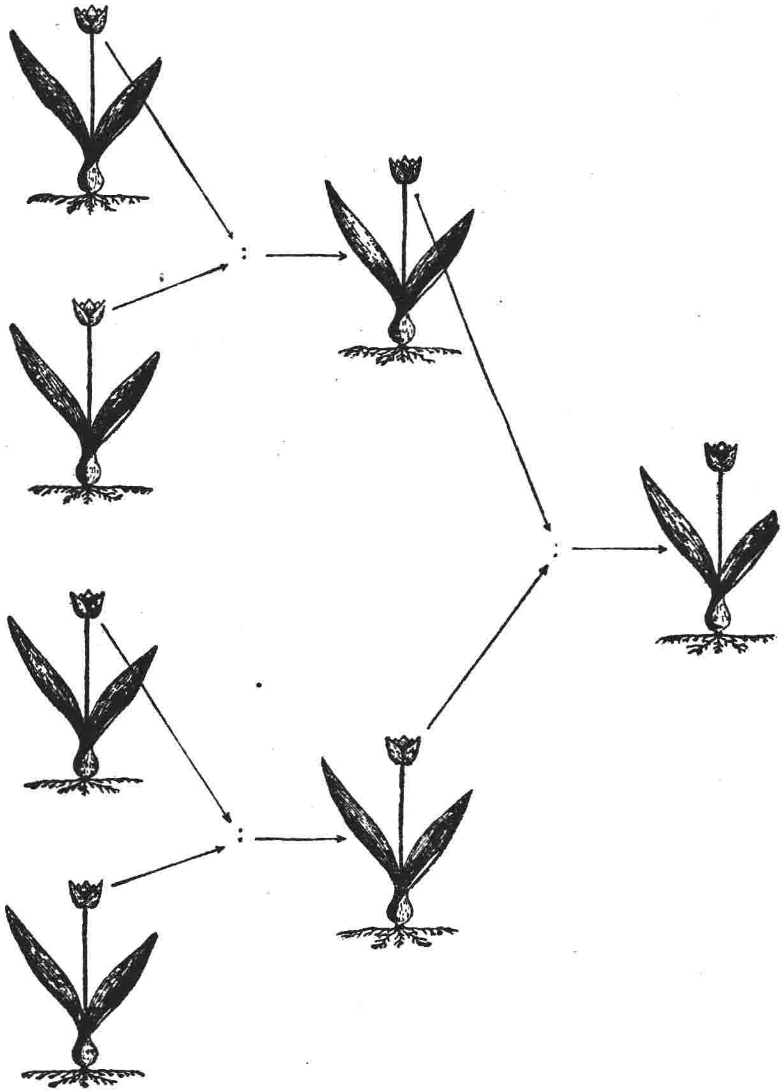

FIG. 1.—The narrow hereditary bridge. The plant at the right receives from each of its parents only one minute sexual cell, a male gamete from one and a female gamete from the other. The parents, in turn, receive from each of the grandparents but one sexual cell. Thus the bridge which connects one generation with the next, and over which the entire inheritance must pass, is an exceedingly narrow one.

In all of these cases of sexual reproduction the essential feature is that a parent contributes to each of its offspring only a *single minute cell*—a bit of living substance so small that it is usually far beyond the limit of vision for the unaided eye. This extremely narrow bridge is the only direct physical link between parent and offspring, and across it everything must pass which is transmitted from one generation to the next (Fig. 1).

Heredity.—As a result of this reproductive activity, a continuous succession of new individuals arises. One of the most remarkable features of the process is that these new individuals *tend to resemble their ancestors very closely.* The offspring of a corn plant develop into corn plants and never into anything else; and those of horses always into horses. Furthermore, any particular kind or variety of corn or horses produces individuals of just that variety. Even very specific characteristics are often transmitted with great exactness through a long series of generations. In man himself the same phenomenon is no less evident than in the lower organisms. In his own family everyone must have observed some instances in which a trait has been repeatedly passed from parent to child or where it "runs in the family," cropping out here and there in one or a few individuals. This resemblance among individuals related by descent is called *heredity.*

Heredity is such a universal and familiar fact that its significance is often not realized. The physical bridge—the reproductive cells or gametes—which connects one generation with the next is an extremely narrow one. The sperms of animals are exceedingly minute, and the effective parts of the eggs, the nuclei, are no larger. It has been estimated that all of the sperm from which the present population of the world (about 1,500,000,000) arose would make no larger bulk than a drop of water, and the nuclei of the same number of eggs would occupy about the same amount of space. In the living substance of the minute sexual elements must in some way be transmitted *all* the characteristics which the new individual inherits from its parents. Any particular adult character, such as size, shape, or color, obviously cannot be found in these cells; but something representing these characters and capable of producing them in the new individual must be there. In the case of man, the color of his eyes, hair, and skin; his susceptibility to various defects and diseases; the size, shape, and proportions of his body; his specific mental traits and capacities, together with many other characteristics, are definitely known to be inherited. In every human sperm, therefore, and in every egg there must be properties which represent each of these characteristics and which, in cooperation with each other and with the factors in the environment, determine what kind of man or woman will develop from the fertilized egg. These minute particles of living substance, into which so much is packed and out of which so much emerges, are certainly among the most remarkable bits of matter in existence.

Variation.—Close as these hereditary resemblances are, however, they are almost never *exact* resemblances. A group of offspring from the same parents may differ among themselves, and some or all of them may differ from their parents or more remote members of their family. In a group of brothers and sisters no two are exactly alike, but each has his distinctive peculiarities, and although all the children may show resemblances to their parents, they do so in different degrees. In the lower animals and in plants, where the number of offspring is usually very great, there often seems to be a much closer similarity between individuals, but even here critical study and increased familiarity will in most cases bring differences to light.

These differences are known by the general name of *variations*. Many of them are due to a parceling out of traits among the various offspring according to a definite method of inheritance. Many others, however, are due to differences in heat, light, moisture, food, or other factors in the environment, for it should be remembered that most characteristics are profoundly affected by the surroundings in which the individual develops. Variations are, therefore, of many kinds and due to many causes, but their presence is one of the most distinctive features of living organisms and indeed has been said to be the only invariable thing in the organic world.

Genetics and Its History.—That branch of the science of biology which is concerned with the phenomena of inheritance and variation and which particularly endeavors to discover the laws governing these similarities and differences between individuals related to one another by descent is called *genetics*. Unlike most of the other sciences genetics is very young, for as a distinct and recognized branch of knowledge its history goes back only about a third of a century. Development has naturally been rapid during that time, and through the activity of a large number of investigators it is still proceeding apace. The first knowledge of the facts of inheritance, however, began at a much earlier date, and what modern genetics is can perhaps best be understood by going back somewhat into the past.

From the earliest times men have recognized the facts that "like begets like" and that offspring differ somewhat among themselves and from their parents. They have long used this knowledge, more or less unconsciously, perhaps, in choosing for breeding purposes those individuals among their domesticated animals and plants which best suited their requirements. Only rarely were deliberate breeding methods used which depended on an empirical knowledge of the methods of reproduction, such as the artificial pollination of the female date palm, which was practiced in Egypt and Mesopotamia many centuries before the Christian era. The early husbandmen bred their animals and plants without any general knowledge of the reproductive processes, and the legacy of valuable cultivated plants, which is the earmark of permanent civilizations, resulted from taming the wild species and selecting fortuitous variations among them. A scientific understanding of the problems of heredity and variation, however, has begun to be reached only recently, and both its beginning and its progress have depended on improved knowledge of the reproductive process and more particularly of the sexual method.

The Discovery of Sexuality.—The existence of sexual reproduction among animals was early recognized, as was the fact that offspring inherit their characteristics from both parents. The ideas entertained by the ancients as to the exact mechanism of the process, however, were often grotesque, and it was not until biology was placed on a modern basis, following the invention of the microscope and the establishment of the cell theory, that the existence of gametes was determined. The male cells, spermatozoa, were recognized by the early microscopists in the latter half of the seventeenth century, and their function as initiators of development in the egg was demonstrated experimentally early in the eighteenth century, although the nature of both egg and sperm as single cells and of fertilization as the union of their nuclei was not made clear until the latter half of the nineteenth century.

Fig. 2.—Joseph Gottlieb Kölreuter (1733–1806). (*Courtesy of Genetics.*)

In the plant kingdom the very fact of sexuality was long unknown, as was the important part played by pollen in seed development. Camerarius, a physician of Tübingen, concluded as early as 1694 from experiments with plants that their reproduction also followed the sexual method known in animals, with the pollen functioning as the male, the ovule as the female, element. In 1760 the German botanist Kölreuter (Fig. 2) performed the first careful experiments in plant hybridization, crossing two species of tobacco by placing the pollen of one on the stigmas of the other. The offspring resulting from this experiment were intermediate in most respects between the two parent species, thus proving not only that pollen performed an essential function in seed production but that parental characters were transmitted both through the pollen and through the ovules. The growth of the pollen tube, the passage down it of the male gametes, the union of one of them with the egg cell in the ovule, and the subsequent development therefrom of the embryo of the seed were established at a later date when microscopical technique had become more highly perfected. Kölreuter performed a number of other experiments in hybridization, endeavoring to find how characters were transmitted from parent to offspring and later generations. He initiated a new direction in biological inquiry—the experimental study of hybridization—and it was the employment of this method which led most directly to the eventual discovery of the fundamental principles of heredity.

In the late eighteenth and nineteenth centuries two other streams of biological interest became well marked, each dealing with what appeared to be problems of greater theoretical importance than the more modest and limited inquiries of the plant hybridizers. One of these dealt with the gradual evolution of animal and plant species and culminated in the publication of Darwin's "Origin of Species" in 1859. The other had for its object the elucidation of the problems of individual structure and development, the whole outlook on which had been altered first by Caspar Friedrich Wolff's epigenetic theory of development and later by the generalization of the cell theory in 1838 by Schleiden and Schwann and its later application to the study of reproduction.

The work of the plant hybridizers who followed Kölreuter showed that offspring tended to inherit equally from the pollen and from the seed parent; that the hybrids, although generally representing an intermediate or average condition between the parents, did sometimes resemble one parent much more closely than the other (Gärtner); and that the progeny of the hybrids might contain individuals very much like each of the parental types (Goss). Naudin in 1862 concluded that a hybrid is a mixture of the potentialities of both parents and that these may separate and be distributed among the progeny of a hybrid. This so-called "splitting" of hybrids was the nearest approach to the great principle of heredity which was discovered by Mendel, who stands at the apex of this group of experimental botanists.

Mendel and His Work.—Gregor Mendel (Fig. 3), whose experiments in plant hybridization laid the foundation for most of the modern work on heredity and may well be said to have established genetics as a science, was a monk, and later abbot, in the Augustinian monastery at Brünn, Austria (now Brno, Czechoslovakia). In the cloister gardens he made crosses between varieties of the garden pea which differed in height, flower color, seed color, and other respects. The discoveries which resulted from these experiments were due not only to Mendel's unusual keenness in observation and clarity in reasoning but to several notable improvements in his method over those of his predecessors. He made repeated artificial hybridizations between plants which differed in various characteristics, but instead of studying inheritance in the whole complex individual as a unit, he singled out separate characteristics and observed them by themselves. He kept accurate pedigree records, which enabled him to know the ancestors of every individual plant. Perhaps more important still, in all cases where contrasting traits appeared in a group of offspring (both red-flowered and white-flowered plants, for example) he *counted* the number of individuals of each type and thus obtained a statistical statement of his results. In short, he applied exact *experimental methods* to the problems of heredity.

The results which Mendel obtained from these hybridization experiments were chiefly important in showing that inheritance was not a hit-or-miss affair but was subject to certain definite rules or laws; and that, consequently, if one knew enough about the ancestry and constitution of two parent plants, he could predict with a considerable degree of accuracy not only what their offspring would look like but the relative

Fig. 3.—Gregor Johann Mendel (1822–1884). (*From A. F. Shull.*)

frequency with which the contrasting characters, brought in from various ancestral lines, would appear among them. Mendel discovered that the individual behaves in inheritance as though it were an aggregation of independent and separable characteristics, each of which is a distinct "unit" and may exist with any combination of other characteristics in a given individual. He also found that when two contrasting characters are brought together by a cross, the hybrid offspring are alike and often resemble one of the parents in this particular character much more closely than they do the other. Still more important, if two hybrids are bred together, both grandparental characteristics appear among the offspring and are sorted out in a definite fashion, a certain proportion of the individuals resembling one grandparent and another resembling the other. The particular combination of characteristics which distinguishes an individual may thus be broken up among its descendants, the various traits being sorted out among the offspring independently of one another, so that all sorts of new combinations may make their appearance, each in a definite and predictable fraction of the whole. Mendel thus formulated the first *Laws* of Inheritance and established the basis on which the later development of genetics has taken place.

Investigations since Mendel.—Important as Mendel's work has proved to be, it was not recognized as such by the scientists of his day. The results of his experiments with peas were collected in a single paper and published in 1866 in the proceedings of the Naturforschender Verein of Brünn, where they remained in obscurity for over thirty years. Meanwhile the great controversy over the theory of evolution had begun, following the publication of Darwin's "Origin of Species" in 1859, and the attention of biologists was centered upon argument and speculation rather than upon a careful experimental study of plants and animals themselves. Rather fantastic theories, based on little or no experimental evidence, were put forward, one of them by Darwin himself, to explain how parental traits were transmitted to offspring. The facts of heredity and variation were recognized, and indeed the Theory of Natural Selection was based upon them, but there was no establishment of anything like general laws of inheritance. In this period, however, the German zoologist Weismann (Fig. 4), an able supporter of Darwin, called attention to the fact that some traits of an individual are due to the inherent characteristics of its living substance and that others are produced by the surroundings in which it has developed. Weismann believed that the latter type, which are now called "acquired" characters, are never inherited, and he performed a series of experiments to determine the fact. This problem of the "inheritance of acquired characters" has since received a great deal of attention, and most of the evidence obtained supports Weismann's contention.

Fig. 4.—August Weismann (1834–1914). (*Courtesy of Genetics.*)

Weismann also correctly identified the material basis of heredity with the nuclei of the gametes and showed that, in many animals at least, the tissues from which the reproductive cells are formed were