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PRINCIPLES OF GENETICS AND EUGENICS

A Study of Heredity and Variation in Plants, Animals, and Man

By

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GINN AND COMPANY

BOSTON · NEW YORK · CHICAGO · LONDON · ATLANTA · DALLAS · COLUMBUS · SAN FRANCISCO

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646.6

The Athenæum Press
GINN AND COMPANY · PROPRIETORS · BOSTON · U.S.A.

DEDICATED

TO

THE F_1 GENERATION

PREFACE

This book has been written as an elementary text for students who desire accurate knowledge and up-to-date information in genetics and eugenics. Special attention has been paid to the factors of heredity, variation, and environment in the production of organisms and to the rôles played by the endocrine glands in normal and abnormal development.

The final chapters of the volume deal exclusively with genetics applied to man, for the purpose of finding out the forces necessary for the emergence of a finer race of men and women. This, of course, embraces the modern science of eugenics, which has been shown to bear a very important relationship to many of our educational and social problems. Wherever possible, human illustrations have been utilized to emphasize points which have been stressed.

Most books on genetics and eugenics are written from the point of view of the specialist, and because of this, undergraduates who attempt to read them find themselves hopelessly lost unless they have had considerable preparation in the sciences dealing with plants and animals. In writing this volume the author had in mind the average student who, without much background in biology, possibly no more than an elementary course, is desirous of obtaining an understanding of the essential principles of genetics and eugenics and of discovering in what ways these sciences affect the human family. The present textbook is intended for the following classes of students:

1. Those who have become interested in the subject matter of genetics and eugenics after a preliminary discussion of these topics in the beginning biology course.

2. Those general students in the liberal arts, social sciences, education, commerce, and home economics who have been attracted to genetics and eugenics because in some of their other courses certain aspects of these subjects have been considered.
3. Those who anticipate majoring in biology, as well as those who intend following the elementary genetics course with special studies in plant or animal breeding.

In the preparation of the volume many sources have been called upon for material, and the writer desires to express his appreciation and thanks for the courtesies shown him. Although such acknowledgments have been made in their respective places within the text, the writer wishes to acknowledge here his particular indebtedness to the American Genetic Association and its official organ, the *Journal of Heredity*; the Wistar Institute of Anatomy and Biology; the Science Press; the American Eugenics Society; and the Eugenics Research Association. To Professor Earl N. Bressman, formerly plant geneticist of the Oregon State Experiment Station, and now scientific adviser to the Secretary of Agriculture, United States Department of Agriculture, he owes a special debt of gratitude for critically reading the entire manuscript and offering many helpful suggestions. To Professor Helen M. Gilkey, of the Botany Department of Oregon State College, he is indebted for drawings of Figs. 22 and 23, showing the structure of a flower and the cycle of gamete formation and fertilization in the seed plants. To Mr. John C. Burtner, of the Division of Information, Oregon State College, he is grateful for supplying the photograph of the three pairs of identical twins shown in Fig. 42. Also to Professor Charles E. Owens, of the Department of Botany, and Mr. Alfred Taylor, of the Department of Zoölogy, both of Oregon State College, thanks are due for reading critically various portions of the manuscript. Finally he wishes to express his gratitude to his wife, Frieda Mayer Fasten, for her painstaking reading and correction of the entire manuscript.

NATHAN FASTEN

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PRINCIPLES OF GENETICS AND EUGENICS

CHAPTER I

The Scope and Need of Genetics

IT IS astonishing how few persons have an intelligent understanding of the rôles played by heredity, variation, and environment in the development of organisms. This becomes apparent just as soon as one begins to inquire into an individual's ancestry. Who are your parents? Who are you? Simple questions, yes, but how many people can answer them adequately? In a recent investigation, conducted for the American Eugenics Society, specially prepared genealogy sheets were distributed to about two hundred students for the purpose of finding out how far back they could trace offhand their ancestry. Surprising as it may seem, very few of them could go beyond their immediate grandparents. On the whole, most of these students had rather vague notions regarding the ancestry responsible for their coming into existence, and, at the very best, they could not go beyond the second generation of grandparents. This portrays accurately the situation which exists among the vast majority of the human family, and we are forced to the conclusion that they know little regarding the ancestors who contributed to their make-up.

What does this mean? Just this: that while professional breeders have zealously traced and guarded the pedigrees of many species of domesticated plants and animals, the human family has given little thought to itself, paying almost no attention to the question of human breeding.

"Breeding" may not seem a suitable word to use in speaking of human individuals; nevertheless that is exactly what the process is, — one of reproducing the next generation through the mating of adults of opposite sex, the immediate parents. They in turn have been conceived in similar manner, through a union of the grandparents — their immediate parents. After all, the problem in its simplest terms is similar to the one with which every breeder deals, namely, the mating of individual organisms for purposes of reproduction and improvement of species.

At this point one might be permitted to ask, Why bother about considerations of heredity and improvement of the species? Such considerations bear directly on individual, social, and national welfare. Although we may rail against heredity, still species are what they are mainly because of the operation of this factor. The environment acts on the stuff which is found in the individual organism, stimulating it to respond in one way or another; but it must be emphasized that those who are familiar with biology are convinced that the fundamental entities responsible for the characteristics of any individual must be inherent within the make-up of the organism from the start, and that the environment is powerless to produce them where they are lacking. It is quite true that environmental influences may tend to emphasize, minimize, or completely interfere with the expression of certain traits, but this factor alone is powerless to produce such traits in cases where they were absent in the combination that formed the living organism.

The present-day biologist emphasizes both heredity and environment and believes that the most satisfactory results can be obtained only when an organism has the fullest advantages of the best of both of these factors. The quaint old saying that "a silk purse cannot be made out of a sow's ear" applies adequately to this discussion. No matter how one may treat a sow's ear, basically it will remain the organ which it was in the first place, without any fundamental change in its nature. One must not forget that by and large these same

principles hold good for the rest of the organic kingdom. Organisms are what they are because of their heredity, and the environment only maintains and stimulates certain traits to play a larger degree of importance in the life of the individual species. Likewise the environment establishes limits within which heredity works. In actuality, both good heredity and good environment are absolutely necessary for the finest development of any living form, and this fact must be stressed with as much emphasis as possible!

The Meaning of Genetics

Genetics is primarily a study of heredity. Environment, variation, and kindred subjects are embraced in this biological science. Since about the beginning of this century genetics has become such an important branch of biology that many students have been specializing in this field, devoting all their energies to discovering the laws and principles which will enable one to understand more adequately the fundamental nature of organisms. The word "genetics" itself is derived from the Greek root *genesis,* meaning "origin," and when literally applied it refers to the origin of the various kinds of living forms that populate the globe. Strictly speaking, the science of genetics deals with the (resemblances, *heredity,*) and (differences, *variation,*) which characterize the large number of existing plant and animal organisms. In its broad implications, genetics deals with the origin and relationship of groups of organisms, whereas in the restricted sense it deals with those resemblances and differences exhibited by individuals related by descent. This latter phase may be said to be the strict province of the field of modern genetics, while the former considerations are dealt with largely under the heading of *evolution.* Inasmuch as all groups of organisms are made up of individuals, it is extremely difficult to draw any sharp line of distinction between the broad field of evolution and the restricted one of genetics. Both of these branches of science are concerned with the principles of heredity and

variation, and as such apply to living forms whether they be related to one another individually or collectively.

Genetics and Education

There is great need for knowledge of genetics from numerous standpoints, such as education and sociology. Education is the most important social means for developing to the utmost our biological inheritance. It is the method by which we train the organism to make use of its heredity and adapt itself to its environment.

From the standpoint of education, genetics tells us that we have been putting the cart before the horse. School boards and the public in general have often been interested primarily in the physical equipment of their educational systems, and have concentrated most of their attention on school buildings and plants, rather than on the human material enrolled in them. The impression must not be obtained that this phase of education is not important, for, on the contrary, it is extremely so. But it must be remembered that the factor of greatest significance in education is the child himself. The ideal to be followed should not be the present one of merely fitting the pupils into the school, but rather the reverse, of building the school and the system around the pupils. Unfortunately this has not been the case in the past, but many educators are beginning to realize that this condition must be changed if the best results are to be obtained. The principles of genetics reveal that organisms differ in both physical and mental capacities, and that the only equality which may be said to exist among human beings is the manner in which they are conceived and brought into existence. When once they make their appearance in this world, organic differences as well as surroundings soon assert themselves to such an extent as to make every individual a distinctly recognizable entity.

At the present time *age* is too frequently made the factor of greatest consideration in segregating pupils into grades. Students of psychology and genetics have shown quite con-

clusively that among a large number of children of the same age there are to be found salient physical and mental differences, enabling us to classify them into numerous distinctive groups. Needless to state, age also must be considered. Per-

FIG. 1. How the Average Dollar in Taxes is Spent[1]

haps the most efficient means of educating children would be to segregate those of approximately the same age into grade units in accordance with their physical and mental levels, their home surroundings, and their individual accomplishments, and then to give each group the fullest and best training possible. In most instances the present organization of

[1] Courtesy of the *Chicago Tribune*.

our school system does not permit of such handling of the human material, and the inevitable result is that the more capable pupils are not given the right opportunity for fullest development, and at the same time the duller pupils are hindered from progressing because they cannot keep pace with the average, normal group in the class.

Every now and then one reads of the vast sums of money which are being spent on education. The aggregate amount, no doubt, is large, and yet it is woefully insignificant when compared with the expenditures for such items as war, crime, and the care of the socially inadequate population. Everywhere nations are now spending huge sums for armaments and implements in preparation for future wars. A single modern superdreadnought costs approximately forty million dollars to construct. What present-day university receives such a huge sum for its annual support? It has been estimated that in the United States somewhere between 70 and 80 per cent of our national taxes are used for the army and navy, including pensions for disabled war veterans or their relatives and the various other details connected with war and the preparation for it. This is vividly depicted in the illustration shown in Fig. 1.

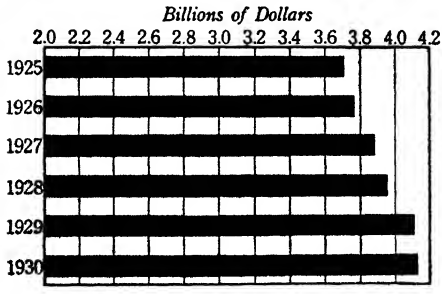

FIG. 2. World Expenditure for National Defense, 1925–1930[1]

According to figures given in the League of Nations Armaments Year Book for 1930–1931 (*Bi. 131*),[2] the world spent $4,157,931,958 during this single year for armaments, and of this amount the United States spent over one sixth, or $707,425,000. Fig. 2 shows the huge amounts expended for

[1] Courtesy of the *New York Times*.

[2] The abbreviation *Bi.*, followed by a number and inclosed in parentheses, refers to specific references in the Bibliography at the end of the book.

armaments during the years 1925–1930 inclusive by the various nations of the world. If in some way these sums could be reduced materially and a large share of them utilized for educational purposes, along lines looking toward the creation of conditions which would make it possible for every child to obtain the finest opportunity for self-development, it would result in untold improvements which would greatly benefit civilization.

Conservative estimates place the cost of caring for our socially inadequate population at five billion dollars a year. This is the direct cost, which, when added to the indirect cost, of the loss in wages of these nonproducing units, causes the sum to increase to probably twice the stated amount or more. James H. S. Bossard (*Bi. 17*), sociologist of the University of Pennsylvania, in speaking of this item asserts:

> Five billion dollars a year is the price we pay for those who falter or mutiny in the ranks of our rapidly changing society. This is a conservative estimate, based on such data as are available, and treatment of the dependent and delinquent elements in our population.
>
> This is equal to three times the annual expenditures for the maintenance of the public school system of this country, is nearly double the amount of the budget of the federal government in recent years; and it exceeds slightly the total value of all the products of the entire automobile industry of the United States in 1927.
>
> Then there are the indirect costs. Anything like a complete accounting of the cost to society of social ill-being must include, of course, many items in addition to the direct costs just alluded to. There is, for example, the loss of possible contributions by the individuals concerned — both as producing units in the economic organization of society and as personalities in its communal life. The former of these may be translated into monetary terms and measured in multiples of the average man; the latter item, that of possible social contributions, has to do with life's intangibles, and these clearly are beyond the scales of the statistician.
>
> Four dollars of indirect cost for each dollar of direct cost seems conservative on the basis of recent studies. This would place the indirect costs of social ill-being at twenty billion dollars a year. This amount approximates the total capital invested in the railroads of the country.[1]

[1] James H. S. Bossard, "What We Pay," *People*, Vol. 1 (1931), p. 10.

Or consider the following assertions (*Bi. 24*):

The annual crime bill in the United States is in excess of $16,000,000,000 compared with a $5,000,000,000 child welfare bill, the Committee on Youth Outside the Home and School declares in a report to the White House Conference on Child Health and Protection. While expenditures for welfare touch 50,000,000 young people, those on account of crime touch less than 1,000,000 of the population. "Every time we 'grow' a criminal," says the committee, "he costs us as much as the welfare influence in the lives of 160 normal boys." To combat the influences of disintegration which foster delinquency and other evils, the committee calls for "wider support of the basic institutions of home, church, and school, and those social agencies operating outside the home and seeking to influence character development." [1]

Certainly it must be apparent to all interested in the future welfare of civilization that expenditures for education should be ample to secure for our youth the very best direction from the standpoints of teaching and guidance. In this connection it is encouraging to note the progress that some communities have already made along these lines by giving school children opportunities afforded by such agencies as clinics for standard health examinations, for mental testing, and for vocational guidance.

Genetics and Sociology

The discussion of our socially inadequate population naturally leads to a consideration of the need for genetic knowledge from a social standpoint. Sociology deals with many of the problems confronting our present-day society, such as pauperism, feeble-mindedness, insanity, and criminality. In the past the remedies advocated for the solution of these problems have been largely curative rather than preventive and have consisted in providing adequate institutions for housing and treating these unfortunates. The philosophy which motivated those who proposed such remedies was embodied

[1] "Food for Thought," *College Bulletin of the Chicago Fisk Teachers Agency*, Vol. 4, No. 1 (January, 1931), p. 8

in the conviction that in many cases the right treatment of these individuals would gradually overcome their defects, so that in due course of time they could be liberated as normal and efficient citizens. This object has not been realized; on the contrary, in many instances the socially inadequate individuals have multiplied to such an alarming extent that within recent years public taxes for their maintenance in state institutions have increased enormously. Geneticists have repeatedly pointed out that such treatment has failed to decrease the defective population, and they have insisted that the only way to better social conditions is so to organize our charities that while help is given defective individuals, at the same time something is done to stop up the source of their heredity, thereby preventing them from reproducing offspring similar to themselves. Studies in human heredity have indicated that many paupers and many feeble-minded, insane, and criminal individuals are produced through a combination of hereditary factors brought in by the parental germ cells, and that permanent relief can be obtained only if in some manner this defective population is prevented from reproducing its kind.

Some authorities (*Bi. 93, 109, 111, 116, 167, 173*) believe that there must be close to eighteen million such defectives in the United States, who are contributing largely to our institutional population, and they have pointed out repeatedly that if in some way these persons could be prevented from having offspring, the danger of their perpetuating their kind would be removed. The ultimate result would be a tremendous saving of money because of the decreased costs of maintaining the various institutions for the support of such defectives. In a recent pamphlet on sterilization the problem which confronts the American people is described as follows (*Bi. 114*):

> Careful studies indicate that there are 6,000,000 in the United States who have been, are now, or at some time will be legally committed as insane to state institutions. The number who suffer from equal mental disease sufficient at some time to incapacitate them for work but who are never legally declared insane is about

as great, making 10% of the population or 12,000,000 persons subject to mental disease in one of its most serious forms. Altogether apart from the undesirability of perpetuating such forms of mental disease, it needs no argument to maintain that many of this vast number should not have children either for the welfare of those children or for their own welfare, not to mention posterity.

But these 12,000,000 mentally diseased persons are not the whole story. There are 6,000,000 additional who, though not mentally diseased, are so deficient in intellect, with an endowment in this respect that is more than 30% below the average, that they are often described as feebleminded. . . .

This, then, is the situation which America faces now: 18,000,000 persons who are or at some time during life will be burdened by mental disease or mental defect, and in one way or another a charge and tax upon the rest of the population.

It challenges every thoughtful person.

The misery resulting from this insanity and feeblemindedness provides the first reason for grappling with the problem. No stratum of society is immune from such suffering.

The economic burden is tremendous and steadily growing worse. A billion dollars a year would be a low estimate of the cost of caring for these unfortunates, either in or out of institutions. The cost to the community of those who are not cared for,— who are furnishing a large part of the staggering crime bill and the losses due to accidents,— is much greater.

Finally, what sort of a government can be expected,— what progress can be looked for,— when so large a part of the voters are mentally abnormal?[1]

Genetics and Popular Misconceptions

There is great need for a more general knowledge of genetics. The average individual has so many misconceptions regarding the subjects of heredity and environment that he needs to acquire accurate, scientific information along these lines.

One of the beliefs which is common among a large proportion of people is that the environment is the all-important

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[1] *Human Sterilisation*, a publication of the Human Betterment Foundation, Pasadena, Calif., 1932, pp. 4–6.

agency in molding the individual. Often the assertion is emphatically made that irrespective of the heredity the end result will be highly desirable if the surrounding environment is favorable. This, of course, is contrary to what geneticists believe; for, as has been indicated previously, although these scientists do not discount the environment, their genetic studies upon different animals and plants, as well as human individuals, have convinced them that heredity is the fundamental factor in determining the make-up of an organism. No matter how splendid the environment, no good results can be obtained unless the basic material that went into the formation of the individual was desirable. Good traits really depend on a good foundation of heredity, coupled with a desirable environment to allow their full expression. When the entities for such traits are absent, no influences of the environment will incorporate them into an organism. Basically individuals are what they are first because of heredity and then because of environment. One must not get the impression that this latter factor is not of importance, for every scientist knows that it cannot be ignored. However, it is incapable of producing desirable results without a good foundation of heredity to start with.

Albert F. Blakeslee (*Bi. 16*), geneticist of the Carnegie Institution for Experimental Evolution, in speaking of the relationship between heredity and environment, asserts:

> We start life like a photographic plate which has been exposed. There is a potential image ready for development, which corresponds to the heredity. Chemical solutions in the hands of the photographer furnish the environment which reveals the lines already impressed upon the negative. Differences in this environment brought about by changes in the manner of developing the negative may alter the appearance of the finished picture. And yet the development can bring nothing new into the picture. Its outlines were foreordained at the moment the sensitized plate was exposed in the camera. After we are born we cannot change our heredity, though we can change our environment.[1]

[1] Albert F. Blakeslee, "Heredity and Environment," *Scientific Monthly*, Vol. 31 (1930), p. 559.

Another misconception which is widespread is the belief in *prenatal influences*. Many people, even highly intelligent ones, are of the opinion that during pregnancy a child may be branded or influenced in certain directions by external stimuli which happen to impress the mother. Everyone can recall common examples of supposed prenatal influences. The mother is frightened by a mouse, and if the child happens to be born with a large mole on some portion of its body, immediately these facts are believed to be connected; the view is expressed that in a mysterious fashion the fright resulting from seeing the mouse left its impression on the child in the form of a mole. Another illustration of this sort is the supposed connection between an unsatisfied craving by a mother for some berries, such as raspberries, for instance, and the reddish marks found on the body of her child. Many other similar striking examples of supposed prenatal influences might be cited, but, needless to state, scientists believe that they are mainly superstitions, and there does not seem to be any good reason for believing any of them. During pregnancy so many stimuli affect the mother that if all of these left their brand on the developing child, there would hardly be room enough on the body of the youngster to carry all of the impressions. Every biologist knows that pregnancy is a delicate period, in which the child may be influenced through the effects of certain stimuli, but these, in order to produce results, must interfere vitally with the normal development of the body or mind of the child. It is well known that certain diseases and poisons, when they affect the body of the mother, often cause the development of harmful entities within her, which, on coming in contact with the embryo, may injure it and produce abnormalities. But it is hard to conceive how mere impressions might engender the definite transformations which have been mentioned.

Many people have a great deal of misinformation in regard to the question of *sex determination*. Many believe that the environment, period of day when conception occurs, or other similar influences are agents in determining the sex

of the offspring. Naturally such information would be highly desirable as well as beneficial from numerous standpoints. Without discussing the question any further, it must be asserted emphatically that thus far none of these contentions have proved to be scientifically correct. It is now fairly well established that sex is a character similar to other traits and, like them, is conditioned by entities in the two reproductive cells that unite to form the new individual. From the very beginning of conception sex has become established. However, as will be indicated in a later chapter, sex is considered to be a complicated phenomenon, dependent for its completion on the coöperation and interaction of numerous factors within the developing organism.

Still another misconception goes under the name of *telegony*. Briefly described, it is the belief that a former sire may leave his permanent impressions on the reproductive cells of a female, so that when she is later mated to a different sire, her offspring will continue to show the effects of this former union.

Perhaps the most familiar illustration of telegony is the one cited by Lord Morton of England at the beginning of the nineteenth century. Lord Morton crossed a young chestnut mare of seven-eighths Arabian blood with a male quagga, a dun-colored, zebra-like animal possessing distinct stripes on the head, neck, withers, and back (Fig. 3, *A*). The Arabian mare used in this cross had never before been bred from. After being mated to the quagga, she gave birth to a female hybrid which showed distinct stripes on the legs and withers (Fig. 3, *B*). Subsequent to this mating, Lord Morton's Arabian mare was crossed twice to a very fine black Arabian stallion, and she gave birth, successively, to a filly and a male colt. When these foals were examined carefully, it was found that although they had distinctive Arabian characteristics, nevertheless they seemed to show also the effects of the quagga mating, in that they possessed traces of the dun color, definite stripes along the neck, withers, back, and legs, and stiff manes with the hair standing up similar to the mane

FIG. 3. Lord Morton's Quagga, and Offspring

A, male quagga used in experiments; *B*, female hybrid from quagga and Arab mare; *C*, Arab filly. (After Ewart, courtesy of the United States Department of Agriculture)

of the quagga. The filly is shown in Fig. 3, *C*, and when it is compared with the photographs of the male quagga and his hybrid female offspring (Fig. 3, *A* and *B*), the striking resemblances to the zebra-like characteristics of the quagga may be noticed.

For a long time following Lord Morton's experiments, biologists accepted telegony as a fact. However, in the latter part of the nineteenth century, the English biologist Ewart (*Bi. 70 and 71*) undertook a series of extensive investigations to test the contentions, repeating in large measure Lord Morton's experiments. He came to the conclusion that there was nothing to this belief. Ewart pointed out that it was quite common to find striping in the young of many of the Oriental breeds of horses and that unquestionably this is due to the fact that these breeds originated from some wild ancestral type that was striped. Therefore the markings which appeared in the foals, resulting

from the crossing of Lord Morton's mare with the pure Arabian stallion, must be considered a case of reversion to ancestral type rather than one of infection through the medium of a previous mating with the quagga.

Many other experimental breeders, notably those of the United States Department of Agriculture, have conducted similar experiments with various domestic breeds of animals, and they have not been able to uncover a single positive proof in substantiation of telegony. Although this belief is discounted by most modern geneticists, it is none the less true that a large number of people, as well as many practical breeders, still believe in it.

Genetics and Agriculture

Arguments are hardly necessary to convince one of the need for genetics from an agricultural point of view. Modern agriculture depends in large measure on an understanding of various sciences, particularly those that are linked up intimately with plant and animal production. The farmer is constantly seeking better breeds of plants and animals, those which show a combination of the most desirable traits. With the increase of the world's population and the production limits of the agricultural areas of the globe, which, on the whole, are more or less stationary, there is a constantly more pressing demand for the products of the farm. Increased production can come only in one of two ways: either the areas devoted to agriculture must be increased or, if that is not possible, then the production of higher-yielding strains of plants and animals becomes imperative. The agriculturist who understands the laws of heredity is eminently better fitted to plan experiments for the purpose of developing better breeds of animals or higher-yielding varieties of plants utilized by man than the one who is deficient in such knowledge. Genetics thus becomes the key to successful crop or livestock production, and without it the modern farmer would still be following the hit-or-miss methods in vogue in past generations.

Genetics and Civilization

Finally, there is great need for genetic knowledge from the point of view of civilization. Many persons speak of civilization without realizing that what is actually meant by the term is the large mass of achievement made by the human family comprising the various nations of the globe. People constitute nations. The cultures of nations comprise a large part of what is ordinarily meant by the term "civilization." At the present time two events are occurring side by side which are of vital significance to the future welfare of the human family. The desirable, normal, and gifted population is restricting the size of its families to the extent where they are hardly replacing themselves. In fact, many competent observers have pointed out that this branch of civilized society is actually decreasing instead of increasing in numbers. At the same time there is a rapid increase in numbers among those individuals who are abnormal or subnormal in many of the attributes which make for the best interests of humanity. As a general rule, persons belonging to these last-named groups take their social and family responsibilities rather lightly, placing no limitations on the size of their families, with the result that the number of children in each is rather large. Competent observers have pointed out that this undesirable class, as a whole, is increasing so rapidly that it is outnumbering and overshadowing the desirable group in our population. Needless to state, civilization is face to face with a serious problem and unless something is done to check and change the situation, there is danger that our best stocks will be swallowed up by those with mediocre and deficient traits.

CHAPTER II

Theories of Heredity

HEREDITY is the resemblance between organisms related by descent. People always haye noticed similarities between related organisms, and for centuries they have attempted to explain them. So striking is the fact of heredity that it has given origin to many colloquial expressions, such as "a chip off the old block," "like begets like," "the apple does not fall far from the tree," and so on. Early ideas concerning heredity were rather vague and peculiar, so much so that when they are discussed at the present time they invariably provoke laughter. Individuals knew, of course, that there was an intimate bond between parent and offspring, but they were at a loss to understand through what medium, or to what degree, the characteristics of the parents were transmitted to the offspring of the following generations. Since the discovery, in the nineteenth century, of the true nature of germ cells, our knowledge of heredity has been considerably enlarged, and as a direct result emphasis has been placed on the reproductive elements not only as the important entities in producing the new organism but also as being responsible for the transmission of the determiners of individual traits. The history of biology reveals that numerous theories have been propounded to account for the relationship between the germ cells and heredity (*Bi. 25, 187, 207*).

Preformation Theory

One of the earliest conceptions linking the germ cells to heredity goes under the name of *preformation*. This theory came into existence definitely in the seventeenth and eight-

eenth centuries, although prior to that time people held somewhat similar views. We find allusions to this idea all through Biblical and post-Biblical literature. Not until the seventeenth and eighteenth centuries, however, was there a definite formulation of the relationship between the germ cells and the organisms which develop from them. According to the preformation theory, the germ cells have, crammed in somewhere within themselves, miniature models of the organisms which ultimately will develop from them. All portions of the organism, perfect in all respects, are thus preformed even before the mature germ cell undergoes fertilization. Heredity and development are merely the cut-and-dried processes of the growth, enlargement, and elaboration of those traits which the miniature model organism already possesses.

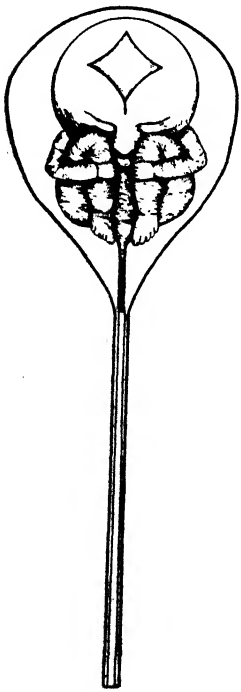

FIG. 4. Human Spermatozoön, showing Preformed Organism[1]

Two distinct schools of preformationists sprang up, known respectively as the *spermists* and the *ovists*. The spermists claimed that the male germ cell, the spermatozoön, carried the microscopic model (Fig. 4), and that the egg merely functioned as a source of food, protection, and stimulation for the miniature organism. On the other hand, the ovists held just the opposite view; namely, that it was the female germ cell, the ovum, rather than the spermatozoön, which contained the minute organism, and therefore the function of the spermatozoön was merely to stimulate the egg to undergo growth and development.

[1] From Fasten's *Origin through Evolution*. By permission of F. S. Crofts & Co., publishers.

Emboîtement (Incasement) Theory

This crude idea of preformation soon gave origin to a theory which goes under the French name of *emboîtement* or the English one of *incasement.* It was propounded in the latter part of the eighteenth century by the Swiss scientist Bonnet, and it asserted that the germ cells carried not only the microscopic models of the immediate individuals but also those of all the organisms which would ever originate from the particular strain in question. This conception of heredity may be compared to the familiar Chinese puzzle box, in which are inclosed a large number of smaller and smaller boxes of the same kind as the outermost one. Applying this theory to the Biblical story that Eve was the first woman to occupy this earth of ours, then the conclusion becomes inevitable that Eve's germ cells contained miniature models not only of her immediate offspring but also of those that followed in all subsequent generations. In the light of modern knowledge this view seems utterly absurd; but it must be remembered that in its day some of the greatest minds of the time devoutly believed in it.

Epigenesis Theory

The above hypotheses were soon proved erroneous by the German investigator Caspar Friedrich Wolff. In the latter part of the eighteenth century Wolff began a careful study of the development of the chick, and succeeded in showing definitely that there was no preformed individual in the fertilized hen's egg, but that only after a certain period of logical development did the adult organism come into existence. He, more than any other biologist before his time, demonstrated conclusively the falsity of the various preformationist views and soon succeeded in convincing biologists. Wolff's conception is often alluded to as the *epigenesis,* or *stuff,* theory, and its chief contention is that the germ cells contain certain definite undifferentiated stuffs which, after fertili-

zation, become organized into the various complex structures and organ systems that ultimately comprise the adult. This hypothesis, although deficient and elementary in a great many respects, nevertheless bears a rather striking similarity to the modern *gene theory* of heredity (discussed in Chapter XI), which has been developed since the beginning of the twentieth century, largely through the studies of experimental breeders and cytologists.

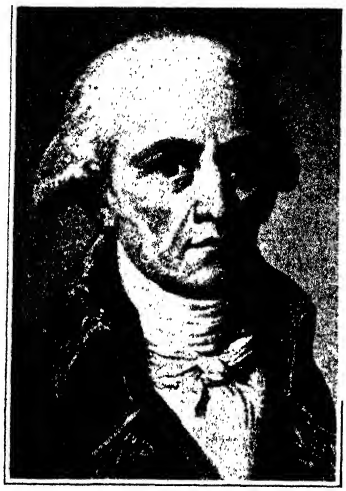

FIG. 5. Jean Baptiste Lamarck[1]

Wolff's work paved the way for the more recent conceptions of heredity, propounded largely in the nineteenth century. Two of these theories deserve special consideration: *pangenesis*, set forth by the great English scientist Charles Darwin, and the *germ-plasm* theory, propounded by the German biologist August Weismann.

Pangenesis Theory

The foundation for the conception of pangenesis rested mainly on the efforts of the two biologists: Wolff, the German, whose view of epigenesis has already been elaborated, and Lamarck (Fig. 5), the Frenchman, who in the latter part of the eighteenth century proposed a theory of the inheritance of acquired characters, or traits, chiefly through the agency of the use or disuse of parts of organisms. Lamarck raised the fundamental question of how animals and plants acquire variations in the first place and how their offspring come to differ from what the parents were at birth. In order to answer this question, he developed the *principle of use*

[1] From Fasten's *Origin through Evolution*. By permission of F. S. Crofts & Co., publishers.

and disuse. He contended that the use or disuse of a structure emphasized or minimized it, so that in time it became either more or less efficient. He believed that the modifications thus engendered in some fashion became incorporated into the germ cells, so that when they participated in reproduction they brought in with them the acquired transformations, thereby transmitting them to the next generation.

In 1866 Charles Darwin (Fig. 6) published his view of pangenesis, which, as already mentioned, attempted to combine the Lamarckian point of view on the inheritance of acquired characters with that of Wolff's epigenesis conception of the constitution of the germ cell as a very simple, unorganized entity.

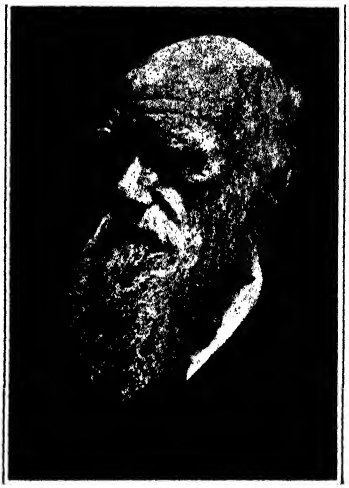

FIG. 6. Charles Darwin[1]

Darwin's pangenesis theory started with the assumption that every organism consists of bodily and germinal elements, and that these, although separate entities, nevertheless are very intimately associated with each other within the individual. Technically the body cells are referred to collectively as the *soma,* and the respective material of which it is comprised is called the *somatoplasm.* Likewise, the reproductive elements are known collectively as the *germ,* and the material which comprises it is spoken of as the *germ plasm.* According to the theory of pangenesis, the reason why there is such a striking resemblance between parents and offspring is because the body elements give off microscopic particles known as *pangens* or *gemmules,* which enter the circulatory fluid and are carried by it to the germ plasm, where they are stored. The pangens are supposed to be representative par-

[1] Courtesy of *Popular Science Monthly.*

ticles, portraying accurately the particular portions of the body cells from which they were derived, so that if any modifications happen to occur within certain regions of the body, then the pangens originating from these localities and later stored in the germinal elements will likewise have the transformation represented within them. Now what is development? Simply a growth of the pangens stored in the germ

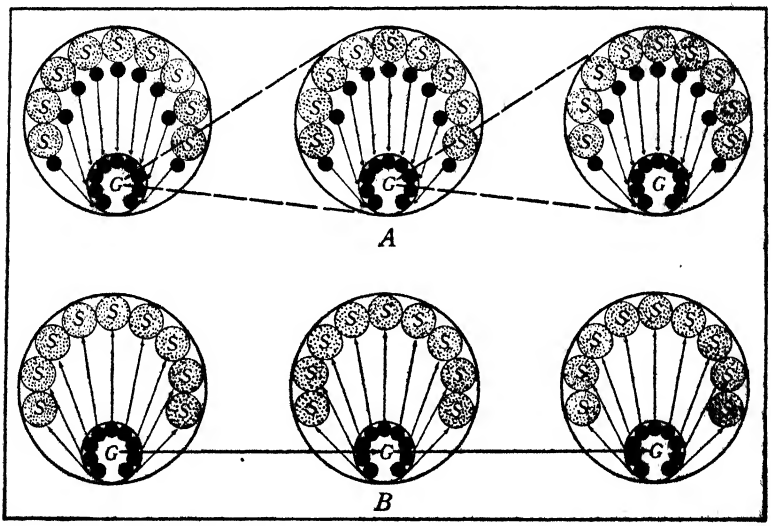

FIG. 7. Diagram of the Pangenesis and Germ-Plasm Conceptions[1]

A, pangenesis view; *B*, germ-plasm conception; *S*, somatic structures; *G*, germ cells. In *A* the black circles designate pangens or gemmules; in *B* they represent germinal determiners

plasms of the uniting germ cells which participate in the reproduction of the new organism. Fig. 7, *A*, is a diagrammatic representation of the pangenesis conception.

This theory of pangenesis was supposed to explain very nicely the manner in which acquired characters were inherited, and it was accepted universally, without question, until almost the end of the nineteenth century. At this time, however, the conception of pangenesis was actually put to the

[1] From Fasten's *Origin through Evolution*. By permission of F. S. Crofts & Co., publishers.

acid test by the German biologist August Weismann (Fig. 8), who seriously questioned the theory and carried on experiments to disprove it. For some twenty generations he docked the tails of mice and then bred them, to see whether he could produce generations with shorter tails. Such was not found to be the case, and the resulting progeny, in each instance, possessed just as long tails as the parents before the docking operations were performed. Inasmuch as these results were negative, Weismann came to the conclusion that heredity did not work in quite the simple manner in which Lamarck and Darwin surmised. Soon the scientific world condemned the pangenesis conception and took an extreme view on the question of the inheritance of acquired characters, asserting dogmatically that under no circumstances could such inheritance ever occur.

Germ-Plasm Theory

Following his experimental results on the tails of mice, Weismann formulated his own explanation of heredity, known as the *germ-plasm* theory (Fig. 7, *B*), which postulates that only those things are inherited which are actually a part of the germ plasms of the parent organisms responsible for the production of the new individual.

In formulating his hypothesis, Weismann, like Darwin, considered the organism as separated into the two entities of germ plasm and somatoplasm. Moreover, he pointed out that since every living form is produced from a combination of two opposite germ cells, it may be asserted positively that these two types of cells are responsible for the expression of both the bodily and the reproductive structures of the next generation. An interesting fact which Weismann discovered from his developmental studies was that very soon after fertilization the bodily and germinal portions of the organism were set off from each other quite distinctly, and because of this he concluded that any changes which would take place in the somatoplasm would have little or no effect on the

germ plasm. At the approach of sexual maturity the germ cells produce the functional reproductive cells, whereas the body cells participate, from the very beginning of development, in the formation of the various parts of the body. Furthermore, the somatic structures, with all their characteristics, terminate at the death of the individual, while the germinal structures, through reproduction, carry on the life and characteristics of the species from generation to generation. The somatic cells are therefore said to be mortal, and the germ cells immortal. According to Weismann, only those entities for traits which are originally a part of the germ cells are inherited.

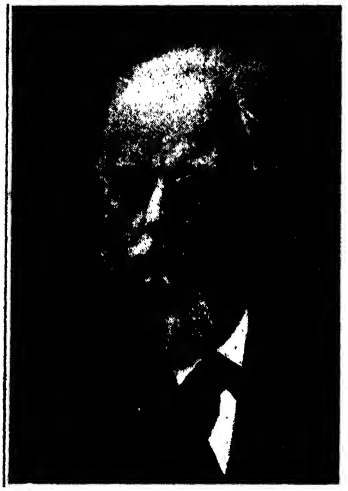

FIG. 8. August Weismann[1]

When this hypothesis of the continuity of the germ plasm was first stated, it immediately met with favor, and before long it was taken up by most of the scientific world. The view was accepted so universally that for a long time no one dared to express any opinion against it. In reality, scientists interpreted the germ-plasm conception so dogmatically that anyone who opposed it and favored another theory, especially one which advocated the inheritance of acquired characters, was considered queer and archaic in point of view. Weismann's experiments seemed to point so conclusively against the inheritance of acquired modifications that everyone forgot to think along Lamarckian lines, and accepted the germ-plasm explanation as the only one which accounted for the manner in which the inheritance of traits could be accomplished.

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[1] From Buddenbrock's *Bilder aus der Geschichte der biologischen Grundprobleme*. By permission of Gebrüder Borntraeger, Berlin, publishers.

But geneticists realized that variations were constantly occurring and in many instances these were inherited in the next generation of offspring. Inasmuch as most scientists had discarded the views advocating the inheritance of acquired traits, the natural question which then arose was, How can such modifications be explained on the basis of the germ-plasm theory? According to Weismann's hypothesis, variations originate in one of two ways: either *de novo*, that is, spontaneously within the germ cells, or through the influence of the germ cells from opposite parents upon each other, during the process of fertilization, which is known as *amphimixis*.

When all is said, however, these explanations remain woefully deficient, explaining little, if anything, in regard to the question of how new traits originate. What makes variations occur spontaneously? What are the influences which cause germ cells to vary during amphimixis? These are the things we are interested to know, but the language used by the Weismannians, while consisting of nicely spun words and phrases, nevertheless explains nothing. It leaves us just as ignorant as ever regarding the causal factors of variation.

It must be admitted that Weismann's theory has been instrumental in initiating a tremendous amount of research in biology, particularly in that branch known as cytology, which has for its special sphere the biology of cells. Since cytology is intimately associated with genetics, it is no exaggeration to state that as a direct result of the investigations initiated by the germ-plasm conception, some of the greatest advances in the fields of cytology and genetics have been made. Weismann was a genius and a remarkable thinker. In spite of the fact that for a good many years he was almost blind, yet in his mind he visualized many of the things which now are accepted universally by all biologists. He possessed such keen powers of insight and such a wonderful imagination that he pictured what was going on within the germ cells; although he was wrong in many minor respects, nevertheless his major contentions were correct, and these influenced the development of modern genetics.

Schools of Heredity

From the standpoint of heredity, present-day biologists may be classified into three groups. The first may be termed *Lamarckians,* or rather *Neo-Lamarckians,* those who stress the inheritance of acquired modifications as advocated by Lamarck. These biologists assert that every influence is important in bringing about changes within the germ plasm. As will be pointed out in the next chapter, dealing with the inheritance of acquired characters, there have been many biologists, since Weismann first propounded his views, who have conducted numerous experiments on animals and plants in the hope of establishing Lamarck's contentions. Most of these scientists, even though they are convinced that Lamarck may have been right in his major premises, nevertheless have had to abandon their views as either inconclusive or faulty.

Another group of biologists may be classified as *Weismannians.* They believe that no acquired characters can ever be transmitted to offspring, and insist that only those modifications are inherited which are already a part of, or originate spontaneously within, the germ plasm. Heredity thus seems to be a fixed thing almost from the very beginning of development, and it is determined by the definite entities within the germ plasm. The somatic structures surrounding the reproductive ones seemingly have little or no influence on them. To show the independence of the germinal and somatic elements of individuals, the experiments conducted in 1911 by Castle and Phillips (*Bi. 23*) may be mentioned. These biologists removed the ovaries of an albino guinea pig, and in their place transplanted the ovaries from a black guinea pig. As soon as this albino female recovered, she was mated to a normal albino male, and her resultant offspring were all black, being similar to those young normally produced when a pure black guinea pig is crossed with an albino (Fig. 9). Apparently the body cells of the albino animal which underwent the operation exerted no influence on the germinal determiners carried by the transplanted ovaries.

In recent years a third group of geneticists has developed, called the *parallel inductionists,* who assert that the germ and body cells of an organism cannot be distinctly segregated

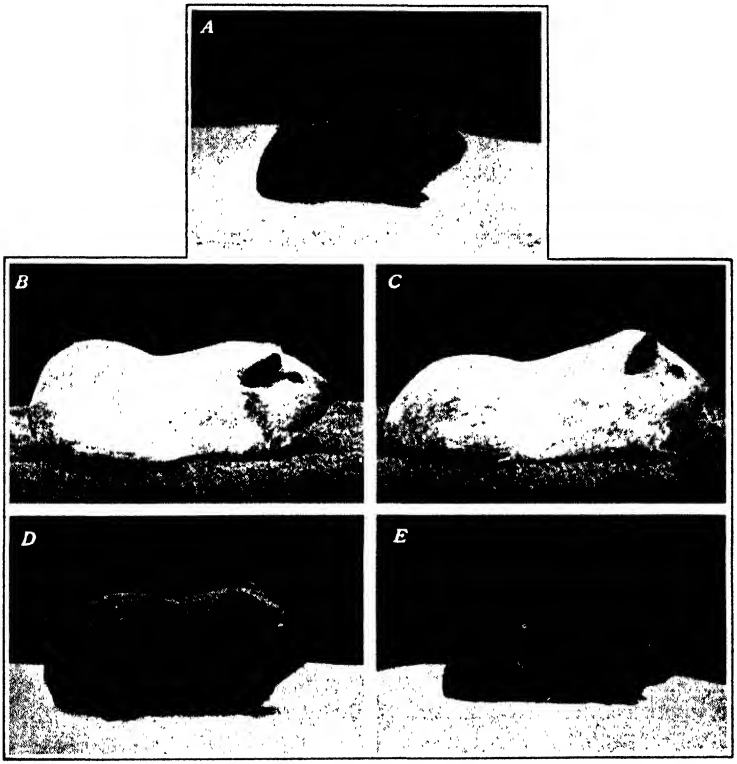

FIG. 9. Ovarian Transplantation in Guinea Pigs[1]

A, black female from whom ovaries were removed for transplantation; *B*, albino into whom ovaries from black *A* were transplanted; *C*, albino male crossed with *B*; *D* and *E*, two of the black young produced from the cross

from each other, for not only are both of these entities integral parts of the united individual but they are also constantly influencing one another, as well as being subjected, in parallel fashion, to similar external agencies of stimulation.

[1] From Castle's *Genetics and Eugenics,* fourth revised edition. By permission of Harvard University Press, publishers.

An examination of organisms shows that the reproductive organs come intimately into contact with all the other organ systems of the body, and therefore it is almost impossible to avoid the conclusion that from the very beginning the bodily and reproductive elements exert an influence upon each other. In the light of this, the parallel inductionists assert that it is ridiculous to think of an organism as being divided into two more or less arbitrary divisions — soma and germ. They insist not only that these are integral portions of a single unified organism, but also that they are subject to similar influences. To some limited extent even the Weismannians have been forced to forsake the strict interpretation of the germ-plasm conception and to postulate a parallel-induction point of view in interpreting the effects of the environment on the evolution of certain adaptive structures of organisms. They admit that they cannot account for such changes unless they assume that environmental influences have exerted a parallel effect on both somatic and germinal structures, inducing them to become modified in parallel directions.

The chief argument of the parallel inductionists may be stated as follows: If a stimulus acts on some somatic structure so as to modify it, and at the same time the reaction resulting therefrom produces a certain chemical substance which, liberated into the circulatory system of the organism, comes in contact with the germinal elements, then permanent modifications may be engendered which will show up in future generations. Another expression of the parallel-induction view is that if the organism affected happens to be pregnant, then a stimulus might influence, in parallel fashion, the same structure in the developing embryo as well as its germinal determiners for the particular structure, thus leading to a permanent modification in succeeding generations.

It is a debated question whether all bodily changes act in the manner outlined. Some undoubtedly produce local transformations which would not be severe enough to produce the chemical messengers necessary for corresponding

changes in the determiners of the germ cells. Then again many modifications are so slight that during the lifetime of the average individual they would produce such a small change as hardly to be noticed; but is it not conceivable that if the stimuli which engendered these seemingly slight transformations acted over a tremendous period of time, say a thousand years or more, they might perhaps be the means of inducing permanent modifications?

It must be admitted that if the effects of the various stimuli of the environment on species are disregarded, then it becomes increasingly difficult to explain adequately the evolution of species. Immediate factors of the environment, such as temperature, pressure, humidity, aridity, and the like, can be controlled in our modern laboratories, and therefore experiments to test out the effects of these agents on living organisms can be undertaken easily. On the other hand, no one has as yet been able to imitate nature so as to conduct continuous laboratory experiments with these factors running over a very long stretch of time, say hundreds or thousands of years. This makes our problem exceedingly difficult, and therefore it is impossible to state what transformations have been produced in organisms by certain of the environmental stimuli acting over the long periods of time in which the earth has undergone its cycles of development.

In passing, it must be pointed out that modern genetics now places its emphasis on mutations as the changes responsible for modification of organisms in one direction or another. Since the beginning of the present century, mainly because of the work of the Dutch botanist Hugo De Vries, many geneticists have been studying mutations, and have indicated the origin of such transformations in a large number of plants and animals. As will be seen in later discussions, particularly in Chapter XIV, mutations are distinct changes resulting from various chance rearrangements of the physicochemical system within the cell, especially the germ cell. But what the stimuli are that induce mutations is a question which as yet is hard to answer.

Retrospect and Prospect

The relationship existing between that which has already been considered and that which is to follow will now be indicated. Our discussion began, in Chapter I, with a consideration of what constitutes the subject of genetics, as well as its importance. There it was learned that heredity is of primary consideration for an understanding of the principles of genetics. In the present chapter the theories accounting for heredity were reviewed, and also the methods of explaining the origin of the characters of organisms. Then these were appraised from the standpoint of the evolution of varieties and species. Toward the end of the chapter the question was raised as to what part the various internal and external factors of the organism played in the evolution of characters. In Chapter III, where inheritance of characters is considered, particularly the so-called acquired characters, the evidence for and against such factors is appraised.

Following the consideration of the inheritance of acquired characters, the modern theory of the cellular basis of inheritance is developed in chapters dealing with the cell (Chapter IV), the germ cells (Chapter V), and the determination of sex (Chapter VI). Since sex is dependent for its expression on specific factors within the chromosomes of the germ cells, the natural question which arises is, Why not the other characters of the organism?

In the following chapters, Chapters VII and VIII, the recent work on twins and monsters is considered for the purpose of showing that even though heredity is a matter of combination of entities within the chromosomes of the germ plasms of the gametes, yet environmental and glandular factors may be of equal importance with the hereditary ones in directing the course of development.

Fundamentally, however, the basic entities for the emergence of traits are present within the chromosomal complex of the germ cells, and the chief reasons for this belief are summarized in Chapter IX, entitled "The Immortal Germ

Plasm." Incidentally this lays the foundation for Chapters X–XIII, dealing with Mendelian principles of heredity, the gene hypothesis, sex linkage and nondisjunction, and linkage and crossing over. These considerations of heredity are followed by a chapter on variation and its importance in the origin of varieties and types of organisms (Chapter XIV). In Chapter XV there is an appraisal of the different methods of breeding practiced by geneticists and practical breeders. The final chapters of the volume, Chapters XVI–XIX, are devoted to discussions of heredity as applied to man, including, among other things, such topics as the history, aims, and program of eugenics.

CHAPTER III

Inheritance of Acquired Characters

THE traits, or characters, of organisms are the chief things with which genetics is concerned. How traits originate, which ones are transitory and which are permanent, which ones are transmitted from one generation to the next, and particularly how new characters arise to supplant the older ones, are all questions more or less involved in the topic of the inheritance of acquired characters. In Chapter II the various theories of heredity were considered, and also the different schools of heredity — each attempting to explain the manner in which traits originate — were outlined. In the present chapter the hereditary rôles played by characters acquired by organisms will be outlined more completely. It must not be forgotten that such considerations are largely an outgrowth of discussions between the Neo-Lamarckians and the Weismannians.

By an *acquired character* is meant a trait which originates in some bodily structure during the normal course of the existence of an organism. According to Weismann, it is a bodily modification which does not have its origin in the germ cell and therefore cannot be transmitted to offspring. In this connection it must be recalled that prior to the time of Weismann the idea that acquired characters were inherited was universally accepted. The French biologist Lamarck, more than any other individual, called attention to the somatic modifications produced through the use or disuse of bodily structures; these he believed to be inherited. On the basis of such inheritance, he propounded his theory of the evolution of the various traits possessed by species. Charles Darwin espoused Lamarck's point of view and developed the conception of pangenesis to explain the man-

ner in which acquired characters were transmitted to offspring. It remained for Weismann to question seriously the Lamarckian viewpoint by means of a series of extended experiments on mice, in which he seemed to show quite conclusively that somatic modifications which were acquired during the normal lifetime of the parent were not transmitted to the offspring.

Weismann's experiments so completely negated all the existing evidence for the inheritance of acquired modifications that since his time biologists have viewed with skepticism all new claims in this direction. Within the last few years, however, the question has been attacked with renewed vigor, and many workers have been trying to bring forth conclusive experimental evidence to show that such cases of inheritance are common in nature and also that they play a very important rôle in evolution. No attempt will be made to give an exhaustive account of the work along this line; only a few of the more striking experiments will be indicated.

Mutilations

By a mutilation is meant some transformation through physical means of the normal structure or appearance of some part of an organism. Numerous attempts have been made in recent times to modify organisms through mutilating various parts of the body. Breeders of animals have been docking the tails of dogs, cats, lambs, and other animals for many years, and these operations seemingly have had no influence on the offspring. As will be recalled, Weismann's experiments on the tails of mice produced no effect on the following generations. But one need not consider only such experiments on the lower forms, for many branches of the human family have been mutilating various parts of the body, for countless ages, without any apparent effect on the offspring. Instances of this sort which may be mentioned are circumcision among different Semitic races; modifications of the face, forehead, scalp, and other portions of the body by

numerous barbaric tribes; the binding of Chinese women's feet; and so on. In none of these cases have the modifications appeared to have left any permanent effects on the race.

During the latter part of the nineteenth century, the Brown-Séquard experiments were hailed enthusiastically by some biologists as good examples of the inheritance of acquired characters. In these experiments the nervous systems of guinea pigs were mutilated, particularly by cutting the spinal cord or the sciatic nerve of the hind limb, and this seemed to induce such abnormalities as epilepsy and eye defects. When these individuals reproduced, it was found that some of the young revealed the same afflictions as the parents; and these transformations appeared without any further treatment. Brown-Séquard therefore came to the conclusion that these were cases of the inheritance of acquired modifications. When investigators carefully checked up on these experiments, they found that such animals as guinea pigs seem to have a normal predisposition to epilepsy, eye defects, and other abnormalities, and that in many instances the cutting of the nervous structures was unnecessary to produce the effects observed.

When all the evidence in regard to mutilations is examined carefully, it seems safe to conclude that, in general, these modifications do not seem to have any effect on the germinal constitution of the organism, and therefore it is doubtful whether any of them are ever inherited. Of course there are species of animals in which some of the modifications which have been mentioned are normal germinal traits, such as short tails and epilepsy, and where this happens these traits are found to be hereditary, being transmitted to future generations in a manner similar to other hereditary characters.

Use and Disuse

According to the theory of acquired characters, the use or disuse of structures is believed to have produced definite effects which are in the nature of acquired modifications of

the germ plasm. These are supposed to be inherited. It must not be forgotten that Lamarck built up his entire conception of the origin of traits on the basis of the use and disuse of various portions of organisms. Using a structure emphasizes it, and in some manner this increased efficiency becomes incorporated into the germ plasm to be transmitted to the next generation. The disuse of a portion causes atrophy and the dwindling of the part, with the result that this modification likewise is transmitted to the next generation. A number of investigators have attempted to bring forth proof of acquired modifications and their inheritance, asserting that many of the structures of organisms, including man, owe their origin to use and disuse. For example, Darwin, Romanes, and others cite the instance of the thickening of the skin on the sole of the human foot as a case of such inheritance. The argument is that the pressure produced through the use of the feet has thickened the skin on the soles and gradually this trait has become a part of man's normal inheritance. An examination of the foot of the human fetus from five months upward distinctly shows that the skin is thicker on the sole than on the reverse side.

FIG. 10. Callosities on the Foot and Ankle of an Ostrich Chick Shortly before Hatching[1]

A number of years ago Duerden (*Bi. 56*) published a paper in which he indicated that the ostrich has developed callosities on those portions of the body which come in

[1] After Duerden, courtesy of the *American Naturalist.*

contact with the ground and concluded that these modifications must be inherited traits because they are found present in all the embryos before they hatch. Fig. 10 shows callosities on the foot and ankle of an ostrich chick a few days before hatching. Duerden's argument is that the callosities undoubtedly first were developed through the agency of use, but after many generations of the appearance of the character, it finally became incorporated into the hereditary mechanism of the species. Other biologists object to such an interpretation and account for this and other similar variations by assuming that selection weeded out those individuals which did not possess the character, leaving only those forms to survive which happened to have it. Gradually more and more individuals showed the trait, until it became the normal thing for the entire species.

Effects of Environment

By environment is meant such agencies as climate, food, chemicals, and all other similar stimuli which surround the average organism. The various factors of the environment are supposed by many biologists to have evoked in organisms definite transformations which have been inherited. This has been the case particularly where the environmental stimulus has been slow, persistent, and lasting over a long stretch of time. In recent years numerous biologists have been studying the effects of the various agencies of the environment upon different organisms. In some of the single-celled animals, the Protozoa, biologists have succeeded in showing experimentally that surroundings can induce permanent changes which are inherited. Here, however, conditions are somewhat different from those in the higher forms because, as a rule, there is no segregation of somatic and germinal structures. The entire organism invariably participates in reproduction, which is accomplished through the asexual process of direct division. Therefore, if a modification sets in, it will be transmitted directly to those individuals formed

from the portion affected, whereas the other individuals will be minus the change. It is significant to note that when the transformed organisms were brought back into the normal environment and kept there for a long period of time, they did not seem to lose the modifications induced. In higher organisms, those that reproduce sexually, the situation becomes more complicated, and it is questionable whether changes in the environment bring about transformations within bodily structures which become permanent acquisitions through heredity. Before rendering a verdict it is necessary to consider some of the more striking experiments in this direction.

Climate

A great many biologists believe that the factors of climate (moisture, temperature, amount of light, and so forth) have a great effect on organisms and that the results which they induce are inherited. This is largely the view of historians and geographers, who assert that the temperaments, dispositions, and cultures of the different races of people that populate the earth have been molded directly by climate.

Many experiments have been performed to test the effects of temperature and light on organisms. The German botanist Nägeli, years ago, took Alpine plants, which are rather short and stocky, with thick, hairy skins, and transplanted them to the Munich Botanical Gardens, where the temperature was warmer, and soon they changed to look like different forms, the individuals becoming much taller and their leaves possessing much thinner skins. So long as the plants remained in Munich their offspring showed the changed appearance, but when they were transferred back to Alpine soil, they soon reverted to their original state and again took on the Alpine appearance. Certainly this cannot be claimed to be a case of the inheritance of acquired characters!

Sumner's experiments (*Bi. 200*) on white mice may also be cited in this connection. White mice were kept in cold and in warm rooms. Those kept in the cold developed shorter limbs and tails than those kept at ordinary room tempera-

ture. When the modified animals were transferred to rooms with normal temperature, their offspring showed, for three following generations, similar transformations of the limbs and tails. In the fourth generation, however, conditions were reversed, and the resulting organisms had as long tails and limbs as the untreated ancestors. This also does not appear to be a case of inheritance of acquired characters but, rather, a temporary change due to the environment. The transformations lasted for only a few generations, and so the problem remains whether the transformations would become permanent if the environmental stimulus or stimuli which first invoked them persisted for a very long stretch of time — say many hundreds or thousands of years.

Tower (*Bi. 202*) subjected potato beetles to changes of temperature and humidity and obtained modified individuals with different pigmentation. He argued that the environment was responsible for modifying the germ cells, whereas others have questioned his interpretation.

Fischer (*Bi. 73*) subjected butterflies and moths to low temperatures and found that they became darker. The offspring from these, when raised under a normal environment, were like the parents, darker in color, and therefore he argued that this was a case of inheritance of an acquired character. It has been pointed out, however, that the color of these insects varies considerably under normal conditions, so that it is not clear whether the color changes were mere coincidences or actual permanent modifications were induced. In fact, some investigators have shown that these same modifications in color can be produced when the developing insect larvæ themselves are exposed to different degrees of temperature, or when their pigments are extracted into a test tube and subjected to heat or cold. This seems to indicate that it is the soma rather than the germ that is modified.

In this connection must be mentioned the work of the Austrian biologist Paul Kammerer, as it has been given a great deal of publicity and has attracted considerable attention. Kammerer subjected various animals, such as salamanders,

toads, lizards, and the like, to radically different conditions of the environment, especially those of light, temperature, and humidity. He has reported induced modifications that persisted to a marked degree in succeeding generations under normal conditions. Only a few of his experiments can be discussed here. For a fuller treatment the reader is referred to Kammerer's *Inheritance of Acquired Characteristics* (*Bi. 125*).

Kammerer also subjected the European salamander, *Salamandra maculosa,* commonly called the spotted or fire salamander because its normally black skin is covered with brilliant yellow spots, to changes in the color and temperature of its environment and found that some of the offspring were modified. Those which were placed on a yellow background developed larger patches of yellow, whereas those placed on a dark background lost many of their brilliant yellow spots and became more uniformly dark in appearance.

In some other experiments Kammerer dealt with the reproductive habits of these same salamanders, *Salamandra maculosa,* in which the fertilized eggs normally develop within the females for a considerable period of time, and then are deposited in water as larval forms with well-developed, functional gills for breathing purposes. Here they continue to transform for a period of several months until they reach their adult appearance, when they migrate to land, lose their gills, and develop lungs for air-breathing purposes. By preventing these adults from coming in contact with water for several generations, Kammerer forced them to take on the characteristics of the Alpine, land-dwelling species, *Salamandra atra,* in which fewer young are produced and these are retained within the females for a longer period of time, so that when they are actually born they possess dwarfed gills and functional lungs, making it possible for them to live on land right from the start. Moreover, these modifications were retained and inherited by some of the offspring, even though the animals were returned to their normal moist surroundings. The significant thing in regard to these experiments is that the young, although deposited in the water, remained there

for an insignificantly short period of time, a few days at the most, and then migrated to land to lead a terrestrial existence, similar to that of the Alpine species mentioned.

In other experiments Kammerer reversed the conditions which have been outlined, forcing the normally land-dwelling Alpine species, *Salamandra atra*, to change over until it resembled *Salamandra maculosa*, in which a larger number of

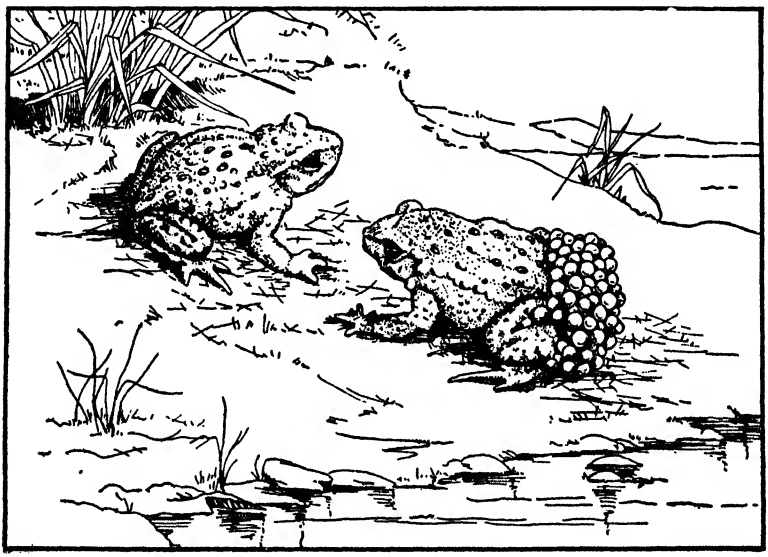

FIG. 11. The Midwife Toad, *Alytes obstetricans*

After the female lays the eggs, the male attaches them around his body near the thighs, where they are carried until they are hatched. Daily the male migrates to the water's edge to moisten the eggs. The female is the specimen without the eggs

young are produced and these are deposited in water, where they continue to develop for a number of months before they become permanent land-dwellers. Here also Kammerer claimed that the acquired modification persisted in many of the offspring.

One of the most interesting of Kammerer's experiments concerned another amphibian, the midwife toad, *Alytes obstetricans*, which does not deposit its eggs in water, but on land. These become attached to the upper portion of the

hind limbs of the male, where they undergo development until they are tadpoles (Fig. 11); from then on their further progress is in water and is similar to that of other tadpoles. This peculiar habit of the midwife toad, of depositing its eggs on land in contradistinction to most other Amphibia, has modified the male to the extent where the so-called *nuptial pads* on the first toes of his fore limbs, which ordinarily are used for the purpose of clasping the female during reproduction, have dwindled to inconspicuous structures with little or no pigmentation. By increasing the temperature considerably, Kammerer forced the midwife toad to take to the water, where it gradually acquired the habit of mating and depositing its eggs like ordinary water-dwelling forms. The eggs remained freely extended in the water and underwent development without being first attached to the lower limbs of the male. At the same time the males themselves showed ordinary mating behavior, and soon developed the instinct of clasping the females. Gradually the nuptial pads became more prominent, increasing in size as well as becoming darker in color, due to an increase in the pigmented areas. Kammerer described these new acquisitions in the following words (*Bi. 125*):

> Possibly to be better adapted to the more difficult seizing of the female in the water, the male of this, and, to a certain extent, the male of a previous, generation also develop a rough blackish nuptial pad on their fingers and forearm. Besides, the muscles of the arm are strengthened, which in turn results in giving the fore limbs a more converging position. All these are exterior sex characteristics, to be found in all frogs and toads, which mate in the water, but are ordinarily not to be observed on the midwife toad, which normally mates on land.[1]

The modifications which these animals acquired not only seemed to persist but became intensified in following generations. Kammerer therefore concluded that they were examples of the inheritance of acquired characters.

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[1] Paul Kammerer, *Inheritance of Acquired Characteristics*, pp. 53–54. Boni & Liveright, New York, 1924.

Kammerer's experiments, although suggestive, nevertheless aroused considerable skepticism in the minds of many scientists. An American biologist, G. Kingsley Noble, Curator of Amphibians and Reptiles in the American Museum of Natural History, New York City, who happened to visit Kammerer's laboratory, had an opportunity to see some of the animals with which the Viennese biologist was experimenting, particularly the salamanders and toads. Upon carefully examining the midwife toad, he found that while the nuptial pads in the male had increased in size, the darker pigment areas were the products of the artificial injection of some dark coloring matter under the skin. This fact immediately threw suspicion on all Kammerer's experiments. Shortly after this incident, Kammerer wrote a pathetic letter to the officials of the Moscow Academy of Sciences, which was later published in *Science*, in which he denied any knowledge of the falsification of his experiments, declaring that someone in his laboratory must have played a trick on him, probably for spite. Kammerer soon afterwards committed suicide.

In passing, it must be asserted most emphatically that an individual who would falsify his experimental results has no place in science. Inasmuch as the facts in Kammerer's case seem to warrant such a conclusion, his work must be viewed with considerable skepticism. In spite of all this, there are some biologists who are convinced that Paul Kammerer was honest in his efforts, and they are willing to accept the major results which he obtained. In any event, Kammerer's experiments were stimulating and suggestive. Some scientists have advocated the appointment of an impartial board of investigators to repeat these experiments under controlled conditions, for the express purpose of proving or disproving the validity of Kammerer's contentions.

Chemical Substances

A number of biologists have surrounded organisms or injected them with certain substances in order to observe whether the modifications induced were inherited. Some have

fed certain organisms, particularly guinea pigs, poultry, and caterpillars, with Sudan red III, and found that this coloring material was deposited in the yolk of the eggs, so that when the young developed, their cells were tinged with a typical reddish hue. However, this change cannot be claimed as an instance of the inheritance of an acquired modification because the coloring matter was deposited in all cells of the organisms experimented with, both body and germ cells alike. When such germ cells participated in the reproduction of new

FIG. 12. The Effect of Alcohol on Guinea Pigs

Two male guinea pigs of about the same age. The runt at the left, weighing 132 grams, was the product of an alcoholic father and a normal mother. The guinea pig at the right, weighing 221 grams, was derived from normal parents. (After Stockard, courtesy of *Journal of Heredity*)

individuals, they merely brought the dye in with them, thereby transmitting the same color characteristic to the offspring. Moreover, the character did not appear much beyond one generation, decreasing in intensity and soon disappearing entirely.

Stockard and Papanicolaou (*Bi. 196*) exposed guinea pigs to alcohol fumes and found that for about three generations following exposure defective offspring were produced. The fourth-generation offspring, however, while fewer in number than those in litters from normal parents, were entirely normal and showed none of the defects. Undoubtedly the alcohol injured many of the germ cells, thereby producing deficient offspring, which again gave origin to weak germ cells, and these, in turn, developed defective individuals (Fig. 12).

Raymond Pearl (*Bi. 165*), on the other hand, subjected fowls to the effects of alcohol and found that no defective offspring were produced. In reality, the resulting individuals, while fewer in number than those from untreated parents, were on the whole larger in size and more vigorous in constitution. Here the alcohol seemed to kill off the weaker germ cells, leaving the more vigorous ones to survive and participate in reproduction.

Following Pearl's experiments, Stockard and Papanicolaou (*Bi. 197*) reinvestigated their earlier results on the effects of alcohol on guinea pigs and came to more or less the same conclusion as Pearl, that alcohol injured and ultimately killed off the weaker germ cells, leaving the more vigorous ones to participate in reproduction. In some animals, frogs, for instance, the reverse seems to be true, the alcohol killing off many of the normal germ cells and, at the same time, stimulating the weaker ones to greater activity, so that in later generations a larger number of defective offspring are produced than ordinarily.

Cole and Bachhuber (*Bi. 26*), of the University of Wisconsin, studied the effects of lead poisoning on rabbits and fowls, and found that this element caused injury to the germ cells, thereby accounting for the production of weak and defective offspring. Other investigators have indicated similar effects on human individuals with lead, sulfur, and other poisonous substances.

In line with this work must be mentioned the experiments of MacDougal (*Bi. 136*), botanist of the Carnegie Institution, who injected metallic salts directly into the ovaries of evening primroses, thereby modifying them permanently in one direction or another. By this means lasting changes were produced, and these were inherited without further treatment. The advocates of the theory of inheritance of acquired characters sometimes cite MacDougal's experiments as illustrations of such transmission, but when the facts are examined critically, it becomes obvious that such a conclusion is not warranted, inasmuch as no changes were first

induced in any bodily structures which, in turn, were the causal factors responsible for bringing about any of the permanent modifications within the germ cells. The transformations were engendered by injecting the chemical solutions directly into those structures of the plants which contained the germinal material, the treated plants themselves showing no visible differences whatsoever. Of course, it is highly significant that by this method permanent modifications may be invoked in species of organisms.

Antibodies

Since MacDougal's experiments some geneticists have been wondering whether certain changes in bodily structures may not also, at times, be the means of producing definite internal reactions, with the resultant manufacture of certain entities which, when circulated within the body so as to come in contact with the germ cells, could induce, in similar fashion to the metallic salts, permanent modifications in the germinal determiners for the respective characters in question. It seems logical to assume that this has occurred in the past, leading to the production of many types of organisms.

Perhaps the most important research along this line has been conducted by Guyer (*Bi. 96–98*) and by Guyer and Smith (*Bi. 99–101*) at the University of Wisconsin. It was based largely on a certain fact well known to biologists, — that if toxic substances or injurious organisms invade an animal, almost immediately certain reactions are set up within its body and an attempt is made to counteract the injurious effects by building up chemical entities known as *antibodies*, which can then act on the invaders and either destroy them or reduce their harmful effects. In doing this the body becomes accustomed, or, as we say in biology, becomes *sensitized*, to the invading entities, and at the same time it also builds up a resistance toward them that stands it in good stead in case other similar invading organisms ever enter it again. We say, technically, that the body has built up an *immunity* to the specific injurious substance in question.

Another very well-known fact which has been established is that when any foreign tissue is injected into the body, it evokes responses similar to those following the injection of toxins or bacteria. At first the treated organism becomes sick, but soon it develops antibodies, called *cytolysins*, which act on the invading structures and attempt to destroy them. From the facts revealed by the above studies, it becomes evident that the body builds up not only antitoxins but also cytolysins for the purpose of destroying certain invading substances.

Guyer and Smith, being aware of these principles, undertook to solve the problem whether, by injecting a certain tissue (say that of the lenses of the eyes of rabbits), they could produce parallel modifications in the lens tissue of the adult eye and also in the germinal determiners of the reproductive cells responsible for the development of lenses, so that when these germ cells participated in the formation of a new individual they would bring the entities for defective lenses with them. In other words, the experiment resolved itself into discovering whether similar parallel changes can be produced in both somatic and germ cells. The chief reasons why Guyer and Smith picked out the lens of the rabbit's eye for experimentation were, first, because they desired to work with a structure that apparently was normal; and second, because they wished to use a structure in which any transformations that should arise could be seen easily. Upon carefully questioning a large number of rabbit-breeders, they learned that the lens of the eye was, on the whole, considered to be a very normal, resistant, and stable structure, so that in case any modifications were set up within it they could be detected readily with the naked eye.

In their first experiments the Wisconsin investigators took the lenses of rabbits' eyes, pulped them up in a weak salt solution, and then injected the mixture into the circulatory systems of chickens. Some of these animals became very sick and died, while others recovered and soon accustomed themselves to the injections. Guyer and Smith then killed

some of the latter chickens, bled them in order to procure the clear liquid of the blood, the serum, and injected this into female rabbits shortly after they had been mated to normal males. When the litters of rabbits were finally born and examined, some of them were found to possess defective eyes. In later experiments the investigators dispensed with the chickens, injecting the pulped-lens extract directly into pregnant adult rabbits, and obtained exactly the same results.

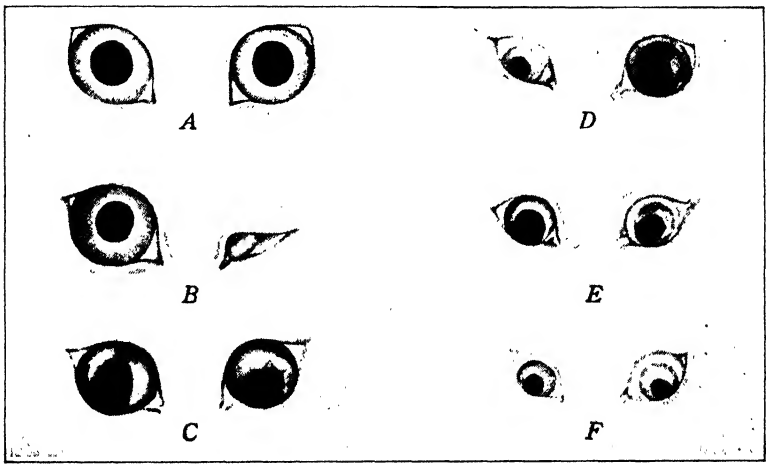

FIG. 13. Normal and Defective Eyes in Rabbits

A, normal pair of eyes; *B–F*, pairs of eyes showing induced defects. (After Guyer and Smith, courtesy of *Journal of Experimental Zoölogy*)

As mentioned previously, before Guyer and Smith began their experiments, they made an exhaustive investigation concerning the eye defects of rabbits and found that a large number of rabbit-breeders all over the world had never noticed such eye defects in normal stock. They therefore concluded that the malformation was not the outcropping of a covered-over racial defect, which remained hidden and dormant, but rather the appearance of a newly induced defect.

After modification the eye itself looked dwarfed, with that portion of it in the vicinity of the lens highly defective,

so much so that in many instances the lens itself appeared to be liquefied (Fig. 13). The interesting thing about this defect is that when it is once induced, it reappears, generation after generation, without further treatment. Moreover, it crops out in an increasing number of individuals — becoming intensified rather than showing a tendency to diminution.

The question which naturally arises is, What has actually happened here? Did Guyer and Smith first produce a modification in the eye of the adult animal and this in turn cause the formation of certain entities in the circulating medium, which when they came in contact with the germinal determiners for the structure in question, induced them to change in a similar direction? Or, if they did not alter the adult eyes, did they produce a stimulus which modified the eyes of the developing young in the placenta and at the same time also induced alterations in the eye-producing determiners within the germ cells of the young? The second explanation appears to be the more plausible one, namely, that of a parallel induction of a similar modification in both somatic structures and their corresponding germinal determiners. In order to test whether a temporary injury or an actual permanent modification in the germ cells had been produced, these investigators took two normal-appearing adults of opposite sex, derived from their treated strain, and mated them together. When the young were born and examined carefully, some of them showed defective eyes, indicating that the germ cells themselves had been permanently modified so as to carry the determiners for the induced trait. In another cross a normal, untreated female was mated with a normal-appearing male derived from the defective strain, and some of the offspring possessed defective eyes.

In later experiments Guyer (*Bi. 96*) needled the lenses of the eyes of adult rabbits and, after mating them, found that some of the offspring showed various eye defects similar to those induced through the injection of serum sensitized to rabbit lenses. These experiments have not been carried far enough to be conclusive, but if they should prove to be relia-

ble, they would afford important evidence for the inheritance of induced somatic modifications. In any event, regardless of the interpretation, there does not seem to be any doubt that Guyer and Smith have induced a defect which has been inherited. Both of these investigators are inclined to interpret their results as merely another case of parallel induction, in which the stimulus has modified the eyes of the young while undergoing development within the membranes of the mother and, at the same time, has also brought about a corresponding modification within the determiners of the germ cells of the embryos responsible for the expression of the somatic structures in question. In passing, one must remember that those who advocate the parallel-induction view believe that it is at least one method, and an exceedingly important one, which accounts for the acquisition of new traits by organisms.

In contrast to these results it must be pointed out that numerous investigators have attempted to repeat the experiments and have been uniformly unsuccessful. Furthermore, since Guyer and Smith's experiments, some investigators have succeeded in showing that in rabbits occasionally defective-eyed individuals are born to normal parents. They are therefore of the opinion that Guyer and Smith have possibly uncovered a defective trait which, while it is a part of the normal heredity of the rabbit, nevertheless has been covered over effectively by other hereditary factors.

In this connection attention is called to the recently published paper by Ibsen and Bushnell (*Bi. 119*), in which are described the results obtained in attempting to repeat Guyer and Smith's experiments. While these investigators noticed some eye defects in treated stock, nevertheless their percentages were much lower than those obtained by Guyer and Smith. Not only that, but they also found that untreated stock gave several instances of similar eye defects; when these results were tabulated, it was noticed that the difference between the per cent of defectives in the treated and in the untreated stocks was negligible. Ibsen and Bushnell

therefore concluded that it was not at all certain that the treatment received by the animals was instrumental in inducing the abnormalities observed.

Because of such apparent contradictions as these, geneticists are holding in abeyance their judgment in regard to Guyer and Smith's investigations until further proof is obtained.

Before dismissing these researches mention must be made of Griffith's experiments (*Bi. 94*), in which he rotated adult white mice in revolving cages in a horizontal plane, and found that they developed peculiar twisting movements of the body, particularly the head, which seemed to be inherited by some of their offspring. These investigations were conducted from a psychological, rather than from a genetic, point of view, but in order to increase the rat colony many of the rotated individuals were mated together so as to have larger numbers available for experimental purposes. A careful examination of the parents revealed that the rotation produced a defect of the ear, invariably showing itself by a swelling around the organ, as well as a discharge of secretion from it. Since some of the young born to these parents showed similar defects, Griffith interpreted the phenomenon as a case of inheritance of an acquired modification and explained it on the same basis as did Guyer and Smith. Griffith's argument was that rotating the animals not only disturbed their inner ears to the extent where these structures became defective, but also led to the manufacture of certain entities which found their way into the circulating medium and on reaching the germ cells singled out the determiners responsible for the expression of the inner ears and modified them in a like direction. In criticism of these results it must be pointed out that other investigators, notably Detlefsen (*Bi. 49*), carried on similar experiments with white mice, and while they obtained results comparable to those of Griffith, nevertheless they also succeeded in showing that white mice were normally subject to afflictions of the ear and that rotation was not necessary to produce any of the defects observed.

Congenital Diseases

By a *congenital* disease is meant one which originated in the parent and has been transmitted to the offspring through the medium of infection while in its embryonic state, still surrounded by the fetal membranes within the uterus of the mother. An example of such a disease is syphilis. Instances of congenital diseases are often cited as cases of inheritance of acquired characters. When they are examined critically, it is found that no heredity of weakened structures or dispositions toward disease are involved similar to the cases discussed in Chapter XVII. As pointed out above, congenital diseases are due to direct infections of the embryos through the medium of one or both of the parents who possess the diseases. Although the factor of heredity may not be involved in congenital diseases, yet these maladies may be the means of inducing just as serious malformations and disturbances within the body as any of the ordinary diseases which depend for their emergence on hereditary dispositions.

Effects of Training

A number of years ago the distinguished Russian physiologist Ivan P. Pavlov (*Bi. 164*) startled the biological world by publishing a paper entitled "New Researches on Conditioned Reflexes," in which he tabulated the results of the process of teaching mice to come for food upon hearing the ringing of a bell, and the inheritance of this conditioned acquisition.

Before giving these results it must be pointed out that reflexes are of two kinds: *inborn* and *conditioned.* Inborn reflexes are those which are part of the racial heredity of the organism; that is, they are born with the individual. Conditioned reflexes, on the other hand, are those which are acquired during the normal lifetime of an individual. Pavlov tried to teach mice to come to meals at the sound of a bell. By training and inbreeding the individuals, he claimed that he actually obtained five successive generations of individuals who responded more and more rapidly to rings of the bell, so

that the last litter of mice came to meals in a very much shorter time than the original animals with which he started. Pavlov believed that he was dealing with a conditioned reflex that was first acquired and then inherited. The following tabulation shows the results which he obtained:

Generation	Lessons Required, to Respond
First	300
Second	100
Third	30
Fourth	10
Fifth	5

Pavlov gave very few details regarding the experiments, and many geneticists viewed them with considerable skepticism. Everybody was looking forward with anticipation to finding out how the mice behaved in the sixth generation, but nothing further in regard to them was forthcoming. At the International Physiological Congress in Boston in 1929, Pavlov, who attended as a delegate, was questioned concerning these experiments, and, much to the disappointment of the out-and-out Lamarckians, he withdrew his first contentions, asserting that the chief cause for the improvement in the learning ability of the mice was really due, in large measure, to the improvement in the teaching ability on the part of the investigator.

The results of experiments of a similar nature to those of Pavlov have been announced by the psychologist William McDougall (*Bi. 137, 138*). This investigator trained rats to escape from a water tank through certain well-defined channels, and maintains that the effects of this training were inherited by the offspring that followed. After being thrown into the tank, two avenues of escape were open to the rats, one brightly illuminated and electrified, and the other darkened and nonelectrified. A rat that chose the illuminated exit would receive a shock, whereas if it chose the darkened one, it would escape unmolested. The training process continued for something like twenty-three generations, and by

keeping accurate data McDougall showed that it took not only less time to train the later generations to escape through the correct exit, but also that the time period required for them to escape from the tank was diminished considerably.

McDougall's experiments have been repeated extensively by F. A. E. Crew (*Bi. 34*), Director of the Institute of Animal Genetics of the University of Edinburgh, with inconclusive results. His data were presented at the Sixth International Congress of Genetics, held at Ithaca, New York, during August, 1932, and revealed that litters of rats, and in some instances even individuals within the same litter, showed considerable differences in behavior within the tank. Crew summarizes his studies as follows:

> I think that I must try more accurately to classify the rats according to their behavior for I have been greatly impressed by the fact that in one and the same litter one can get two or more different behaviors exhibited and that those individuals who behave alike have scores that are very similar. On the other hand one can get litters of which all the individuals exhibit the same habit in the water, all rushing, all floating, all hopeless or all eager, and then it has been possible to identify the litter to which an individual belonged by reference to the behavior in the tank. It may well be that as this experiment proceeds I shall find myself studying the mode of inheritance not of capacity for learning but of a peculiar behavior pattern. For indeed it would seem to be the case that there are rats that persistently leave the tank by one route, rats that turn to right or left indiscriminately; rats that tend to avoid the light, rats that do not mind it; rats that are quick to associate light and shock, and rats that are slow. It must be my task to examine the possible genetic bases of these attributes which certainly distinguish rat from rat.[1]

Although Crew did not venture any conclusions and McDougall asserted that he did not choose his animals with regard to speed of reaction, others suspect that selection undoubtedly played a very important rôle in the results obtained by McDougall.

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[1] F. A. E. Crew, "Inheritance of Educability," *Proceedings of the Sixth International Congress of Genetics*, Vol. 1 (1932), pp. 133–134.

X-Ray and Radium Effects

By the use of X rays, as well as other rays, various permanent, heritable transformations have been produced in organisms. Hermann J. Muller (*Bi. 148, 149*), of the University of Texas, has been the leader in this field of investigation. By exposing vinegar flies (*Drosophila melanogaster*) to strong emanations of X rays, Muller caused the progeny of these organisms to vary 15,000 per cent more than under normal conditions. These changes have proved to be permanent modifications that are inherited. Figs. 14 and 15 show some of these induced modifications in vinegar flies after exposing them to radium emanations. Other investigators, notably Stadler, Hanson, Goodspeed, Mavor, and Patterson (*Bi. 102, 104, 162, 194*), have obtained similar results in numerous plants and animals. Recently Babcock and Collins (*Bi. 8*), of the University of California, and Hanson and Heys (*Bi. 103*), of Washington University, placed vinegar flies in natural locations where the rate of radioactive emanations was approximately two and a half times as great as in normal surroundings. The California investigators exposed their organisms in a small lateral branch opening off Twin Peaks tunnel in San Francisco, while the Missouri biologists placed theirs in an abandoned carnotite mine in Colorado. When the offspring were examined, it was found that these locations

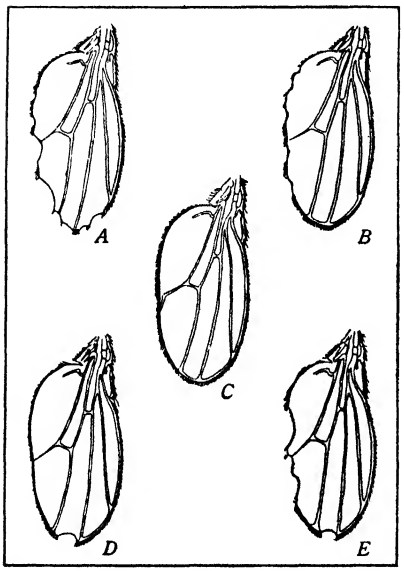

FIG. 14. Mutations in Wings of Vinegar Fly

A-E, five distinct mutations induced by radium emanations. (After Hanson and Winkleman, courtesy of *Journal of Heredity*)

had caused them to vary permanently to about twice the extent of spontaneous variation in normal surroundings.

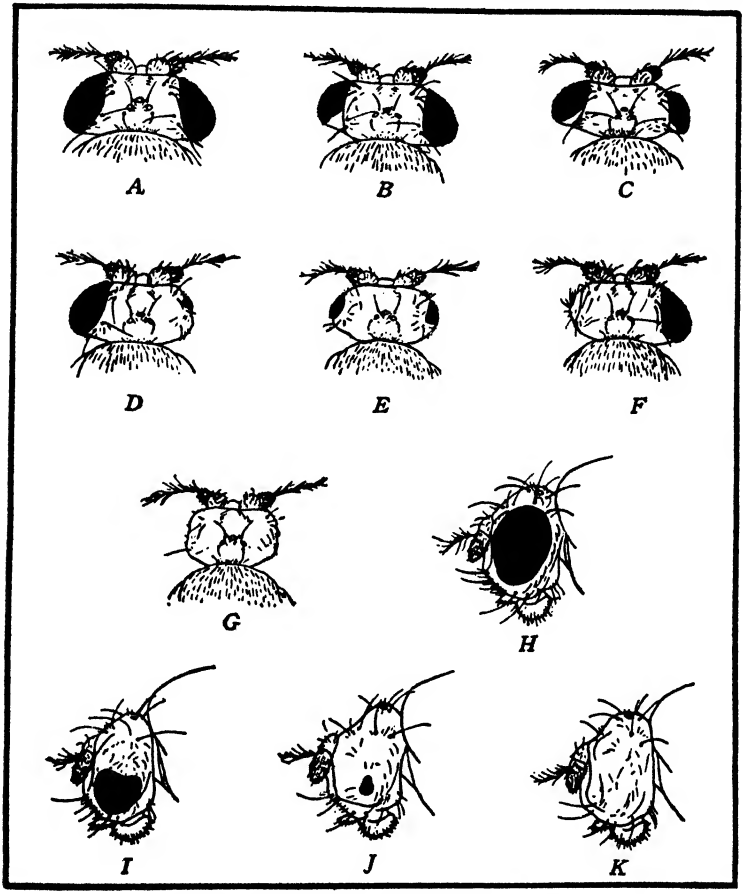

FIG. 15. Mutations in Eyes of Vinegar Fly

A, normal eyes, top view; *B–G*, top views of different eyeless mutations; *H*, normal eye, side view; *I–K*, side views of different degrees of eyelessness. All mutations were induced by radium emanations. (After Hanson and Winkleman, courtesy of *Journal of Heredity*)

Furthermore, all the induced changes were of the nature of mutations, that is, they were germinal modifications, which, once they put in an appearance, came out again in later generations.

In all cases of such experiments the important thing which has been observed is that the rays do not seem to affect the somatic structures, but pass directly through them to act on the germ cells so as to induce permanent transformations in some of the hereditary materials which are carried there. The investigators who have given their time and attention to these experiments are of the opinion that a great many of the permanent changes in organisms, if not perhaps all of them, are brought about in this manner. We know definitely that such emanations as X rays are all around us and that organisms are constantly coming in contact with them. If variations which normally crop out in organisms can be produced experimentally or speeded up by exposure to larger amounts of the rays, why is it not logical to assume that this is the manner in which nature also functions to bring about permanent modifications?

While these experiments on X-ray and radium effects cannot be considered instances of acquired characters in the sense that they first make their appearance in somatic structures, yet they bear on the problem of the origin and acquisition of characters by the organism, because they reveal that certain environmental factors may cause entities in the germ plasm to become modified in such a way as to reveal themselves as changed structures in the offspring. Is it not conceivable, therefore, that somatic changes may at times be the means of producing chemical agents which, when they come in contact with germinal determiners, act in a manner similar to X rays, so as to bring about permanent modifications? It must be admitted that all characters which arise are acquired at some time and in some manner. In closing this portion of the chapter it should be pointed out that this field of research with X rays and other similar emanations is just in its infancy, and we ought to expect some very interesting results from it during the next few years.

Summary

From the foregoing discussions it becomes evident that since Lamarck's time there have been many attempts to show that somatic changes can induce germinal modifications which are inherited. As has been pointed out, when most of the investigations along this line are considered critically, they are found to be either deficient or inconclusive. After Weismann's experiments on the tails of mice and his propounding of the germ-plasm conception, the question of the inheritance of acquired modifications remained closed for a considerable period of time. Within recent years many biologists have renewed interest in the subject and have been attacking the problem from a number of new points of view.

In spite of the fact that there is no more vital problem in all genetics than this one, the results on the whole have been very disappointing. Nevertheless there is no basis for the claim that the arguments in favor of the inheritance of acquired modifications are absolutely without foundation. All that one can say is that up to the present time no one has succeeded in proving such inheritance. In passing, it is well to remember that all variations are really of the nature of acquired modifications, but the question of vital importance is that which concerns itself with the manner in which these acquisitions originate. It is no exaggeration to state that this is one of the most fundamental topics, and that if we can ever solve it adequately, we shall have the answer to the problem of species formation. In reality, this problem concerns every biologist, particularly the geneticist and evolutionist, for it deals with the origin, degree of expression, and permanence of the traits of organisms. Thus far all our attempts at a solution have proved unsatisfactory in one respect or another, so that we are still face to face with the great mystery of how variations originate and, more particularly, how they are incorporated into the normal hereditary stream of the organism.

Detlefsen (*Bi. 50*) ably summarizes the present status of opinion on the question of the inheritance of acquired characters in the following words:

If an opinion must be pronounced, we can say without hesitation "insufficient experimental proof as yet"; but there remain the following grounds for regarding this question with tolerant open-mindedness:

1. The suggestive or circumstantial evidence drawn from the data of embryology, paleontology, and ecology still remains just as suggestive, for we have found in natural selection a formal but not complete cogent acceptable explanation for many hereditary adaptations and cases of high specialization.

2. The alacrity with which the strict Weismannian could postulate "parallel induction" in the face of such meager experimental evidence is a fatal admission that some element of Lamarckism is convenient after all, that is, that evolution is guided directly by environmental change.

3. While no one doubts the effectiveness of natural selection or that its existence is categorically determined by the very nature of things, organic evolution is nevertheless no simple matter but on the contrary an enormously complex process in which natural selection is hardly a cause of variation. The whole concept of evolution has been greatly amplified since its inception by additional important information and points of view derived from intensive biological study, but without any doubt much remains to be discovered.

4. It is conceivable that the experiments devised up to the present time have failed to demonstrate conclusively the inheritance of somatic induction by such experimental evidences as are available; the fact also remains that the results of a number of experiments have not been fully and adequately "explained away."

5. We have accumulated a huge array of important biological facts, but we have not discovered many general laws. Of first causes in evolution we know next to nothing. When we know more about endocrinology, serology, and neurology, then we may hope the inter-relationships between various parts of the organism, the control of development, the basis of adaptive behavior, habit and instinct will be clearer to us. At present, it seems to me more important to recognize the situation than to take a dogmatic position.[1]

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[1] J. A. Detlefsen, "The Inheritance of Acquired Characteristics," *Physiological Reviews*, Vol. 5, No. 2 (1925), p. 275.

CHAPTER IV

The Cell

THOSE who are familiar with the organization of living things know that in the final analysis all organisms may be broken down into those units of structure known as cells. The simplest forms of life consist either of single cells or of many cells organized into a colony, with little differentiation or division of labor. The more advanced forms possess specialization, and here the various parts become highly differentiated in order to participate effectively in the division of labor that makes for the best interests of the species. The cells become arranged as tissues, and these in turn combine to form the organ systems that coöperate in the functioning of the united organism. The cell, therefore, must be regarded as the fundamental unit of organization of all living forms, and as such it is of tremendous importance in genetics. In order to understand the material basis of heredity it is essential that the cell be analyzed for the purpose of finding out what mechanism makes possible the transmission of old characters and the origin of new ones.

Our knowledge of the cell does not go back very far beyond 1838–1839, when two German biologists, Schleiden and Schwann, enunciated the doctrine known as the *cell theory.* This theory asserts that basically all organisms, both plants and animals, are similarly constructed, being composed of the minute units already alluded to, — cells. This conception has proved to be one of the most fundamental in all biology. It has marked an epoch in the history of science. It has given origin to a distinct branch of biology known as *cytology,* which has for its special field the study of the cell. At present cytology is regarded as one of the most important branches upon which the science of genetics rests. In

order to understand modern genetics one must obtain a thoroughgoing understanding of the structure and function of the cell, particularly the reproductive cell.

Importance of the Cell

When the cell doctrine was first enunciated, little was known of the real make-up and function of the various parts of the cell. Most of our knowledge along these lines has developed subsequently, especially during the last sixty years. At the present time the cell is regarded as the vital entity within the organism, from three points of view. In the first place, it is important in *morphology*, the subject that deals with the form and structure of organisms. Biologists realize that the cell is the unit which they must analyze before they can hope to understand the complete living machine. Secondly, the cell is important in *physiology*, the branch of biology that treats of the functions of living things. In the main, the functions of an organism may be said to be the summation of the functions of its individual cells. Therefore cellular physiology is the real key to an understanding of how the various parts of the united organism operate. Lastly, the cell is of great significance in *embryology*, the field which concerns itself with the early development of living forms.

All organisms start out as cells. The higher forms come into being through the medium of specialized reproductive cells, one from the male parent and the other from the female parent, uniting during the process of fertilization to produce the *zygote*, or *oösperm*, a single-celled structure which is the beginning of the individual plant or animal. Each independent reproductive cell loses its identity when it combines to form the single-celled zygote, and the latter structure is then found to possess the necessary capacities for further development into the complete organism. This is accomplished chiefly through the medium of a rapid multiplication and specialization of cells.

Structure of the Cell

Cells are constructed more or less similarly, and therefore to know one cell is to know them all. The following description will not confine itself to the structure of any single specialized cell, but rather will refer to that of a generalized, typical cell (Fig. 16). The living substance of cells is the

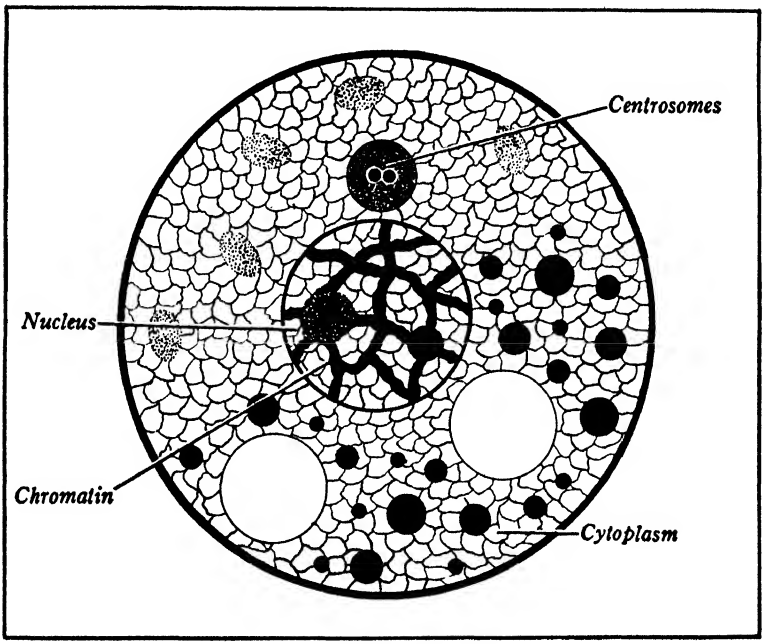

FIG. 16. A Typical Cell[1]

semifluid *protoplasm*. This is specialized in accordance with the need of the particular kind of cell.

Within the interior of each cell, located either near the center or to one side, may be recognized a condensed globular structure, the *nucleus*. This is limited by a distinct nuclear wall and is filled with a liquid material known as the *nuclear*

[1] From Fasten's *Origin through Evolution*. By permission of F. S. Crofts & Co., publishers.

sap. Within this sap may be seen threadlike structures known as *linin,* along which larger masses generally are condensed, which stain heavily with nuclear dyes. This is the *chromatin* material, and, as will be described subsequently, during cell division these chromatin masses become organized into a definite number of distinct bodies, the *chromosomes.*

Surrounding the nucleus, and composing the rest of the cell, is the *cytoplasm,* or, as some biologists call it, the *cytosome.* This also consists of specialized protoplasm, in which are suspended numerous elements of one kind or another, such as vacuoles, yolk, pigment granules, mitochondria, and Golgi bodies. Finally, in every cell of the animal kingdom, and also in those of many plants, especially the lower groups, there is found the *centrosome,* or *centriole,* which may be either a single or a double granule, lying within the cytoplasm next to the nuclear wall. It is surrounded by a condensed mass of material, called the *centrosphere,* or *idiozome.* The combined structure of centrosome and centrosphere are designated as the *central body* of the cell.

Functions of the Cell

The nucelus is looked upon as the dynamic center of the cell. Experiments have indicated clearly that it is the center of all those activities, known as *anabolism,* which have to do with the building up of living matter.

As already mentioned, during cell division chromatin granules become organized into a definite number of chromosomes. Modern geneticists regard the chromosomes as the structures which carry invisible units responsible for the phenomena of heredity and variation. The specific reasons for considering them as such will be discussed in Chapters IX–XIII. These units for traits are called by various names, such as *factors, genes,* or *determiners,* but they are believed to be the cellular representatives which, under the stimuli of development, become organized into the distinctive characters found in the adult forms. In recent years much posi-

tive proof has been accumulated to convince the geneticist that the chromosomes are the vital centers for the transmission of characters, so that he, in common with other biologists, regards the nucleus of the cell not only as the center of anabolism but also as the chief center of individual heredity and variation.

The cytoplasm, or cytosome, is considered to be that part of the cell in which most of the breaking down, or *catabolism*, takes place. This constant flux that goes on in living cells, involving the processes of both catabolism and anabolism, is spoken of collectively as *metabolism*. From the standpoint of heredity, it is believed that the general species characteristics of the organism are determined, to a large extent, by the cytoplasm. Compared with the nucleus, the cytoplasm may be said to influence the racial development of the organism, whereas the nucleus determines its individual development. In reality, both are essential for the normal progress of the organism. This matter will be considered in greater detail in Chapter V.

The central body seems to have no influence on heredity, but in organisms where it is found it appears to have some importance in controlling the motion and division of the cells that carry on the life processes of the individual. In such instances it seems to regulate movement within the cell, playing its biggest rôle during the period of the growth and multiplication of cells.

Types of Cells

In the many-celled organisms, particularly those in which tissues are developed, two general types of cells may be recognized: first, those which constitute the chief organs of the body proper and are grouped under the general heading of *somatic* cells; and second, those which comprise the reproductive glands exclusively and are known as the *germ* cells. The somatic cells make up those structures which play their parts in the feeding, transportation, protection, and responses of the organism. These are referred to collectively

as the *vegetative* structures, and in the many-celled animals they are generally grouped under the headings of epithelial, connective, vascular, muscular, and nervous tissues. Fig. 17 illustrates a few cells in some of these typical tissues of the higher animal. On the other hand, the germ cells are highly specialized units known as *gametes* (Fig. 18), and their only

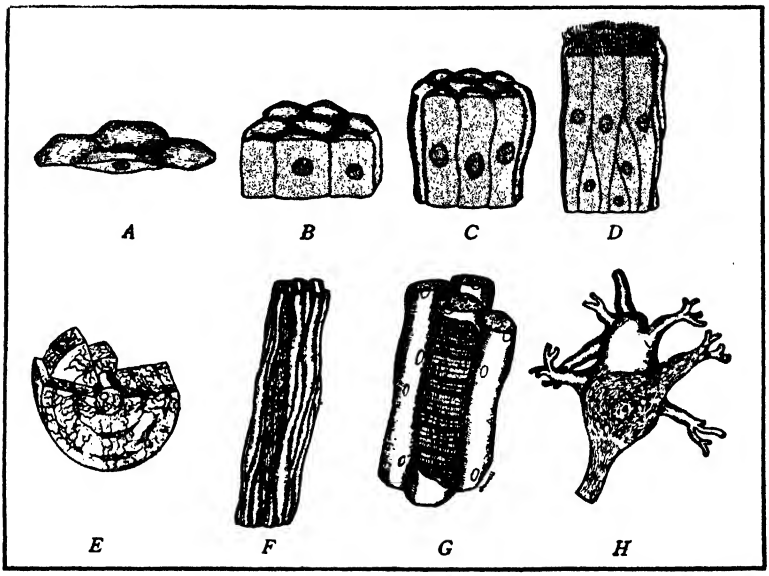

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FIG. 17. Somatic Cells of Typical Tissues

A-D, different types of epithelium; *E*, bone; *F*, smooth, or involuntary, muscle; *G*, striated, or voluntary, muscle; *H*, nerve cell

function is that of reproducing the new organisms of the following generations, thereby perpetuating life.

The somatic cells of each individual invariably pass out of existence at the termination of the life span of the organism, whereas the germ cells, by participating in reproduction, carry on the chain of life, with all its traits, from one generation to the generation that follows. Because of this the somatic cells are often alluded to as mortal and the germ cells as immortal, the latter being the means of perpetuating species

from generation to generation. Such biological immortality has made possible the continuity of the traits and characteristics of individual species in one endless stream of life.

Cell Division

As indicated at the beginning of this chapter, all forms of life may be said to originate through cells. An organism obtains all its traits through the increase of cells or, more specifically, through an increase of the determiners which originally were within the zygote, the product resulting from the combination of two germ cells. This leads us to a discussion of cell heredity, or the question of how a cell multiplies and passes on its entities to the other cells that go to form the whole of the complex organism, with its different systems.

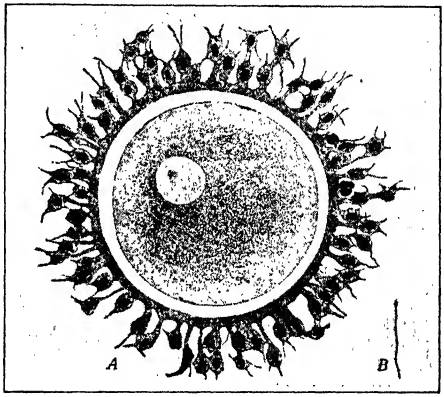

FIG. 18. Human Germ Cells[1]

A, an ovum (after Waldeyer); *B*, a spermatozoön

In general, two methods of cell division are known. The first is the direct one called *amitosis*, in which there is a splitting of the adult cell into two more or less equal parts. As will be seen from the description later on, this is accomplished by a rather simple process. The second method is the indirect one known as *mitosis*.[2] This is more involved, and invariably it is accompanied by a rather complicated nuclear reorganization. The end result, however, in both amitosis and mitosis is exactly the same — two cells being produced through the splitting of a single one.

[1] From Arey's *Developmental Anatomy*. By permission of W. B. Saunders Company, publishers.

[2] The older cytologists used the term *karyokinesis* for indirect cell division.

Amitosis

Amitosis at one time was believed to occur as a normal process in many of the cells of the lower organisms. In recent years it has been shown that many of the supposed cases of amitosis really may be resolved into true instances of mitosis. It is believed now that amitosis occurs in certain cells that are undergoing degeneration, in cells of transitory structures which function for nutritive or protective purposes during embryonic development and later are abandoned. The nutritive cells in the testis of the crayfish may serve to

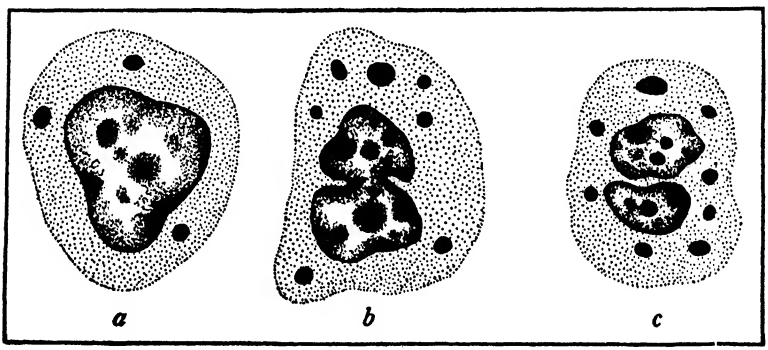

Fig. 19. Amitosis

a-c, successive stages illustrating the process in the nutritive cells of the testis of a crayfish

illustrate what happens during amitotic division (Fig. 19). The first thing to be noticed is a drawing out of the nucleus into two nearly equal parts. Soon a distinct constriction may be seen, which splits the original nucleus into two portions of approximately equal size. The cytoplasm may or may not separate around each of the newly formed structures.

Mitosis

In the majority of organisms whenever there is a multiplication of cells, from the very beginning of reproduction to the end of the organism's existence, it occurs through the more complicated process of mitosis (Fig. 20). As a rule, mitosis is

accomplished by the five general steps of *prophase, mesophase, metaphase, anaphase,* and *telophase.* These are not distinct and isolated steps but continuous ones which fade into each other so gradually that it is difficult to determine where one begins and the other ends.

Prophase

This is the stage in which the resting cell is prepared for division (Fig. 20, *A–D*). The first changes to be noticed are those occurring in the nucleus and central body. The centrosome divides into two granules, and soon these separate and begin to migrate away from each other. At the same time definite ray-like lines make their appearance around each granule, arranging themselves after the fashion of beams of light emitted from stars, and called *asters.* As the process proceeds, each centrosomal granule wanders completely away from the other, and at the same time distinct *spindle* fibers form between them. The astral rays and the spindle fibers together constitute the so-called *achromatic figure.* While this is going on, the nucleus becomes organized in such a manner that the chromatin masses spread out into either a continuous skeinlike structure known as a *spireme* or, more often, into distinctly separate, elongated threads, into which every spireme eventually breaks down. These individual threadlike structures soon shape up to form the compact, distinctive chromosomes. In the final moments of the prophase, the nuclear wall completely disintegrates. At the same time the spindle fibers radiating from the centrosomes become attached to the chromosomes, and seem to influence them to migrate toward the equator of the cell.

Mesophase

Here (Fig. 20, *E*) the processes initiated toward the end of the prophase have been completed. The centrosomes have terminated their migration to the poles of the cell, and at the same time the radiating fibers have arranged themselves in spindle fashion between them. The chromosomes have wan-

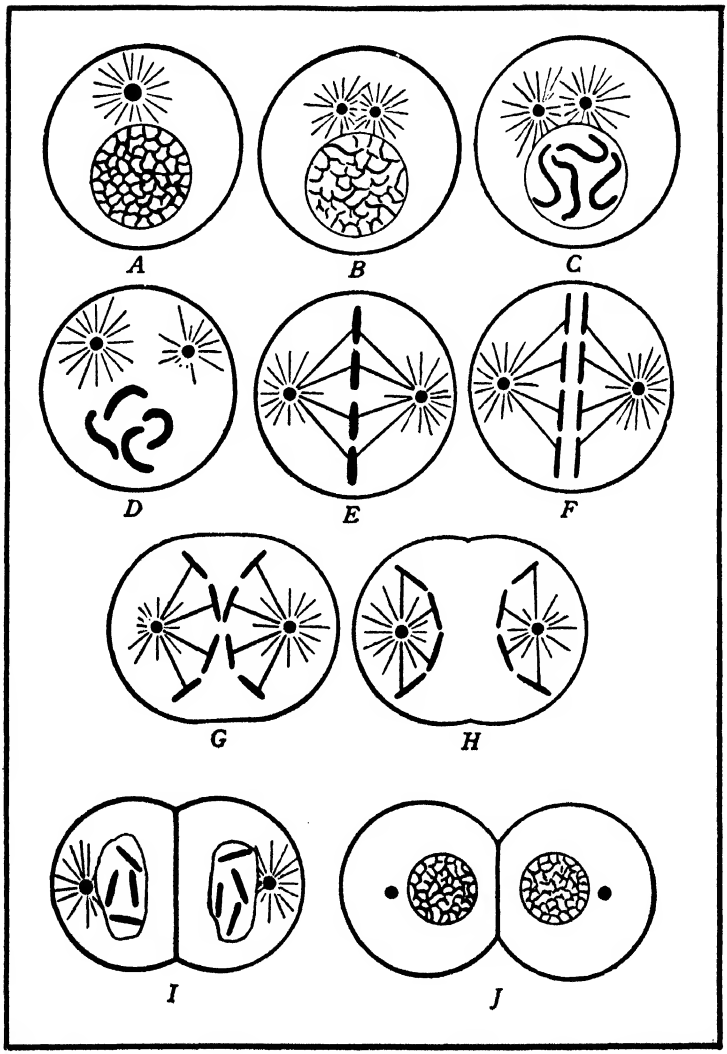

FIG. 20. Mitosis[1]

A–D, prophase; *E*, mesophase; *F*, metaphase; *G–H*, anaphase; *I–J*, telophase

[1] From Fasten's *Origin through Evolution.* By permission of F. S. Crofts & Co., publishers.

dered toward the center of the cell, and soon come to lie in the equatorial plane between the spindle fibers, in readiness for the actual division process.

Metaphase

In this stage (Fig. 20, *F*) a definite split appears in each of the chromosomes, ultimately dividing all of them into two full sets of *daughter chromosomes*, arranged side by side, in horizontal fashion, in the equatorial plane of the cell.

Anaphase

In the anaphase (Fig. 20, *G–H*) the chromosomes migrate toward opposite poles and take positions around each of the centrosomes. Soon a definite constriction makes its appearance in the middle of the cell, indicating the region in which the final split will occur.

Telophase

The telophase (Fig. 20, *I–J*) is the final stage in mitosis. Here the central constriction which showed itself in the previous stage becomes a distinct cleft which may be recognized very readily. The chromosomes, which meanwhile have been pulled very close to the centrosomes, now become surrounded by distinct nuclear walls. Shortly the compact, independently appearing chromosomes within the nuclear walls of each newly formed cell disintegrate and soon participate in the formation of a nuclear structure. The cytoplasm also becomes more definitely organized, with the centrosome of each cell taking its customary position near the nuclear wall. The final result is that the two newly formed cells come to look like the old one from which they were derived.

Cell division has thus been accomplished through the medium of the exact splitting and segregation of the cellular contents, particularly the chromosomes. As already intimated, these chromosomes are really worlds in themselves, consisting of those ultra-microscopic units responsible for traits (the *genes*, *factors*, or *determiners*) whose nature, or

composition, has not as yet been determined. While biologists have never succeeded in seeing these entities, they are convinced that they are in existence and that they are arranged in linear fashion within the chromosomes, somewhat like a series of beads strung on a string. In fact, in some organisms investigators have shown the existence of small granules, *chromomeres* (*Bi. 6, 15*), arranged logically along the chromosomes after the fashion here described. By the equal splitting of the chromosomes during mitosis, there is brought about an equal cell heredity through an equal distribution to the newly formed cells of the similar hereditary units.

In closing the discussion of cell division it may be well to point out that when the body cells divide, they do so equationally; that is, all parts of the cell — central body, cytoplasm, chromosomes, and so on — participate in the division process. On the other hand, during *maturation*, the period of the development of the germ cells (to be discussed in the following chapter), there is one stage in which the division, while in all other respects similar to mitosis, differs markedly — the division of the chromosomes. Instead of the chromosomes' dividing equally, they become reduced in number through the migration of a full half of the entire set into each of the two cells resulting from the division process. This sort of division is spoken of as a *reduction division*. All other divisions during the development of the germ cells are of the equational type, exactly similar to those taking place in all the somatic cells.

CHAPTER V

Germ Cells and Heredity

AN ORGANISM, with its many structures, usually comes into existence through the combination of two special reproductive cells, the so-called germ, or sex, cells, known technically as *gametes*. In animals the male gamete is called the *spermatozoön*, and the female gamete, the *ovum*. Fig. 18, on page 65, shows the relative differences in the shape and size of the human spermatozoön and ovum. In plants the corresponding names given to the male and female reproductive elements are, respectively, *sperm cell* and *egg cell*.

From the point of view of heredity and variation these reproductive cells are the most important structures to be considered. The gametes may be regarded as the keys which unlock the secrets of genetics. When one realizes what goes on within them during their process of development toward maturity and, more particularly, the rôle they play in fertilization, then one ought to have little difficulty in understanding the basic principles upon which the science of genetics rests. Inasmuch as individuals come into existence through the agency of germ cells, these reproductive elements must be looked upon as bringing in with them the capacities responsible for the traits of the completed organism. All the cellular structures produced during the life of the individual can be traced to the original combination which started the organism. The germ cells must be considered, therefore, as the units of greatest significance in any discussions of heredity, variation, sex, and those principles which go under the name of Mendelism (*Bi. 29, 187, 207, 208*). During the last thirty years especially, these facts have been definitely established. This will become more apparent after a consideration of the material in the present and following chapters.

Sexuality

In most forms of life the sex cells are invariably produced in separate individuals, the male giving origin to the male gametes and the female to the female gametes. Sex, therefore, may be said to be a condition directly associated with, as well as dependent on, the differentiation of the gametes. In some of the lower animals differently sexed individuals do not exist, but each organism produces both male and female reproductive organs within the same body. Such a bisexual individual is termed a *hermaphrodite*, and the condition is alluded to as *monœcious*. Most of the higher forms, however, are unisexual, developing the two distinct sexes, each specialized to produce its respective gametes — a condition which is referred to as *diœcious*. Even though this latter condition is the normal one, occasionally something will go wrong during development so as to lead to the formation of an individual showing the monœcious condition. The fact is that the zygote of every animal starts its development with sets of capacities for both sexes, but before development has progressed very far a set of determiners for one sex assert themselves to the extent where they predominate over the other set, with the result that the individual soon proceeds definitely to unfold into either a male or a female. When something goes wrong in normal development, it may happen that those determiners which make for just one sex are in some manner prevented from dominating the situation, giving the factors for the opposite sex an opportunity to express themselves and resulting in the production of an abnormal individual in whom the reproductive organs of both male and female have become more or less apparent. Sometimes the characteristics of one sex are more prominent than those of the other, so that the individual is more of a male than a female, or vice versa. In other instances the traits for both sexes are reduced to the extent where the individual cannot function in a normal sexual manner and remains sterile. Such instances will be considered more fully

in Chapter VI, under the heading "Gynandromorphs, or Sex Intergrades," and in Chapter VIII, where the freemartin is described.

The sexual condition encountered in practically all plants is monœcious, or hermaphroditic, but the most common method of reproduction is through *cross-fertilization,* by means of which the male elements of one plant fertilize the female elements of a different plant. Such is often the situation in those animals that are normally hermaphroditic. Cross-fertilization is insured through nature's precaution of having the male and female elements of each hermaphroditic organism ripen at slightly different times.

When the mature gametes are examined, they are found to possess one half the number of chromosomes that are contained in the somatic cells (see page 77). This gametic number is known variously as the *germinal, simplex,* or *haploid* set, whereas the somatic number is correspondingly called the *somatic, duplex,* or *diploid* set. From the standpoint of genetics, it is very important to know not only how each gamete gets its reduced number of chromosomes, but also the exact significance of this maturation, or reduction, process.

After fertilization the zygote, or oösperm, is produced. This is the product resulting from the union of two gametes, each one of which has contributed its haploid number of chromosomes to restore the diploid number common to both the somatic and the immature germ cells. Every species of plant or animal is characterized not only by distinct bodily characteristics which anyone can recognize, such as color and height, but also by the possession of a specific number of chromosomes within its cells. Man (*Homo sapiens*), for instance, possesses forty-eight chromosomes within the somatic cells and twenty-four within the mature germ cells. The edible crab of the Pacific coast, *Cancer magister,* has a hundred and twenty chromosomes in the diploid set, and half that number, sixty, in the germ cells. Furthermore, besides mere number, there are other distinctions within the chromosomes, such as size, shape, and the nature of the genes.

The zygote is the beginning of a new organism, and from it all the body and germ cells will eventually be produced. The zygote may be said to start everything the biological individual will possess. It begins its development with a full double set of chromosomes and represents the dual parentage that contributed the mature germ cells, with their single sets of chromosomes, to the formation of the zygote. Inasmuch as in many species the chromosomes are all of characteristic size and shape, it is evident that the single sets contributed by the gametes are similar and are arranged within the zygote in a set of *homologous pairs.*

At first all cells formed within the individual, including the immature germ cells, contain this complete double set of chromosomes. We know, however, that the mature germ cells, the gametes, possess only half this number. Therefore the question which arises is What has happened to bring about such a reduction? When all phases of the development are studied carefully, it is discovered that at the approach of sexual maturity many of the immature germ cells undergo, as mentioned on page 77, a reduction division known as *maturation* (Fig. 21), during the beginning stages of which there occurs a rapid growth and realignment of the pairs of homologous chromosomes. This is then followed by a division which is reductional rather than equational, so that each of the resulting two cells receives one half the number of chromosomes present in the immature germ cells at the beginning of the maturation process. By this means the dual hereditary factors for traits carried by the pairs of homologous chromosomes, and representing the dual parentage, become segregated into single sets.

It is a well-established fact that before an individual organism reaches sexual maturity, all its cells are alike as far as chromosome number is concerned. Very early in embryonic development the germ cells become segregated from the body cells. During the sexual immaturity of the organism, the immature germ cells merely go on dividing, thereby increasing their number. During the organism's

span of sexual maturity, various numbers of immature germ cells undergo maturation to form the gametes. Those which do not undergo maturation continue to divide by mitosis, although some of these may undergo maturation later on during the period of sexual maturity.

The length of sexual maturity varies with the species and the sex of the individual. In the human family the male is sexually functional for a period of about fifty years, the period coming on between the ages of fourteen and sixteen and lasting ordinarily to the age of sixty-five, whereas the female is mature for about thirty years, maturity beginning between the ages of twelve and fourteen and ending near the age of forty-five. Of course, individual variations from these figures do occur, dependent on racial and environmental factors. Ordinarily people living in warmer climates mature earlier than those dwelling in colder ones. It has been estimated that during this period of sexual maturity the human female is capable of producing about four hundred ova, whereas the human male is capable of producing over three hundred billion spermatozoa.

Concurrent with the onset of sexual maturity the secondary sexual characters express themselves, by means of which the male can be distinguished readily from the female (*Bi. 63, 128, 161*). For example, in the human family, the boy develops a deeper voice, a beard, firmer muscles, a more pronounced chest, and increases considerably in size. At the same time he becomes more aggressive and develops a keener interest in individuals of the opposite sex. The girl, likewise, undergoes a transformation. Normally, sexual maturity is established with the onset of the monthly or menstrual periods, during which the ripened ova are discharged from the ovary. The form of the body undergoes transformation, taking on the characteristic rounded, feminine appearance. The hips and pelvis broaden out. The breasts become enlarged and highly glandular in structure. Going hand in hand with these physical changes, many mental transformations take place leading to distinct differences in the emotional

behavior of the individuals. As will be indicated in Chapter VIII, these secondary sexual characters are controlled largely by secretions from the male and female glands of reproduction.

Maturation of the Germ Cells in Animals

Maturation of the germ cells is a universal process occurring in both plants and animals. With minor differences the stages are practically the same in all organisms. Maturation of the germ cells of animals will be discussed first, and this will be followed by a description of the maturation process in the germ cells of the higher plants.

Before a detailed discussion of maturation is undertaken, it will be well to summarize briefly what has already been stated. All cells of an organism owe their origin to the zygote, produced by a combination of two mature germ cells derived from opposite parents. The zygote soon undergoes development through a rapid process of cell multiplication. At first all the cells are more or less alike, but before long differentiation sets in and a certain number of them are set aside as a compact mass of immature germ cells, called *spermatogonia* in the male and *oögonia* in the female. At the same time the other cells produce by specialization and organization all the so-called vegetative tissues of the body — those which have to do with the response, feeding, and protection of the organism.

During the period of sexual immaturity, the immature germ cells multiply by mitosis, but form no other cells except immature ones. At the approach of sexual maturity numerous of these cells undergo development and become mature reproductive elements capable of functioning in the process of fertilization. The maturation of the male germ cell is called *spermatogenesis*, whereas that of the female is termed *oögenesis*. Fig. 21 is a schematic representation of the principal steps in both of these processes.

Broadly speaking, when germ cells, whether male or female, start on the process of maturation, they undergo a

number of very definite transformations, the general features of which may be outlined as follows: First, each immature germ cell grows, and at the same time the similar chromosomes of its homologous pairs temporarily join, fuse, or entwine around each other in the process known as *synapsis* or *syndesis*. These pairs then line up in the equator of the cell, and when division occurs whole chromosomes, corresponding in size and shape to one of each homologous pair, migrate to the two newly formed cells. This is the reduction division. Following it, each of the two cells containing the single set of chromosomes divides again, this time equationally, with the result that four cells are ultimately formed, each possessing the reduced number of chromosomes. In some forms, especially those belonging to the insect order Orthoptera, these processes may be reversed, so that where the reduction and equation divisions are indicated, there occur the equation and reduction divisions. The end result, however, is just the same, bringing about a reduction in the number of chromosomes from the double to the single set. Finally, by a complicated process some or all of these cells transform into mature gametes, which differ considerably in appearance from the immature germ cells that gave origin to them.

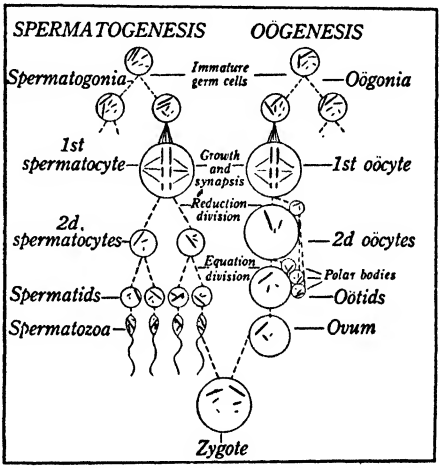

FIG. 21. Maturation Stages of the Germ Cells of Animals[1]

Spermatogenesis is maturation of the male gamete; oögenesis is maturation of the female gamete; zygote is the union of the male and female gametes in the process of fertilization

[1] From Fasten's *Origin through Evolution*. By permission of F. S. Crofts & Co., publishers.

Spermatogenesis

The moment that the immature, primordial male germ cell, the *spermatogonium,* starts its maturation, its name is changed to *primary spermatocyte.* It grows in size and at the same time the pairs of similar chromosomes which it contains line up together, either side by side or end to end or by twisting around each other in the process of synapsis, or syndesis. Then follows the reduction division, during which the pairs of homologous chromosomes become assorted, or segregated, into independent cells, so that only a single set find their way into each of the two *secondary spermatocytes* which have been formed. There has been complete division of the cytoplasm, but not so of the chromosomes; instead, entire chromosomes of every homologous pair have become separated from each other, thereby reducing the double set to single ones. Each of the secondary spermatocytes now divides once more, this time completely, through an equational mitosis, resulting in the formation of two *spermatids* of equal size. Four spermatids, then, are eventually produced from each immature spermatogonium; these spermatids, through a very complicated process of transformation, become mature functional male gametes, the *spermatozoa,* capable of uniting with female gametes in order to reproduce new members of the species.

Oögenesis

With some minor differences, the process of oögenesis is quite similar to that of spermatogenesis. When the immature germ cell, the *oögonium,* begins to develop, its name is changed to *primary oöcyte.* This undergoes growth, synapsis, and reduction to form two *secondary oöcytes.* However, these cells are not of equal size, like the secondary spermatocytes, one of them being considerably larger than the other. It so happens that in most instances the smaller secondary oöcyte is formed at one pole of the larger one, and because of this it is usually designated as the first *polar body* or *polocyte.* In spite of the relative difference in the size of the secondary oöcytes,

the number of chromosomes which they possess is exactly the same, the size difference being due to the amount of cytoplasm in each. These secondary oöcytes then divide equationally, giving rise to four *oötids*, one of which is much larger than the other three, which are extremely small and called second *polar bodies* or *polocytes*. Of these oötids only the large one develops into the functional *ovum*, whereas the smaller ones, the polar bodies, invariably are nonfunctional and soon disintegrate.

Cycle of Gamete Formation in Plants

In plants, especially in the higher forms, gamete formation, although a little more complicated than in animals, is nevertheless accomplished by a similar process. The complications are due to the fact that plants ordinarily undergo an *alternation of generations*, consisting of a nonsexual generation known as a *sporophyte*, in which the cells all contain the diploid number of chromosomes, and a sexual generation, known as the *gametophyte*, the cells of which all bear the haploid number of chromosomes. The gametophyte generation produces the mature male and female gametes, which, upon uniting, form the zygotes, which give origin to the sporophytes once more. In the highest plants, the so-called seed plants, those that geneticists deal with mainly, the gametophyte generation is much reduced. Most of the plant, including roots, stems, leaves, and visible portions of the flowers, consists of the sporophyte generation, whereas the pollen tubes and embryo sacs of the blooms, or flowers, constitute the gametophyte generation.

When the flower of such a plant is examined (Fig. 22), it is found that it consists of an outer layer of leaves called *sepals*, the whole layer being known as the *calyx*. Immediately next to the calyx is the *corolla*, consisting of a row of leaves similar to the sepals, and called *petals*. The calyx and the corolla form the cup of the flower, and within its center are found the male and female reproductive structures. Those that lie nearest the petals are the slender *stamens*, the male portions,

which bear the *pollen grains*, with the haploid number of chromosomes that give origin to the mature male gametes. Next to the stamens, in or near the exact center of the flower, are the *carpels*, the female portions (which usually are united into a composite structure known as the *pistil*), which produce the mature female gametes, the *egg cells*, contained within the ovules. It is of interest to note that in most plants the stamens and carpels invariably are borne by the same flower. Sometimes, however, they may be developed by different flowers, one kind possessing stamens and the other kind, carpels or pistils. The former are referred to as male flowers, and the latter as female flowers. In some instances these separately sexed flowers may be found on the same plant; or they may occur on different plants. In the latter case the plants themselves are designated as either male or female.

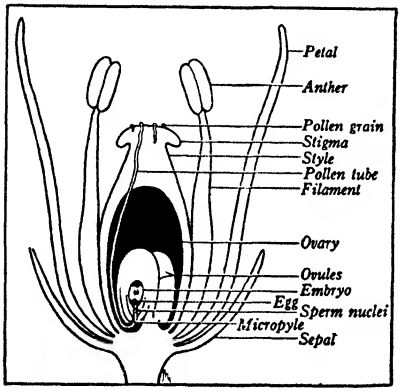

FIG. 22. The Structure of a Flower

With the above explanation in mind, let us now examine a little more intimately the male and female portions of a typical flower for the purpose of finding out how the mature gametes are formed and also how these unite to form the zygotes in the seeds, which produce the plants of the new generation.

Each stamen consists of a long filament, at the tip of which is the *anther*, containing several *microsporangia*. Each microsporangium contains many immature male germ cells, known as *sporocytes*, which possess the diploid number of chromosomes. As in animals, each sporocyte undergoes synapsis and two maturation divisions, thereby forming four cells, which in plants are called *microspores* or pollen grains. Each of the miscropores possesses the haploid number of chromosomes.

The female portion of the flower, the pistil, consists of three regions: an outer part, the *stigma*; a slender middle part, the *style*; and a spacious, hollow basal part, the *ovary*. Within the ovary are the *ovules*, varying in number from one to many, depending on the species. These are also called the *megasporangia*, and within each one of them a sporocyte, or diploid immature germ cell, soon undergoes synapsis, followed by two divisions forming four cells, a large one and three smaller ones, each with the haploid number of chromosomes. The large cell, called technically the *macrospore* or *megaspore*, remains functional, whereas the three smaller ones as a rule disintegrate in a manner comparable to the disappearance of the polar bodies during the maturation of the female gamete of animals. Following this, the nucleus of the megaspore divides three times to form eight nuclei, while at the same time the cytoplasm divides into seven portions. Six of these surround single nuclei located at the poles, and the seventh portion of cytoplasm surrounds two nuclei situated in the center. We thus obtain six cells each with a single haploid nucleus and a seventh one with two haploid nuclei. One of the single nucleated cells is a little larger than the others, and this becomes the functional *egg*. The whole structure thus enumerated and formed from the division of the megaspore is spoken of as the *embryo sac*.

Fertilization occurs when the ripe pollen grains of the stamens fall on the stigma of the pistil. Each pollen grain grows into a tube that extends down through the style and into the ovary, where it comes in contact with an ovule. While this is happening, the nucleus of the microspore divides into two nuclei, one of these forming a *tube nucleus* and the other a *generative nucleus*. This generative nucleus divides once more into two sperm nuclei, the true male gametes, each retaining the haploid number of chromosomes. Inasmuch as these nuclei are confined to the tip of the pollen tube, they are brought along with this structure as it grows into the embryo sac. Soon a double fertilization occurs, in which one of these sperm nuclei unites with the egg cell to

form the zygote, with the diploid number of chromosomes, whereas the other sperm nucleus unites with that cell of the embryo sac which contains the double nucleus, forming a structure with a triploid number of chromosomes. This triploid cell forms the basis of the nutritive, or *endosperm*, tissue which surrounds the zygote and forms the rest of the seed. The five other nuclei of the embryo sac ordinarily also serve

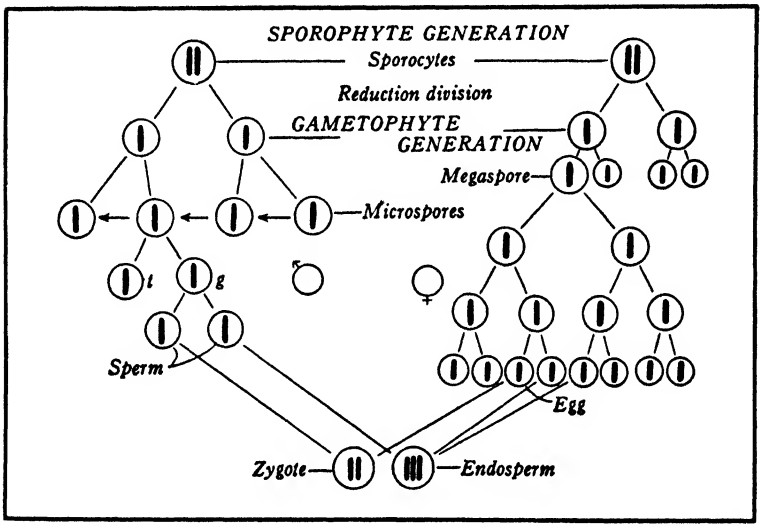

FIG. 23. Gamete Formation and Fertilization in Seed Plants

The rods indicate the condition of the nuclei, one representing a haploid cell, two a diploid cell, and three a triploid cell; *g*, generative nucleus; *t*, tube nucleus

as reserve food supply for the embryo within the seed. Fig. 23 shows in diagram form the processes of the maturation and fertilization of the gametes in seed plants.

Through the above phenomenon of double fertilization common in the seed-bearing plants, the mature seeds are obtained, each of which consists of two parts: a zygote, or embryo, with the diploid number of chromosomes, from which the sporophyte of the following generation originates; and the endosperm cells with the triploid number of chromosomes, which form the rest of the seed and afford nourishment for

the embryo. In those cases where the external membranes covering the seed are thin, as in corn, the effects of the sperm cell's fertilizing the binucleate endosperm cell may be recognized immediately, indicating the hereditary factors brought in from the male parent. Such an effect of the male gamete on tissues other than germinal ones is spoken of technically as *xenia*. The important fact to remember throughout this discussion is that the pollen grains and egg cells contain the haploid number of chromosomes and have been produced through a process of maturation similar in most respects to that which takes place in animals.

Effect of Synapsis and Reduction

The stages in the maturation of the germ cells during which growth, synapsis, and reduction of chromosomes occur are the ones of greatest importance, for at these times the entities from parents responsible for the expression of characters may become shuffled around and segregated in different ways, thereby determining the ultimate hereditary constitution of the mature gametes that participate in reproduction. Of particular significance is that stage which has already been alluded to as synapsis or syndesis. Geneticists consider this the most important step in the maturation of the germ cells, a step in which an orientation process occurs — bringing together homologous chromosomes from opposite parents, representing factors for similar traits — and during which certain things happen that are most vital for the future construction of the reproductive elements. Fig. 24 shows the sixteen possible ways in which four pairs of homologous factors may become segregated, accounting for sixteen different types of gametes.

This discussion may be made very concrete by means of Fig. 25, which illustrates what actually occurs during the synapsis stage of a pair of homologous chromosomes. The members of the pair were brought into the cross by the male germ cell's giving, in the process of reproduction, one member and the female germ cell's giving the other member. In order

to distinguish these chromosomes, let us represent the one brought in by the female gamete as unshaded and the one contributed by the male gamete as shaded. Inasmuch as these are homologous chromosomes, they carry the factors, or genes, which determine similar kinds of traits. During the first stage in the maturation of a germ cell these chromosomes line up together as a pair. When the reduction division occurs, they become segregated in such a manner that each chromosome of the pair migrates into a different gamete. What genes the mature germ cells contain depends on the manner in which the members of each of the pairs of similar chromosomes unite and separate. In cases where they come together side by side or end to end and in the reduction division separate into the same individual chromosomes as in the original pair before they entered synapsis, the germ cells are found to carry complete sets of entities for precisely the same traits as one or the other of the parents. In those instances where some of the genes exchange places,—as happens during the maturation of some germ cells where the paired chromosomes, instead of coming together side by side or end to end, twist around each other so as to cross over,—then, when the reduction occurs, each of the two resulting chromosomes is of a different constitution from that before synapsis, and possesses entities derived from both of the parents. Fig. 25 shows the conditions where there is no crossing over and where crossing over occurs in one or two places. Fig. 26 also shows multiple crossing over

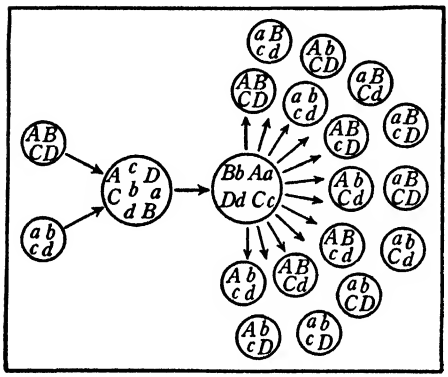

FIG. 24. Possible Gametes resulting from Various Factors

This diagram shows the sixteen types of gametes possible where four pairs of factors, *A*, *B*, *C*, *D* and *a*, *b*, *c*, *d* (that is, *Aa*, *Bb*, *Cc*, *Dd*), are considered. (After Wilson, courtesy of *Science*)

between the genes of homologous chromosomes. In this way it becomes possible to get new combinations of characters, accounting for many of the phenomena observed in breeding, or crossing, experiments.

As will be shown in Chapter XIII, when two genes of a chromosome are widely separated from each other, the

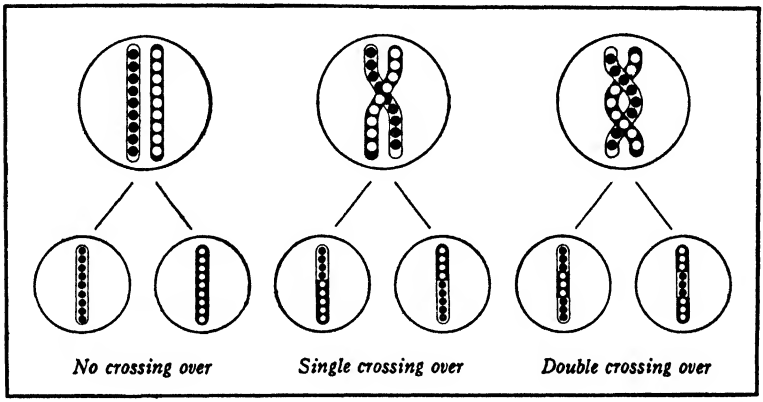

FIG. 25. Synapsis and Reduction of a Pair of Homologous Chromosomes

The dark chromosome with the light genes represents the maternal heredity, and the light chromosome with the shaded genes, the paternal heredity. The end results show how the chromosomes will segregate into the gametes where (1) no crossing over occurs, (2) where there is a single crossing over, and (3) where a double crossing over takes place

chances are increased for them to become segregated in the process of crossing over; on the other hand, if they lie close together within the chromosome, the probability is that they will not become separated during crossing over and will remain linked together in heredity. Sometimes the determiners for certain characters are closely linked within those chromosomes which have been discovered to be concerned with sex determination, and in such instances these characters have been found to appear more often in individuals of one or the other sex. Such phenomena are spoken of in genetics as cases of *sex-linked heredity*. The other chromosomes, besides the sex chromosomes, also have been found to possess linked genes, as will be indicated in Chapters IX and XIII. On rare occasions even the most closely linked

characters may become segregated through crossing over and splitting of pairs of homologous chromosomes during synapsis, accounting for some of the cases which have actually been observed in various breeding experiments.

Since the beginning of the present century biologists have been able to explain many phenomena of inheritance by understanding what goes on during the growth, synapsis, and reduction stages of maturation. In particular, these crossing-over and linkage phenomena have been of great aid in helping us to understand many hitherto unexplained cases of heredity. As a result of such studies geneticists have been able to determine fairly accurately, in some species, exactly where in the chromosomes the genes for certain traits are located, with the result that they have been able to develop chromosome maps (Fig. 60, p. 155), indicating the locations of a large number of genes within the specific chromosomes. The most extensive work along this line has been done by Thomas Hunt Morgan and his co-workers, notably Calvin B. Bridges, Hermann J. Muller, A. H. Sturtevant, T. Dobzhansky, Alexander Weinstein, Harold H. Plough, and J. W. Gowen, on various species of vinegar flies belonging to the genus *Drosophila*, and also by Cornell University geneticists under the able leadership of Rollins Adams Emerson on corn (*Bi. 3, 7, 22, 118, 133, 140–146, 190*). Such knowledge has been extremely helpful in understanding the constitution of the germ cells and the parts which they play in the production of the new organism.

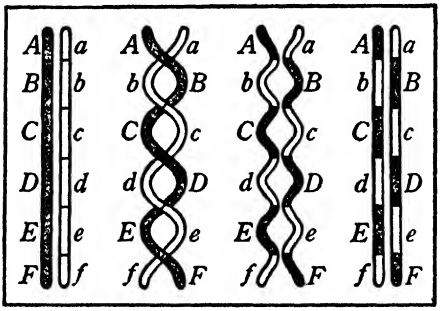

FIG. 26. Multiple Crossing Over among Chromosomes

Six pairs of factors are involved, *A*, *B*, *C*, *D*, *E*, *F* and *a*, *b*, *c*, *d*, *e*, *f*, in the multiple twisting, crossing over, and separation of this homologous pair of chromosomes during synapsis and the reduction division of the maturation of the germ cells. (After Wilson, courtesy of *Science*)

Fertilization and its Significance

By fertilization is meant the coming together of two germ cells of opposite sex, and their union to form that single organic whole, the zygote, or oösperm, — the beginning of the new individual. The organism's development thus starts as

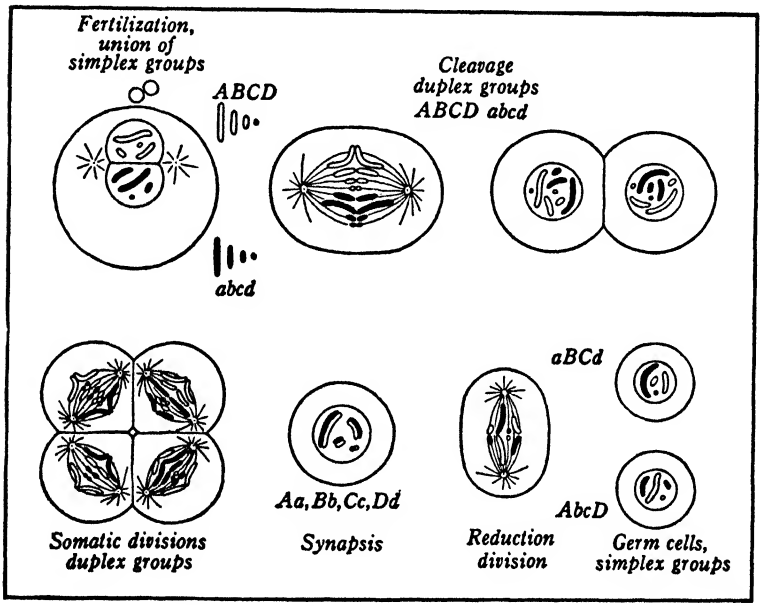

Fig. 27. Fertilization and Cleavage Stages of the Developing Embryo

The single sets of chromosomes, *A*, *B*, *C*, *D* and *a*, *b*, *c*, *d*, brought in by opposite germ cells, unite to form the duplex set, and these are equally distributed in the formation of the body cells and immature germ cells. In the maturation of the germ cells this double set is reduced to the single, or simplex, set through synapsis and the reduction division. (After Wilson, courtesy of *Science*)

a single cell in which there has been a restoration of the duplex number of chromosomes by each participating gamete's contributing a simplex set (Fig. 27). All development from the zygote proceeds in much the same fashion: at first there is a rapid multiplication of cells, all undifferentiated, called *blastomeres*, and these, through further multiplication and

differentiation, develop into the various tissues and organ systems. This remarkable development of the single-celled zygote, starting, as it does, from such humble beginnings and unfolding until it has arrived at the stage of the mature organism, with perhaps millions of specialized cells, is one of the most awe-inspiring phenomena in all nature. Its real significance can be comprehended only when all phases of the developmental process are traced. When thus studied, fertilization is found to be significant in the four following ways.

In the first place, fertilization is the agency for bringing about the reproduction of the new individual. But this process is not absolutely necessary for this purpose, because under certain conditions the egg alone may be stimulated to develop into the complete organism, without the aid of the spermatozoön. Such development is spoken of as *parthenogenesis* and among certain species it is found to occur in nature, or it may be induced artificially by means of various agents within the laboratory. The honey bee among animals and the dandelion among plants may be cited as good examples of such development. The case of the honey bee is especially interesting, as normally there are found to exist in this species both males and females. Investigators have shown that the females are of two types, sterile workers and fertile queens, both of which are produced from eggs that have been fertilized. It seems that the food which surrounds the fertilized eggs determines whether they shall develop into queens or workers. The males, on the other hand, are all of one type and fertile, but they are produced from unfertilized eggs through the process of parthenogenesis.

In the second place, fertilization is significant because it brings about a rejuvenescence of the protoplasm of the species through the union of the gametes. The word "rejuvenation" means to make young again. It is true that in the process of fertilization the germ cells lose their independent identities, but at the same time each one of them is stimulated to participate and fulfill its destiny in the formation of the new organism. Fertilization, therefore, while prevent-

ing the death of the germ cells, at the same time brings about their rejuvenation through participation in species formation.

This rejuvenescence theory was propounded mainly by the early investigators of the Protozoa, who noticed that after these organisms carried on their normal functions for some time, reproducing asexually, they slowed up and showed signs of degeneration unless they underwent a process comparable to fertilization, known as *conjugation*. During conjugation two individuals temporarily join and exchange nuclear portions, after which they separate and seem to have been rejuvenated, with the result that once more they can carry on the functions of life in a normal manner.

In recent years, however, experiments have been carried on by numerous investigators on Protozoa which have cast doubt on the theory that fertilization or conjugation is necessary for rejuvenescence. Some of these investigators, notably L. L. Woodruff, of Yale University, have found that if environmental conditions are good, certain strains of *Paramecium* can carry on normal functions of life without ever undergoing conjugation. For perhaps twenty years or more, Woodruff has been able to carry strains of these organisms through many thousands of generations without conjugation and without loss of vigor. Herbert S. Jennings, of Johns Hopkins University, also has studied the differences in vigor between conjugating and nonconjugating members of the same stock of Protozoa and has found that there was no decline whatsoever in the vigor of the nonconjugating individuals.

In the third place, fertilization is important in that it is the means of transmitting traits from parents to offspring. The newly produced organism thus becomes the possessor of the hereditary factors from the two parents, as represented in the chromosomes of their combining gametes. At sexual maturity this organism then becomes the hereditary bridge which links the past with future generations. Offspring may be said to inherit equally from both parents, although in reality certain traits dominate over others or interact with others to form different-appearing types.

Finally, fertilization is of great significance from the standpoint of variation. Some biologists believe that in large measure it is the process which is solely responsible for bringing about variation. As will be recalled from our previous discussion, in the admixture of germ cells during the process of fertilization there is always a shuffling and realigning of determiners for traits, with the result that new combinations are apt to appear.

From the point of view of genetics, the insurance of the transmission of heredity and the production of some degree of variation are considered the most significant functions of fertilization. In fact, the whole science of genetics is based on a thoroughgoing understanding of the various stages in the maturation of the germ cells and, more particularly, on the rôles played by the nuclei and cytoplasms of the mature gametes in the formation of the new offspring.

Nucleus and Cytoplasm in Heredity

As already indicated in Chapter IV, the nucleus and cytoplasm play somewhat different rôles in heredity. This becomes apparent especially when the functions of these structures are studied in germ cells.

Inasmuch as the male gamete possesses a negligible quantity of cytoplasm in comparison with the female gamete, it is chiefly the latter germ cell which contributes the main quantity of cytoplasm for development. Students of the problem are of the opinion that the cytoplasm of the egg determines such general characters as polarity, symmetry, and position or pattern of certain of the organs of the individual. The nuclei of the ovum and spermatozoön influence the production of individual characters such as sex, color of skin, hair, eyes, stature, and mental traits.

Even before fertilization, many eggs show distinct zones of differentiation, indicative of symmetry, polarity, and pattern that characterize the species. That the spermatozoön is not necessary for development is obvious in those forms

where parthenogenesis occurs. Within the egg, therefore, the foundation is laid, before fertilization, for the development of the general bodily features which have been mentioned. Since the egg contains only chromosomes contributed from the mother, such groundwork must be looked upon as being laid down under the influence of maternal genes. When fertilization occurs, the fundamental general plan and symmetry of the body have already been determined. The only male influences contributing toward the characteristics of the egg cytoplasm have been those from the male parent of the female who produced the ova. Since this is the case, it may be said that the generalized features have been influenced by the grandfather's genes rather than by those of the immediate father.

All in all, both cytoplasm and nucleus must be reckoned with in heredity. Needless to state, the genes of the nucleus of the germ cell constantly interact with the cytoplasm. Not only that, but environmental factors also coöperate to produce the effects observed in the adult organism.

CHAPTER VI

Sex and its Determination

IN PRACTICALLY all the higher forms of life sex invariably involves the development of specialized types of individuals, male and female. These have distinctive organs of reproduction capable of manufacturing the sex cells, or gametes, which play the all-important part in the creation of the new generation. Associated with sex are *primary* and *secondary* sexual characters.

The primary characters are those which give the individual its immediate stamp as male or female, being represented by the reproductive glands (testes or ovaries), vasa deferentia or oviducts, penis or vagina, and other parts which make up the remainder of each reproductive apparatus.

The secondary sexual characters are those which normally accompany the primary ones. While they begin their development at about the same time that the sex of the individual is definitely charted, nevertheless they come to full fruition chiefly around the time of sexual maturity. They are bodily traits which enable us to recognize one or the other of the sexes readily. Examples of secondary sexual characters are familiar to all persons. For instance, the cock is distinguished from the hen by the possession of more brilliant plumage, a lustier voice, more prominent spurs, and so on. In Chapter V the secondary sexual characters which distinguish the human male from the female were mentioned. In fact, such bodily differences may be noticed throughout the entire animal kingdom. That there is an intimate relationship existing between the sex characters, especially the primary ones, is borne out by observation and experiment. As will be shown in Chapter VIII, if anything goes wrong during the development of one sex, so as to interfere radically with the develop-

ment of the primary sexual characters, not only may the sex structures be vitally affected and even altered, but more particularly the accompanying secondary ones may be changed.

Aside from the primary and secondary sexual characters, some investigators, notably Havelock Ellis (*Bi. 63*), have established a third group known as *tertiary* sexual characters. These are present in both the male and the female, but their degree of expression in each of the sexes is distinctly different. The tertiary characters become apparent only when they are studied comparatively. Obvious tertiary sexual characters which differ in the sexes are the size of the thyroid gland, the size of the skull, the number of red blood corpuscles, rates of growth of the body, and the width of the pelvis, as well as mental and emotional behavior.

Although such distinctions as indicated may be made statistically, still at the present time biologists pay little attention to the tertiary sexual characters, believing them to be intimately linked with the primary and secondary ones. On the whole, the tertiary group of characters has been discarded, and the emphasis is now laid on the primary and secondary sexual characters which distinguish males from females.

Historical

The topic of sex is an exceedingly important one. It is no exaggeration to state that for centuries it has been one of the great biological mysteries which thinking men have been attempting to solve. Until the beginning of the present century almost nothing was known about sex determination. Of course there existed many pet theories, something like five hundred of them, each attempting to account for the determination of sex after its own particular fashion, and practically all of them formulated on the basis of the effects of various environmental stimuli on the developing embryo. It was thought that alterations in the surrounding medium of the transforming embryo could induce modifications in its sex and, in spite of the mass of accumulated evidence to the

contrary, this view has persisted to some degree even to the present time. There are still many doctors and practical breeders who insist that the sex of an organism can be determined through such agencies as feeding and temperature. Some are even so bold as to claim that they can prophesy the sex of developing individuals. They are in entire agreement with Geddes and Thomson (*Bi. 84*), who, writing in 1889, asserted:

> The factors which are influential in determining sex are numerous, and come into play at different periods. The constitution of the mother, the nutrition of the ova, the constitution of the father, the state of male element when fertilization occurs, the embryonic nutrition, and even the larval environment in some cases, these and yet other factors have all to be considered.[1]

Sex determination has so many theoretical aspects, as well as practical applications, that it is considered of great importance in genetics. Since the beginning of the present century it has been fairly well established that sex is a character of an organism, depending for its expression on certain factors within the chromosomal combination brought into the zygote by the participating gametes at the time of fertilization. Accordingly, sex is now regarded as a character, like any other trait, and it is determined chiefly by certain factors within the germ cells which unite to form the individual.

Before the present century most biologists believed that all the germ cells of a species were alike, and that they contained the same, even number of chromosomes. It is true that a few exceptions to this general rule had been discovered, in which one half of the male germ cells possessed one more chromosome than the other half, but all such cases were dismissed as due to either faulty technique or mistaken observation on the part of the investigator who reported them. Some of these exceptions, however, seemed to persist even though the technique was of the very best and the ob-

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[1] P. Geddes and J. A. Thomson, *The Evolution of Sex*, pp. 84–85. Charles Scribner's Sons, New York, 1900.

servers were the most proficient in this field of research. The exceptions could no longer be ignored or overlooked. In 1891 Henking (*Bi. 106*) showed that in the insect *Pyrrhocoris apterus* two kinds of male gametes were formed, differing from each other by a single chromosome. Without knowing the nature of this extra chromosome, Henking called it the X element. A few years later, in 1899, Paulmier (*Bi. 163*), working with the male of the squash bug (*Anasa tristis*), also found a dimorphism of the spermatozoa, in which two types were produced, one of them containing one more chromosome than the other type. He thus confirmed Henking's discovery but, like him, could not explain its significance.

Fig. 28. Clarence E. McClung

In 1902 Clarence E. McClung (Fig. 28), at the present time professor of zoölogy in the University of Pennsylvania, discovered that likewise in the common locust *Xiphidium fasciatum* two kinds of male germ cells develop, one possessing an even number of chromosomes and the other an odd number, consisting of the even number of chromosomes already indicated for the first type of spermatozoön plus an extra one (*Bi. 135*). McClung called this extra chromosome the *accessory*, or *odd*, chromosome and ventured the suggestion that perhaps it might have something to do with sex determination. He had no direct proof of this, merely putting forth the hypothesis for what it was worth. Moreover, McClung held the erroneous opinion that the germ cell with the extra chromosome, when it fertilized the egg, gave origin to a male, whereas the other germ cell, without the accessory chromosome, when it participated in reproduction, resulted in the formation of a female.

This suggestion of McClung's stimulated one of our greatest cytologists, Edmund B. Wilson (Fig. 29), of Columbia University, to think along these lines. He decided to undertake investigations to test the idea carefully. In 1905 Wilson succeeded in showing that while there was a dimorphism of the spermatozoa, in which two types developed, differing from each other by the accessory chromosome, nevertheless the female gametes, or ova, were all of one type and each contained the accessory chromosome. Wilson, like Henking, definitely designated the accessory chromosome the X-*chromosome*, and then asserted that by studying the chromosomal constitution of the cells of the developing embryos it should be a simple matter to ascertain which combination produced a male and which a female.

FIG. 29. Edmund B. Wilson

It soon became apparent to Wilson that McClung's surmise was just the reverse of what was actually the case,—that the spermatozoön with the extra chromosome was the female-producing one, rather than the spermatozoön without the extra element, which was the male-producing gamete. If N is used to designate the ordinary number of chromosomes in the germ cells, known as *autosomes*, and the accessory chromosome is designated X, then the two types of spermatozoa can be represented by N and N + X, respectively, and the ova by N + X. Wilson showed that a male results when a spermatozoön with N fertilizes an ovum with N + X, giving a zygote of constitution NN + X; and a female results when a spermatozoön with N + X combines with an ovum N + X, giving a zygote with chromosomal formula NN + XX. This condition has also been found to hold good for many other animals, especially insects.

At the present time this extra chromosome is variously known as the extra, accessory, odd, or sex chromosome, and it is represented by the symbol X. It was fortunate that McClung, in his investigations, found this extra chromosome to be but a single element, for had it been more complicated, he might not have recognized it at all, so that any research in regard to its detection, as well as its significance, might have been postponed or completely ignored for a considerable period of time.

Methods of Sex Determination

Since McClung's famous surmise, a great deal of investigation has been carried on along these lines, and many new discoveries have been made which have clarified, in large measure, the whole problem of sex and its determination. Investigators have succeeded in showing that in many animals, as in the locusts mentioned, the male gametes differ from each other by a single accessory chromosome, the X-chromosome, whereas the female germ cells are all of one kind and possess this extra element. In other cases, however, it has been found that all the male gametes possess an extra chromosome but that in one half of them this element is the X-chromosome, whereas in the other half it is a different structure, to which has been given the name of Y-*chromosome*. All the eggs, however, have been found to contain the X element exclusively. If, as before, we designate the ordinary chromosomes, the autosomes, by N and the extra chromosomes, now known technically as *allosomes* or *heterochromosomes*, by X and Y, then the conditions for sex determination may be represented as follows:

CASE 1. Where two kinds of spermatozoa are produced, differing from each other by the X-chromosome:

a. N + X spermatozoön and N + X ovum = NN + XX zygote (female).

b. N spermatozoön and N + X ovum = NN + X zygote (male).

CASE 2. Where all the spermatozoa contain an accessory chromosome, in one half of which it is X and in the other half Y:

a. N + X spermatozoön and N + X ovum = NN + XX zygote (female).

b. N + Y spermatozoön and N + X ovum = NN + XY zygote (male).

A careful examination of the cases cited above reveals that as far as sex is concerned, the X-chromosome is the one which is the important accessory structure; the Y element apparently seems to play no part in influencing the sex of the individual. Biologists who have given considerable thought to the question have come to the conclusion that of the two accessory chromosomes, X is the true sex chromosome, whereas Y plays no real part in sex determination. Although in the fruit fly it was believed, until a few years ago, that the Y element carried no factors for the determination of characters, yet in recent years good evidence has been accumulating to show that at times the Y-chromosome may be the carrier of some genes for characters, as well as certain *lethal genes*, which may be responsible for producing certain defects or abnormalities of one kind or another, leading ultimately to the early death of the affected organisms. In any event, all the evidence indicates that, at best, the number of genes carried by the Y-chromosome is extremely limited.

There have been many striking confirmations of the chromosome theory of sex determination. One of the most interesting cases is that reported by Mulsow (*Bi. 150*) in the nematode worm *Ancyracanthus cystidicola* (Figs. 30–31). In this organism the male (Fig. 30, *A*) has one less chromosome than the female (Fig. 31, *A*). These differences may be observed in the living cells of the developing embryos. When the spermatozoa are examined, a dimorphism is recognized, one kind possessing six chromosomes and the other five (Fig. 30, *F*). All the eggs, however, are found to be similar and to contain six chromosomes (Fig. 31, *D*). Inasmuch as the number of chromosomes may be counted in the mature germ cells, the two types of gametes participating in fertili-

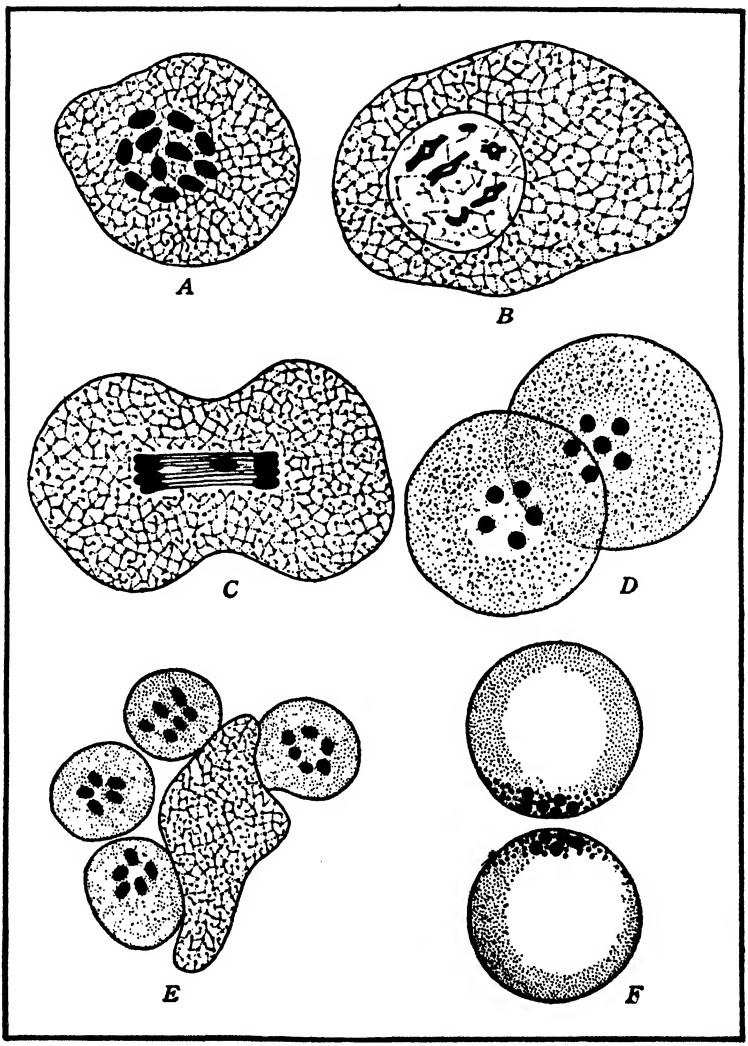

FIG. 30. Spermatogenesis Stages in the Nematode Worm *Ancyracanthus cystidicola*[1]

A, spermatogonium showing 11 chromosomes; *B–C*, stages during reduction division; *D*, two secondary spermatocytes resulting from reduction division; *E*, the four spermatids; *F*, the two types of spermatozoa produced

[1] From Conklin's *Heredity and Environment*. After Mulsow. By permission of Princeton University Press, publishers.

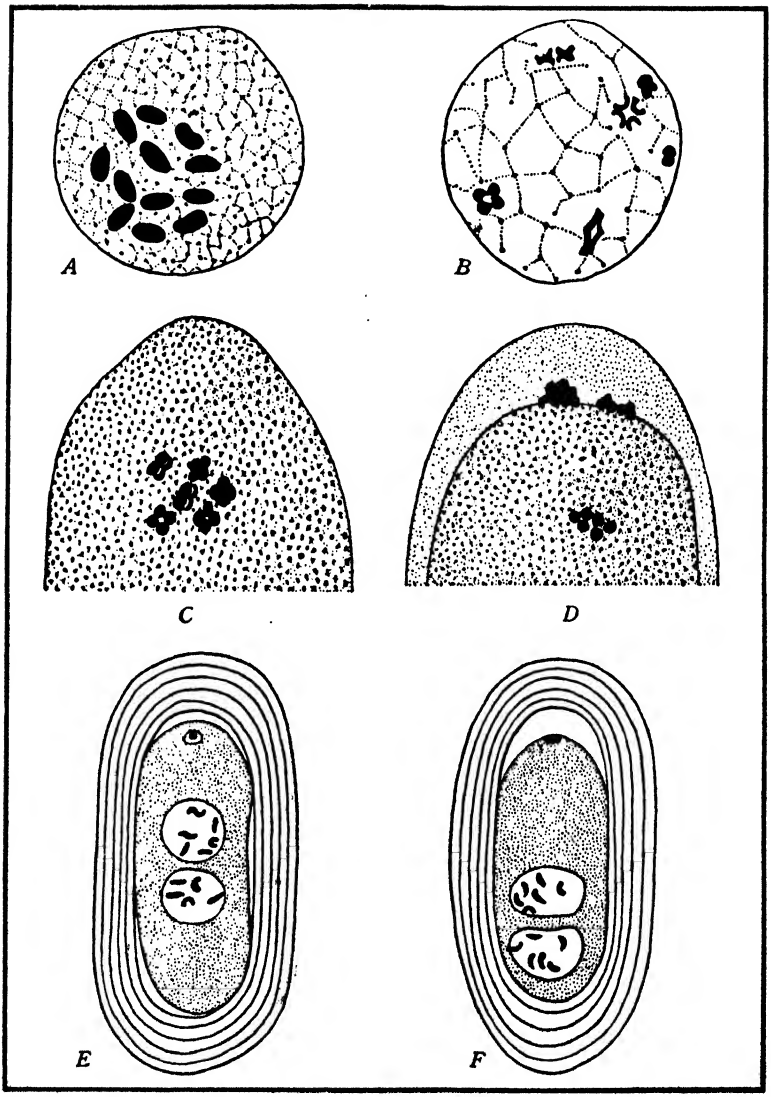

FIG. 31. Oögenesis Stages in the Nematode Worm *Ancyracanthus cystidicola*[1]

A, oögonium showing 12 chromosomes; *B–C*, intermediate stages in maturation; *D*, egg containing 6 chromosomes; *E–F*, fertilized eggs, showing 11 chromosomes in male and 12 in female

[1] From Conklin's *Heredity and Environment*. After Mulsow. By permission of Princeton University Press, publishers.

zation may be recognized readily, so that the chromosomal constitutions of the zygotes to which these reproductive cells give rise may likewise be distinguished, eleven chromosomes being present in the male (Fig. 31, *E*) and twelve in the female (Fig. 31, *F*). The thing of interest here is that the number of chromosomes brought in by the male and female gametes may actually be observed in the living cells of the developing embryo, indicating clearly the numbers present within the cells of the male and female.

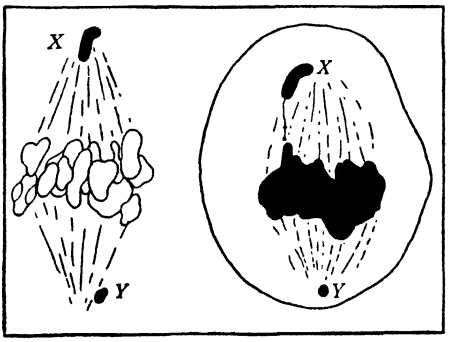

FIG. 32. The X-Chromosome and the Y-Chromosome in Man[1]

Since research along the lines of the chromosomal basis of sex determination began, it has been shown that the sex of a large number of animals, both invertebrates and vertebrates, appears to be controlled in the manner indicated above. In fact, wherever sex chromosomes have been discovered, it has been found that the laws for sex determination as outlined under Cases 1 and 2 always hold true. Most of the higher animals show the constitution of the gametes and zygotes as indicated under Case 2.

Sex Determination in Man

Although the situation in man has been a subject of considerable controversy in the past, the recent investigations by Painter (*Bi. 159*) and Evans and Swezy (*Bi. 69*) have indicated quite conclusively that man also belongs in this second category, Case 2, having 48 chromosomes in the double set, consisting of 46 autosomes and 2 accessory chromosomes. In the human species the male germ cells are of two kinds,

[1] After Painter, courtesy of *Journal of Experimental Zoölogy*.

possessing either 23 + X chromosomes, or 23 + Y; but the female gametes are all of one type, and contain 23 + X chromosomes. The chromosomal constitution of the female zygote

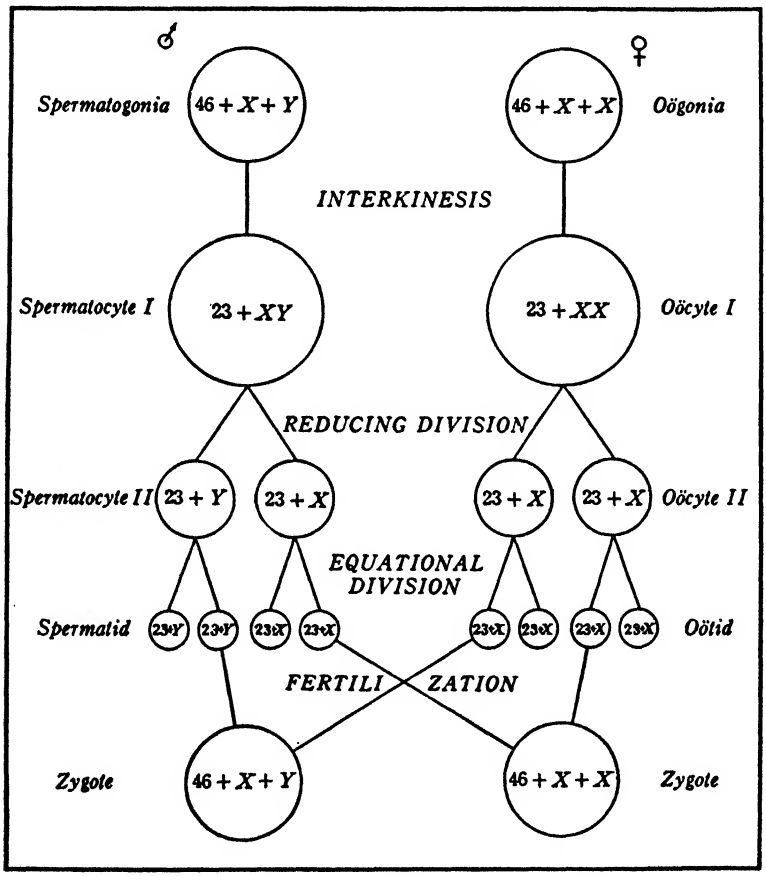

FIG. 33. Maturation and Fertilization in Man[1]

is therefore 46 + XX, and of the male, 46 + XY. Fig. 32 shows the X- and Y-chromosomes in man, and Fig. 33 is a diagram representing the maturation and fertilization stages in the germ cells of man, accounting for the different sexes.

[1] After Evans and Swezy, courtesy of University of California Press.

Reversal of Conditions

Although the methods outlined above are the usual ones for sex determination, there are, however, a number of exceptions, in such forms as moths, butterflies, chickens, and perhaps fishes, where the combination NN + XX, instead of producing a female, produces a male; and, similarly, NN + X or NN + XY, instead of giving origin to a male, produces a female. Here the ova show the dimorphism, possessing either N and N + X, or N + Y and N + X, whereas all the spermatozoa are of one kind, N + X. This, of course, is a complete reversal of the formulas given under Cases 1 and 2. In order not to confuse these exceptions with the ordinary cases, the letters designating the accessory chromosomes have been changed, Z standing for X and W for Y. In these organisms a male will have the constitution NN + ZZ, and a female, either NN + Z or NN + ZW. Fig. 34 shows the male and female chromosomal combinations in the domestic fowl.

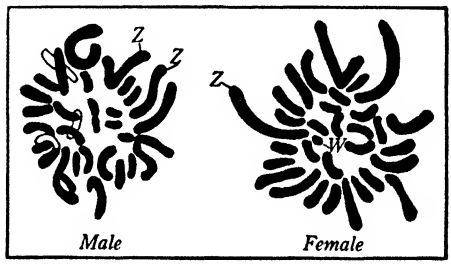

Fig. 34. Male and Female Chromosomes of the Fowl

The male with *ZZ* chromosomes and the female with *ZW*. (After Shiwago)

Sex in Parthenogenetic Forms

A most striking confirmation of the chromosome theory of sex determination has come from work on those forms which normally reproduce both by the sexual method and by the process of natural parthenogenesis. In many animals both of these types of reproduction occur as normal phases of the life history of the species; but it has been shown cytologically that whereas the fertilized eggs always give females, the unfertilized eggs may, in some insects, such as bees, develop parthenogenetically into males exclusively, and in others, like

the aphids and *Phylloxera*, into both females and males. The differences mentioned in these parthenogenetically produced types have been shown to be due to the chromosomal constitutions of the eggs: where they contain the haploid, or reduced, number of chromosomes, as in the honey bee, only males originate; where they possess the diploid, or full, set of chromosomes, as in the aphids and phylloxerans, both males and females come into existence. In these latter cases it has been further shown that while the full double set of ordinary chromosomes, or autosomes, is present in individuals of both sexes, the females contain both of the X elements and the males just one of them.

Biologists thus recognize two kinds of natural parthenogenesis, depending on the number of chromosomes present within the developing ova: (1) the *diploid type* and (2) the *haploid type*. In the diploid type no reduction occurs in the number of chromosomes within the germ cells, so that the eggs are found to possess the duplex set of chromosomes. A single polar body is formed, and this likewise contains the full duplex set of chromosomes common to the species. In the haploid type, however, the simplex number of chromosomes is found within the eggs. Here two polar bodies invariably are formed and a reduction of chromosomes takes place. Good examples of the diploid type of parthenogenesis are the aphids and *Phylloxera* among animals and the dandelion among plants. The haploid type is illustrated by such an animal as the honey bee, and such plants as Jimson weed, tomato, and wheat. To get a fuller comprehension of what actually goes on, let us discuss the conditions existing in the aphids and *Phylloxera*, and in the honey bee.

Aphids and *Phylloxera* (diploid type of parthenogenesis)

Before describing the details of this process it may be well to explain that normally these insects undergo parthenogenesis throughout the summer months, but at the approach of colder weather in the fall, both males and females are developed and the true sexual cycle occurs. The spermatozoa of

the males fertilize the ova of the females, thereby producing the zygotes, which, after remaining dormant throughout the winter, develop into females in the spring. These females then give origin to various generations of summer eggs, which by parthenogenesis develop into other females.

Careful examination of the eggs of these parthenogenetic females reveals that they contain the full double set of chromosomes, those of the aphid *Aphis saliceti*, as pointed out by De Baehr, containing six chromosomes (four ordinary ones and two X-chromosomes, each one of which is single), and those of the insect *Phylloxera fallax*, as indicated by Morgan, possessing twelve chromosomes (eight ordinary ones and two X-chromosomes, each one of which is double). In both of these species, at the approach of fall, two types of eggs are deposited: large ones, which are female-producing; and smaller ones, which are male-producing. When these eggs are carefully examined, it is found that the larger ones, as in the case of the summer eggs, contain the full diploid number of chromosomes, there being six in the aphid and twelve in the phylloxeran. The smaller eggs, on the other hand, although containing the full double set of ordinary chromosomes, possess only one of the X elements, there being present five chromosomes in the aphid and ten in the phylloxeran.

A word of explanation is necessary to clarify this seeming discrepancy. It has already been mentioned that in these parthenogenetic eggs only one polar body is formed and no reduction of chromosomes takes place. Since the smaller, male-producing eggs each have one X element[1] less than the larger, female-producing eggs, something must occur within the smaller eggs to account for the difference. What actually happens is that into the polar bodies accompanying the smaller ova there is extruded, besides the full set of chromosomes, an additional X element, leaving within the small aphid egg four autosomes plus one X-chromosome, making a total

[1] It must be remembered that this X is one chromosome in the aphid and two chromosomes in the phylloxeran.

of five chromosomes, and within the small phylloxeran egg ten chromosomes (eight autosomes plus an X element composed of two chromosomes).

Through parthenogenesis the larger eggs develop into females and the smaller eggs into males. The individuals then produce mature gametes, which after fertilization form the zygotes that remain more or less dormant through the winter months. In the following spring these zygotes develop into females exclusively. Why no males should be developed from fertilized eggs remained a mystery for a considerable period of time, until Morgan and De Baehr succeeded in satisfactorily clearing up the matter. These investigators were able to show that the eggs of the female were all of one type, containing the full set of the reduced number of chromosomes, which may be conveniently represented by the formula N + X. They also succeeded in establishing the fact that although the reproductive cells of the males started out by developing into two types of spermatozoa, one half containing the X element and the other half lacking it, nevertheless only the former came to maturity, whereas the latter atrophied and underwent disintegration. Because of this situation, the only mature germ cells which developed to participate in reproduction were those of constitution N + X. When fertilization took place, the zygotes produced were all of constitution NN + XX, leading to the formation of females exclusively. These were the stem individuals which, in the spring, gave origin to the eggs that were responsible for the development of successive generations of summer females, through the medium of natural parthenogenesis.

The Honey Bee (haploid type of parthenogenesis)

The parthenogenesis which occurs in the honey bee is an illustration of the haploid type, and it also bears out in striking manner the chromosomal basis of sex determination. In this interesting species both females and males occur side by side, and these are produced differently, — the females develop only from eggs which have been fertilized, and the

males from eggs which have not been fertilized, through the process of natural parthenogenesis. As far as chromosome number is concerned, it has been shown by Nachtsheim that the females contain thirty-two chromosomes and the males sixteen. Moreover, all the eggs produced contain sixteen chromosomes, and the spermatozoa also contain sixteen. Inasmuch as the spermatozoa originated from the parthenogenetic males containing a similar number of chromosomes, it is obvious that in the formation of the spermatozoa no reduction division has occurred; instead there takes place an abortive division of the primary spermatocyte, in which the chromosomes appear without dividing at one end of the cell and at the other end a sort of polar mass of material is extruded. The divisions that then follow are all equational, resulting in the formation of spermatozoa containing sixteen chromosomes, similar to the number found in the ova. Fertilization brings in the two simplex sets of chromosomes that unite to form a zygote with the duplex set, thirty-two, and this gives origin to a female. On the other hand, those eggs which develop parthenogenetically have the simplex set of chromosomes only, sixteen, and they develop into males. The females, of course, soon become differentiated into the fertile queens and infertile workers, but this is largely a process of environmental differentiation, owing to the fact that the fertile females develop within queen chambers, receiving richer food than the infertile females, which develop within the worker chambers. Although no sex chromosomes have as yet been established here, it is obvious that the production of males and females lends itself to the regular interpretation, — the males having a chromosomal composition of N + X and the females, NN + XX.

Gynandromorphs, or Sex Intergrades

In connection with our discussions of sex determination the case of *gynandromorphs*, or *sex intergrades* (Fig. 35), in which one side or portion of the body of an organism resembles a

female and the remaining side or portion the male, is extremely interesting. In bilateral gynandromorphs, one half of the body shows male characteristics, and the other half female characteristics. Such abnormalities have been shown to exist in a larger number of animals, chiefly the various types of insects.

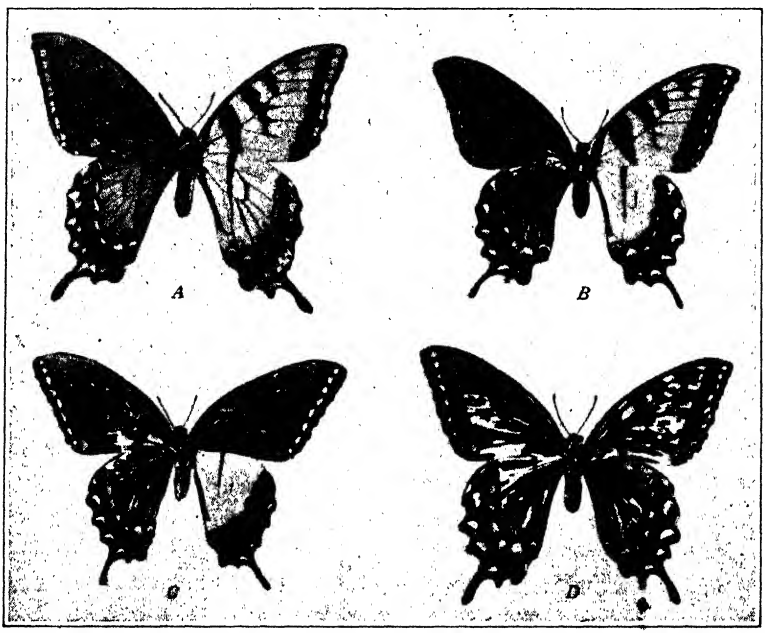

FIG. 35. Sex Intergrades, or Gynandromorphs, in the Butterfly *Papilio glaucus Linnaeus*

A, under side (left half, female; right half, male); *B–C*, upper sides, showing different degrees of gynandromorphism; *D*, upper side of a mosaic, combining the male and female patterns of the wings in a rather haphazard manner. (Courtesy of J. D. Gunder)

In the higher animals also there have been recorded some good examples (Fig. 36) of gynandromorphism. Although it is difficult to give an absolutely satisfactory explanation of gynandromorphism, nevertheless in the last few years considerable light has been shed on the problem, particularly by the workers who have concentrated on the genetics of the vinegar fly. One explanation for bilateral gynandromorphism in bees is the one given by Boveri, that the condition is the

result of the delayed union of the spermatozoön that brought about fertilization with one of the nuclei of the dividing egg, following the initiation of development, so that one half of the cells of the organism contains the duplex set of chromosomes leading to female structures, and the other half the haploid number of chromosomes leading to male structures.

Another explanation, and a better one, is that which was given by Morgan and Bridges for bilateral gynandromorphs in the vinegar fly, namely, that the condition results from the extrusion of an X-chromosome in the early blastomeres of one half of the developing zygote and the retention of the full set of chromosomes in the blastomeres of the other half. The result is that the side which contains the full set of chromosomes develops female characteristics, and the other side male characteristics. Breeding tests and crosses have demonstrated that this latter explanation is probably the more accurate one. There are some *intersexes* which are of the nature of *mosaics* (Fig. 35, *D*), in which part of one structure resembles one sex and its neighboring part the opposite sex. What accounts for such mosaics is difficult to answer. Some investigators are of the opinion that certain of them may be explained on the basis of the peculiar distribution of the chromosomes, especially the sex chromosomes, during the division of a number of the somatic cells of an embryo that is undergoing development.

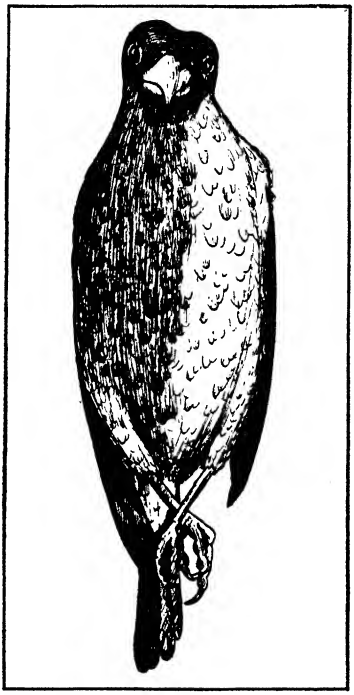

Fig. 36. A Gynandromorph Bird
The darker, male side possessed a testis; the lighter, female side possessed an ovary. (Redrawn after Poll)

Sex Chromosomes in Plants

In recent years some evidence has been accumulated to show that sex in plants is established in the same way as in animals. Charles E. Allen (*Bi. 1*), botanist of the University of Wisconsin, was the first investigator to discover sex chromosomes in a limited group of plants, namely, the liverworts, and since his discovery numerous other investigators also have shown the existence of such chromosomes in the higher plants (Fig. 37). Inasmuch as the number of known cases in plants is

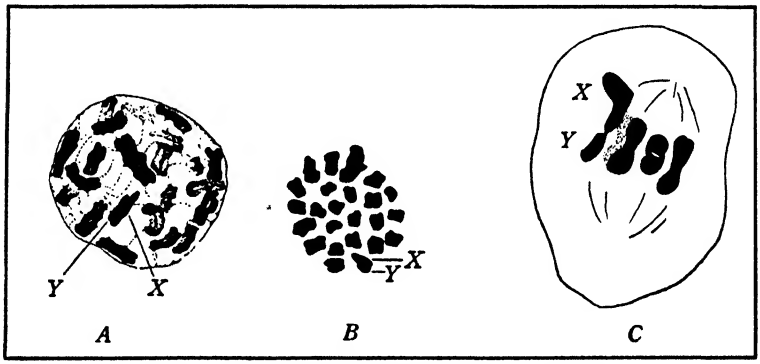

FIG. 37. Sex Chromosomes in Flowering Plants

A–B, the condition in *Elodea gigantea* (after Santos); *C*, the condition in *Melandrium album* (after Winge). (From Bělař)

very limited, we must be careful in our conclusions; but this much is certain, — that in some of the higher plants the conditions which bring about the male and female sexes appear to be similar to those outlined for the animals. Whether this is the case for the other forms in which sex chromosomes have not been discovered is a question which cannot be answered at the present time (*Bi. 213*).

In this connection it must be stated that in a great many animals and in most plants the accessory chromosomes have not as yet been shown to exist. In these organisms perhaps sex is due to a different process, or perhaps the sex chromosomes are present but cannot be distinguished from the ordinary chromosomes. Moreover, it has been established

definitely that in certain animals the sex chromosomes are not always separate entities, but rather are structures which are linked to other chromosomes (Fig. 38); and this may be the situation in a good many other instances where sex chromosomes have not as yet been discovered.

Genic Balance Theory of Sex

Largely through the work on intersexes of the fruit fly (*Drosophila melanogaster*) as reported by Calvin B. Bridges (*Bi. 2*), and of the gypsy moth (*Lymantria dispar*) as reported by Richard B. Goldschmidt (*Bi. 91, 92*), the genic balance theory of sex determination has been developed. There are but slight differences in the theory as propounded by these two investigators.

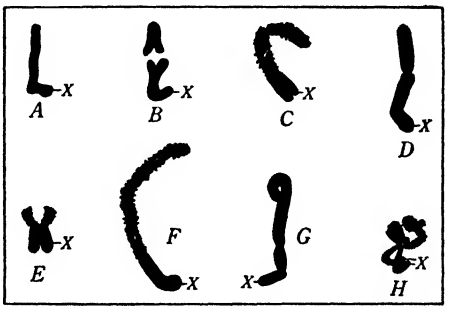

FIG. 38. Linkage of *X*-Chromosomes to Autosomes[1]

Conditions encountered in various Orthoptera. (*A–B*, after de Sinety; *C–H*, after McClung)

According to Bridges, sex is conditioned by the number and strength of the genes not only of the sex chromosomes but also of the autosomes. It is believed that the X-chromosome carries the female tendencies, and the autosomes the male tendencies. The reason why the chromosome combination represented by the formula NN + XY gives origin to a male is that the female tendencies in X are not strong enough to overcome the male tendencies in NN. On somewhat similar grounds, the formula NN + XX gives origin to a female because genes for femaleness in XX are twice as strong and overcome the male tendencies within the autosomes, NN.

[1] From Kellicott's *General Embryology*. By permission of Henry Holt and Company, publishers.

Goldschmidt, from his researches on the gypsy moth, regards sex as a quantitative relationship, that is, a balance, or ratio, between the male and female sex genes. Inasmuch as the chromosomal conditions for sex determination in the gypsy moth are the reverse of those for the fruit fly, Goldschmidt places the male-determining gene in the X-chromosome (here called the Z-chromosome) and that for femaleness outside of this sex chromosome. At first Goldschmidt was of the opinion that this factor for femaleness was found only within the cytoplasm of the egg, but later he was inclined to assign it to the Y-chromosome (here called W).

Present Status of Opinion

Most geneticists are of the opinion that sex is determined either at the moment of fertilization or very soon afterwards. Biologists do not say that the sex chromosomes determine sex, but rather that they are the regulators, carrying certain elements which influence the determination of sex. Most of them are exceedingly careful not to say that the sex chromosomes are the final determiners; for since 1905 they have found that sex is really a very complicated phenomenon, which cannot be determined by any one factor alone, and also that it may be influenced or interfered with by certain other factors outside of the sex chromosomes. We know now, for instance, that in the higher animals, while the major primary characters for sex are outlined by these entities carried in the sex chromosomes, nevertheless there are other influences, such as the secretions of the glands of internal secretion, *endocrine glands*, which also may play their part. If anything happens to upset the normal balance between these external agencies and those initiated through the sex chromosomes, it may result in modifications leading to different expressions. Because of this, it is almost impossible to predict or control the sex of an individual. Sex, therefore, seems to be a rather complicated process, dependent for its expression not only on the sex chromosomes but also on a number of other very important

factors within the organism, particularly those developed by the glands of internal secretion. These latter substances are known technically as *hormones*, and ordinarily they act as messengers which stimulate the sex-determining genes within the sex chromosomes to develop all the characteristics of either the male or the female. In those cases where development is abnormal the hormones may interfere with and even grossly modify the normal progress of the sexual traits so as to give origin to malformed and abnormal monstrosities. Instances of this sort will be dealt with more fully in the next two chapters.

The phenomenon of *sex linkage* also checks up very nicely with the problem of sex determination, helping to establish the fact that the chromosomes are the carriers of the genes responsible for the expression of traits. Not only do sex chromosomes carry genes which influence sex, but likewise they may be the carriers of other genes responsible for the expression of additional characters. Studies in genetics have shown that such genes are linked together with the sex-producing genes inside the sex chromosomes in a manner that accounts for the so-called sex-linkage effects to be considered later on.

Thomas Hunt Morgan, in his presidential address, entitled "The Rise of Genetics," before the Sixth International Congress of Genetics, comments on the genes as sex factors as follows:

All through the 32 years of the present century there have been attempts to isolate (in a genetic sense) the sex-determining factors. At first, when the chromosome mechanism was discovered, the idea prevailed that one X, let us say, made a male, and two X's a female. The sex chromosome itself was then taken as the differential.[1] Very soon after this the idea that the sex chromosome was the carrier of a gene for sex suggested itself, and a search was started to locate such a gene or genes in this chromosome. More recent work on translocations[2] has shown the probable futility of such an interpretation. The tendency at present is rather to look

[1] The cause of the difference.

[2] Transfers of fragments of chromosomes and their attachment to nonhomologous chromosomes, leading to new arrangements of genes.

upon all the genes, or at least on many of them, as sex determining in exactly the same sense, as all or many of the genes have an effect on the development of each character. It may well be, however, that certain genes in the sex chromosome (as in other chromosomes) are more influential than others in turning the balance one way or the other, but even so, it does not at the present moment — in the light of recent evidence — seem probable that a single gene for sex determination is to be found in the X chromosome any more than, in the contrary sense, there is a single gene for sex in any special autosome. Here again, some one or a few genes may be more influential than others, but this is also true to varying degrees of the gene for any other character.[1]

In connection with the above discussions there are numerous other problems which are of great importance from a genetic standpoint, such as the production, sex, and heredity of twins, as well as the phenomena of abnormal individuals and monster formation. These topics will be considered in greater detail in Chapters VII and VIII. How sex is determined in animals has already been outlined. It has also been pointed out that as yet we have not discovered accessory chromosomes in all species of animals, and it is possible that in some cases the conditions for sex determination may be different, although there is no positive evidence as yet to support such a belief. In some species it has been shown that the sex chromosomes are not independent units but are permanently attached to the ordinary chromosomes, the autosomes, so that they might easily be overlooked and believed to be entirely lacking. In plants also it has been shown that, with the exception of a few limited forms, sex chromosomes are not in existence.

In spite of all these exceptions and differences of opinion, most geneticists believe that, in general, sex is determined in exactly the same manner as any other character, namely, through the genes within the chromosomes of the spermatozoön and egg that combine to produce the zygote. However,

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[1] T. H. Morgan, "The Rise of Genetics," *Proceedings of the Sixth International Congress of Genetics*, Vol. 1 (1932), pp. 99–100.

as will be shown in Chapters VII and VIII, where environmental and glandular effects on development are considered, when once the zygote undergoes its process of unfolding toward the finished organism, then the environment may play a very important rôle in influencing the expression and manner of completion of the various structures and organ systems of the adult. Under certain influences of the environment, certain organ systems may be modified, overemphasized, suppressed, or completely obliterated. This holds true for all characters, including sex. As a general rule, normal development should take place under normal circumstances, and abnormal development under abnormal circumstances.

CHAPTER VII

Multiple Individuals

THE term *multiple individuals* indicates the condition where more than a single organism is produced at birth. Two individuals appearing at one birth are spoken of as twins; three individuals, as triplets; four individuals, as quadruplets; more than four, as litters of the respective number of organisms actually born, such as a litter of five, six, seven, eight, and so on. Multiple individuals are invariably of two kinds: *unidentical,* or *fraternal,* and *identical,* or *duplicate.* Where the condition is unidentical, or fraternal, each of the organisms produced has come from the development of a separate zygote, or, to put it differently, as many eggs have been fertilized as the number of individuals born. Here the adult organisms reveal the same degrees of resemblance and difference as ordinary brothers and sisters (siblings). On the other hand, where the multiple individuals are identical, or duplicate, the evidence seems to indicate that they have been produced from a single zygote, and they reveal the most remarkable resemblances to one another. As a general rule, the differences in identical organisms are either nil or so slight as to be negligible.

There are many interesting questions which have arisen in connection with identical and fraternal organisms that are of importance to genetics: What accounts for identical and fraternal individuals, particularly twins? How similar are identical organisms, and how different are fraternal ones? Is the production of multiple individuals, such as twins, triplets, quadruplets, and so on, a hereditary trait which is transmitted in certain strains in a manner similar to such other well-known traits as color, stature, and vitality? Finally, what are the comparative effects of the factors of environ-

ment and heredity on the development of such organisms, particularly in the case of identical twins?

Francis Galton was among the first of the modern biologists really to concern himself with these questions, and in an effort to answer some of them he carried on extensive investigations on human twins, particularly identical ones. Inasmuch as interest along this line has centered mainly on the topic of twinning in animals, especially the production of human twins, it may be well to elaborate at greater length on this subject. It should be mentioned that what is true of twins applies also to triplets, quadruplets, and so on.

FIG. 39. Fraternal Twins

Although at five years of age the larger of these twins was four inches taller and nine pounds heavier than the smaller twin, at birth the other twin was the larger, weighing two ounces more than her twin sister

Fraternal Twins

Twins, like other multiple individuals, are of two kinds, fraternal and identical. Fraternal, or unidentical, twins are just what the term "unidentical" implies. In many instances they are unidentical in regard to sex, although they need not be, many of them being of the same sex; they are usually unidentical in appearance, so that ordinarily one can tell them apart very readily; they are unidentical in regard to various mental and physical capacities; and so on. They may differ as little or as much as any two brothers or sisters born at different times. Fig. 39 shows a pair of such fraternal twins.

Concerning the question of the production of fraternal twins definite and conclusive evidence is available to show that the condition is the result of two separate eggs being fertilized at about the same time. In other words, two zygotes develop simultaneously, each within its distinctive membranes, and the reason why the individuals are unidentical is because each one of them is the possessor of a somewhat different combination of hereditary genes. In view of these facts the condition that produces unidentical twins is known as the *dizygotic condition.*

Identical Twins

Identical twins, on the other hand, are generally alike from practically every standpoint, being of the same sex and possessing the same physical and mental capacities. Moreover, they come into the world at about the same time; live about the same kind of life — physically, mentally, and emotionally; and ultimately die at about the same age, unless an accident carries one off before the other.

In recent years identical twins have been investigated with a great deal of zeal, and biologists have reached the conclusion that the reason the two individuals are alike is because they have originated from the *monozygotic condition,* that is, from a single fertilized ovum. In order to understand what happens, one must realize what goes on during the early development of the zygote (Fig. 40). Although the description that follows is based chiefly on what takes place in the lower vertebrates, nevertheless, with minor modifications, comparable stages have been indicated for all the higher vertebrates, including the mammals.

Ordinarily the fertilized egg undergoes cleavage, segmenting into two, four, and more cells, progressing until it takes on the appearance of a sphere of cells resembling a mulberry and called the *morula.* Following this there is a hollowing out of the interior mass of the morula so as to produce a cavity filled with liquid, and very shortly the zygote takes on the appearance of a single-layered ball of cells, known as

a *blastula*. Through an invagination, or inpushing, of one end of the blastula a two-layered embryo is formed, known as the *gastrula*. From now on differentiation begins to assert itself more markedly and the parts become so definitely specialized that their rôle in the united organism is soon fixed. However, it must be emphasized that previous to the early

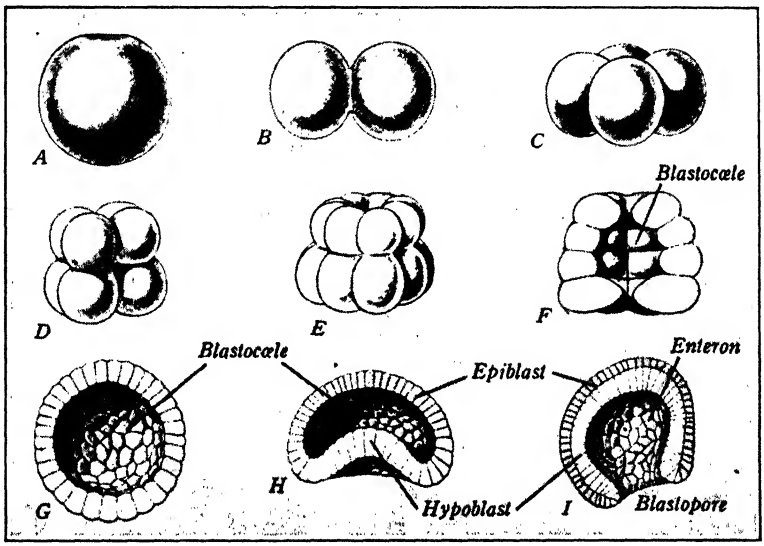

FIG. 40. Early Development of *Amphioxus*[1]

A-E, cleavage; *F-G*, vertical sections of blastula stages; *H-I*, vertical sections of gastrula stages

gastrula stage not much differentiation has set in and all the cells of the zygote are still remarkably similar in structure and function. These early undifferentiated cells are called *blastomeres*, and under normal conditions they remain attached to one another. Occasionally, however, abnormal development may occur, during which the young embryo splits into two equal halves in such a manner that each portion, instead of forming the respective right or left half of

[1] From Dendy's *Outlines of Evolutionary Biology*. By permission of D. Appleton-Century Company, publishers.

the united organism, proceeds to unfold into a perfectly formed individual, giving origin to identical twins. Unlike the products of the dizygotic condition, the two individuals produced from the monozygotic condition are usually surrounded by the same embryonic membranes.

In order to comprehend the resemblances of identical twins it must be remembered that basically they possess the same protoplasmic constitution, having been derived from exactly the same germinal source. In other words, the blastomeres of each of the two halves of the zygote responsible for an identical individual possess exactly the same number and types of genes. This identity is so definite that careful studies on identical twins have indicated that very little modification takes place in them, even though the twins may have become separated widely from each other and also may have had to adjust themselves to different environmental conditions. Such studies have been of tremendous importance in that they have helped to shed light on the age-old problem of which is the more important factor in development, heredity or environment.

During the last hundred years numerous geneticists have published results of their studies on identical twins. These have dealt mainly with the resemblances of such twins when reared in the same environment and also with the modifications, if any, engendered in them when reared apart, that is, in different environments. The work of Francis Galton, Paul Popenoe, Albert Edward Wiggam, Hermann J. Muller, Horatio Hackett Newman, and others may be mentioned in this connection. These investigators have carefully studied numerous pairs of identical twins, and it may be well for us to consider briefly some of their findings.

A number of years ago Paul Popenoe (*Bi. 171*) described an interesting case of identical girl twins (Fig. 41) who were reared apart in different homes and subjected to different environmental influences. The mother died shortly after the twins were born, and each of the girls was adopted by a different set of parents, dwelling in distinctly different parts of

the United States. Although the foster parents in each case were ranchers, their financial means were such that the twin sisters were subjected to different upbringing. The foster parents of one wandered around considerably, so that their adopted daughter likewise came to live in many different localities. This girl, after only a limited number of years of formal schooling, launched upon a business career which involved clerical, secretarial, and administrative work in the states of Montana, Wyoming, California, and New York. During the World War she entered the Food Administration Office in Washington, and from there was transferred to France, where she served for a time during and after the war. Her twin sister remained in the West, mainly in the state of South Dakota, and since her foster parents were in fairly comfortable circumstances she had larger opportunities for education. She attended and graduated from grade and high schools and then began training as a nurse. She also had some summer university work and then taught school for a number of years, withdrawing from that position upon her marriage to a man by the name of Sanders. The year following she gave birth to a son. From Mrs. Sanders, Popenoe obtained most of his information regarding these twins.

FIG. 41. Identical Twins Reared Apart[1]

[1] From Popenoe, courtesy of *Journal of Heredity*.

It appears that following their separation the twins did not see each other or correspond with each other until they were eighteen years old. They have been together but very few times since they were born and then for only short intervals. Of course Popenoe was chiefly interested in studying the influences of the factors of heredity and environment in molding the personalities of the twins. After a very careful investigation of the case, he came to the conclusion that these two girls, even though they were raised under wholly different circumstances and in widely divergent localities, exhibited about the same physical and mental traits. They preferred similar types of books for reading; they had about the same tastes in dress, although, of course, they did not dress alike; they had similar likes and dislikes for certain colors; their companions were more or less of the same type, possessing similar mental and physical characteristics. Finally, they became interested in somewhat the same lines of work. Popenoe describes the likeness between these twins in the following words:

The physical likeness of the two is close. The two, according to Mrs. Sanders, are of exactly the same height, and nearly always weigh within a few pounds of each other. When they have been together, they have worn each other's clothes perfectly and friends found their voices indistinguishable. Their hair is identical in color, and few people can tell them apart. Mrs. Sanders' son has never seen his aunt, but cannot distinguish her photograph from that of his mother. Both have weak lungs "and have been run down from that cause, and nearly always at the same time."

"I am very sorry," the narrator continues, "that I cannot remember exact dates of illness, but many times our letters bearing word of enforced idleness have crossed, until we began to expect to hear of the other's illness as soon as one of us was indisposed."

The mental similarities are perhaps less to be expected than the physical resemblances, but are no less striking. To quote the informant:

"It is almost uncanny, the way we are always doing identical things at the same time. The latest instance is in having our hair cut, each without the other's knowledge. This really took courage, because the majority of our friends do not approve.

"We are both high strung and do not seem to conserve our energy as we should, but I have been resting more gracefully than I ever have before, and in her latest letter she expresses the same mood.

"I believe (and of course say this without conceit) that an intelligence test would find our capacities very similar, and I surely would like to try the experiment if the opportunity presented itself.

"We both favor history, social study 'that functions,' and politics. Neither of us cares for mathematics, and I would not call either of us a good student. We are too 'smattery,' although we learn rapidly and with very little effort.

"I might add that we both seem to show some administrative ability, because we invariably hold an office in every organization we affiliate ourselves with. Last year I was treasurer of our state teachers' association, and am chairman of two county committees now. The latest letter from Bess advises that she has just been elected president of the women's division of a commercial club." [1]

In 1925 Hermann J. Muller (*Bi. 147*), of the University of Texas, reinvestigated these identical twins, particularly from the standpoint of intelligence. He gave them the standardized intelligence tests, and when these were scored he discovered that the scores varied hardly a fraction from each other. The remarkable thing about it was that even though these twins lived in entirely different localities and had never associated much with each other, yet the scores were nearly identical, which not only indicates how similar identical twins really are but also emphasizes the dominance of heredity over environment in the formation of the fundamental physical structures and mental attributes of the adult organism. Muller states:

"Intelligence tests" applied to these twins yielded scores very significantly alike, despite great differences in the amounts and kinds of formal schooling they had had, and other environmental differences dating from two weeks of age onward.[2]

[1] Paul Popenoe, "Twins Reared Apart," *Journal of Heredity*, Vol. 13 (1922), pp. 142–144.

[2] Hermann J. Muller, "Mental Traits and Heredity," *Journal of Heredity*, Vol. 16 (1925), p. 444.

So similar are identical twins that a careful check of the scholastic and activity records of the three pairs shown in Fig. 42, students at Oregon State College, reveals the closest possible identity. A weighted average of the grades, over a period of four years, of the pair wearing dark coats shows a difference of less than .01 of a point between them. These twins majored in the School of Forestry, having taken a very

FIG. 42. Three Pairs of Identical Twins

The physical and mental characteristics of identical twins show remarkable similarities

prominent part in the activities of their school. Their scholastic records have been so uniformly good as to merit their election, at the same time, into the forestry honor fraternity.

The tallest pair of these twins, specializing in civil engineering, have almost exactly the same high-grade average. Their records have been so similar that when the honors committee was selecting the sophomore student most worthy to receive one of the choice prizes awarded by the college, it found the performance of these identical twins just alike, so that it could do nothing else than split the prize equally between them.

Although the third pair of twins, those dressed in the

sweaters, who are enrolled in the School of Education, have practically the same scholastic average, they show their most striking similarities along athletic lines. Both of them are 100-yard and 440-yard men in track, both are backfield performers in football, and both are good wrestlers. Their track coach states that their performance in the events listed is practically identical. Moreover, the only way he can tell these boys apart is that one of them has a mole on the nose, which the other does not possess.

In general, the twins of each of these three pairs are so much alike that it is extremely difficult to distinguish them apart. Their resemblance in height, body build, posture, voice, and general appearance is such that it is not unusual for their friends to mistake one for the other.

One of the most remarkable investigations into the similarity of identical twins is the one made by Johannes Lange of Munich, Germany, reported in his book entitled *Crime and Destiny* (*Bi. 130*). Lange was interested particularly in the problem of finding out what rôle the factor of heredity played in predisposing individuals to crime. His studies embraced thirteen pairs of identical twins and seventeen pairs of fraternal ones, one or both members of each pair having had a criminal record in the prisons of Bavaria. An astonishing fact of unusual interest revealed by this investigation was that out of the seventeen pairs of fraternal twins, in only two cases had both members of a pair been imprisoned, whereas of the thirteen pairs of identical twins ten pairs had been imprisoned and in nearly every instance the crimes for which both members of each pair had been convicted were strikingly similar. Still more remarkable is the fact that in not a single instance were the two members of any pair associated together in the particular crimes for which they were sentenced. In the cases of the remaining three pairs of identical twins, only one member of each pair had a criminal record, but the circumstances surrounding these crimes were such as to indicate that factors other than hereditary ones may have been the responsible agents. One of these individuals suffered a head

injury at birth, another had a severe goiter, and the third became separated from his twin early in life and thereby was subjected to a radically different social environment. No one can read Lange's book without realizing that the main reason why these identical twins revealed the same criminal tendencies is because, by the very nature of their formation from a single zygote, they were endowed with similar hereditary potentialities.

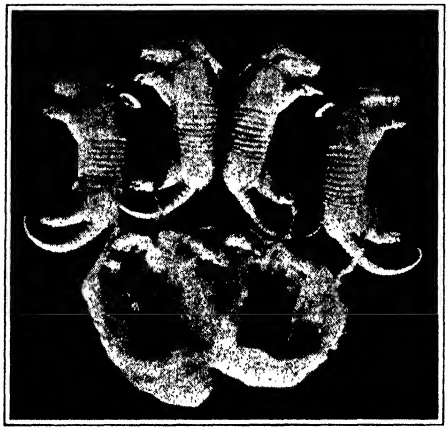

FIG. 43. Four Identical Armadillos from a Single Zygote[1]

Sometimes more than two identical individuals are produced from a single zygote. This is especially true in some of the animals below man. In one species of armadillo (*Bi. 155*) four distinct animals are always developed from the single fertilized egg (Fig. 43). These are identical from all standpoints,—appearance, size, sex, and so forth. In some insects many identical young are produced similarly from the splitting of a single fertilized ovum. When examined, all these organisms show the same remarkable similarities as do identical human individuals.

Importance of Heredity and Environment

Studies on identical twins have helped us in answering the question of which is the more important, environment or heredity. While identical twins are ordinarily alike in practically all respects because of their similar hereditary backgrounds, and tend to remain alike even though they may be

[1] After Newman and Patterson, courtesy of *Journal of Morphology*.

separated from each other by tremendous distances, nevertheless in recent years it has been established that in certain cases the environment may bring about some differences, especially where the individuals have had to live under distinctly different conditions of great stress. During the World War, for instance, it was established that identical twins who became separated from each other for a considerable period of time because one was interned in an enemy prison camp, or both were interned in separate camps, showed the development of differences. The explanation for these modifications is rather difficult, but may be similar to that which Guyer put forth in connection with his rabbit experiments, namely, that, owing to some stimulus of a serious character, a certain chemical agent or toxin was produced in the body of one organism, and this affected certain definite structures or organs so as to bring about their modification. From what we know of the reactions of living protoplasm, this explanation would seem to fit the cases cited. It does not, however, explain other instances where differences have appeared in identical twins reared apart in normal but differing environments. Let us now discuss these at greater length.

In a number of recent studies Horatio Hackett Newman (*Bi. 152–154*), of the University of Chicago, has shown that some identical twins reared apart and subjected to different environmental and educational influences tend to become modified in certain respects. In commenting critically on his results obtained from identical twins reared apart, Newman asserts that

> Nevertheless, the tests do show very definitely that different training, different experiences, and different modes of living profoundly affect the intellectual, temperamental and physical characteristics of the individual. They have a considerable share in determining a given person's mental powers, his character, and his physique — in a word, his individuality. Hence we may conclude that training, social contacts, and living conditions, the main elements of the human environment, actually do have an important influence in determining what kind of person one becomes.

But it would be a great mistake to overemphasize the environment at the expense of heredity, for the degree of similarity that persists in all these twins, even though the environment has worked upon them in diverse ways, is even more remarkable than are the differences noted. Moreover, many of their characteristics, such as coloring, dentition, hair characters, features, general bodily peculiarities, voice, gestures, palm and finger patterns, ears and other traits too numerous to mention, are evidently almost purely hereditary in the sense that they are unmodified by existing differences in the environment. Some of their other character differences, such as those of body weight, muscular development, state of complexion, mannerisms, gait, and a few other traits, seem to be largely environmentally determined, in the sense that they are very plastic and easily modified by actual differences in the environment.[1]

Newman has also studied Siamese, or conjoined, twins (to be considered in the next chapter), and has pointed out the existence of differences between them (*Bi. 151*). He goes on to explain that such differences will appear when the splitting of the zygote to produce the conjoined condition occurs after some differentiation in the early blastomeres has already begun to set in. The more opportunity these blastomeres have had to become differentiated, the greater becomes the possibility that the resulting conjoined twins will be different. This same rule also applies to identical twins.

On the basis of numerous studies similar to those that have been indicated, Newman concluded that resemblances and differences between identical individuals are such that twins may be arranged in a graded series, ranging from those that are so much alike that they are exact duplicates of each other to those that differ considerably. As intimated, these gradations in identities may be explained on the basis of the time of the separation of the two halves of the developing embryo. Ordinarily such separation to form identical twins occurs either slightly before or during the gastrula stage in development. Those individuals formed before gastrula-

[1] H. H. Newman, "Mental and Physical Traits of Identical Twins Reared Apart, Case IV, Twins Mary and Mabel, and a Review of the First Four Cases Studied," *Journal of Heredity*, Vol. 23 (1932), pp. 15–16.

tion has begun, before there has been much opportunity for any degree of differentiation in both sides of the embryo, show the most striking similarities. If, on the other hand, the separation of the two halves has taken place early in the period of gastrulation, after some differentiation has already begun to appear on both sides of the developing embryo, differences assert themselves, and these appear in the two organisms formed. If the splitting off of the two halves of the embryo is completed late in gastrulation, then the most striking differences may be encountered, but it must be remembered that this is exactly what one would expect, because during late gastrulation salient modifications have already expressed themselves on both sides of the developing individual. Moreover, there is little tendency to mirror imaging (the right side of one showing resemblances to the left side of the other, and vice versa), such as is the case in duplicate twins formed during early gastrulation. Instead, both sides of the individual formed from the right half of the embryo resemble the characters normally expressed on this right side. Likewise, both sides of the individual formed from the left half also express the traits normally found on the left side of the embryo. Unquestionably a similar situation exists in many of the other paired organs of the body. In conjoined twins the most striking distinctions have been revealed. According to Newman, the chief reason for these differences in the conjoined individuals is the fact that during late gastrulation, when the two sides of the embryo started their separation, specific modifications had already set in, clearly differentiating the right and left sides of the developing structure.

In a study of the effects of environment and heredity on various kinds of twins, Nathaniel D. Mittron Hirsch (*Bi. 107*), chief psychologist of the Wayne County Clinic for Child Study, Detroit, Michigan, recently came to the following conclusions:

The study demonstrates that heredity and environment both contribute to the intelligence and anthropomorphic[1] qualities of

[1] Possessing human form or human characteristics.

the individual, but that their contributions are far from being equal. Neither the extreme hereditist nor the extreme environmentalist is correct, but the contribution of heredity is several times as important as that of environment.

The study has shown, moreover, that heredity and environment vary in their relative importance in relation to specific or general traits. Thus from our data it was seen that heredity was about five times as significant as environment in determining I.Q.[1] differences between twins, while for weight, heredity was only about twice as potent in its causal effectiveness as environment. Our study did not quantitatively test emotional qualities, but from what scientists have discovered about impulsive and emotional processes, and their general positive correlation with intelligence, it is highly probable that in respect to these qualities heredity would be found to be from two to five times as potent as environment.

Furthermore, it should be added here that several experiments have demonstrated that education and training vary in their influence in proportion to the hereditary type with which they are dealing — the more intelligent the individual the more potent educational and general environmental influence. It may be stated then that the importance of environment increases roughly as we ascend the human scale. In other words, environment becomes more important as heredity becomes higher and more competent, paradoxical as this may seem. This truth again shows that heredity and environment are by no means intrinsically antagonistic.

But there is no doubt that today many of the environmental agencies of civilization are contributing to "The Decline of the West," and that political wisdom can be garnered from a study of twins, and from other experimental studies of heredity and environment.[2]

In bringing this portion of our discussion to a close, it must be emphasized that, after all, the factors of both heredity and environment are important in development. The environment can never be disregarded. A desirable environment must be present to make possible the expression of the germinal entities that went into the formation of the individual.

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[1] This is an abbreviation for *Intelligence Quotient*, a measure of an individual's intelligence based on certain test scores which take into consideration age of persons examined.

[2] N. D. M. Hirsch, *Twins*, pp. 147–149. Harvard University Press, Cambridge, 1930.

On the other hand, the environment alone cannot put a wonderful brain into an individual who does not have the capacities for such a brain. Most biologists are of the opinion that given a good foundation of genes within the germinal stuff to start with, then, to a very large extent, the environment determines which part of the stuff actually expresses itself. Surroundings should be the very best possible in order to give the genes within the zygote the greatest opportunity for full expression.

CHAPTER VIII

Monsters and Abnormal Individuals

THE discussion of the various kinds of multiple individuals in the last chapter has made possible the consideration in this chapter of the formation of monsters and other abnormal types. As will be recalled, the number and kinds of organisms produced from a developing zygote depend, to a large extent, on the number and manner of segregation of the portions into which the young zygote happens to split. When the parts separate completely, normal identical individuals are formed, accounting for identical twins, triplets, quadruplets, and so on. When the separation is incomplete, abnormal development invariably ensues, resulting in the production of many types of monsters. It may be well for us to consider the manner in which some of these monsters are engendered.

Siamese, or Conjoined, Twins

Sometimes the two equal portions of a zygote, which ordinarily produce identical twins, may separate completely at just the anterior end and at the same time remain attached at all other places, resulting in the formation of an individual with one body and two complete heads. On other occasions the posterior portion is the only place of separation, and this gives rise to an individual with one head, one trunk, and two pairs of legs. If the parts should happen to remain attached somewhere in the middle and at the same time should split at both anterior and posterior ends, then *Siamese,* or *conjoined, twins* would be produced (Fig. 44), consisting of two complete individuals united somewhere in the trunk region. Usually it is not possible to separate such twins, since the

place in which they are conjoined may contain vital organs that are essential to the welfare of both of them. In most instances these monsters die soon after birth. Fig. 45 shows human conjoined twins of various types, depending on how the two portions of the zygote separate during early embryonic development.

FIG. 44. Siamese, or Conjoined, Twins

These Siamese twins from the Philippine Islands are shown with their wives, separate identical twins. (Courtesy of *Journal of Heredity*)

The Freemartin

Another very interesting case of an abnormality is that of the *freemartin* (Fig. 46), which invariably appears in connection with the production of dizygotic twins in cattle. The freemartin condition in cattle has been known for a long time, but only within very recent years have biologists been able to explain it. As far as is definitely known, the freemartin occurs in cattle but in no other animals. There may, of course, be other species where the same abnormality exists, but thus far freemartins have not been fully established among any other animals except cattle.

A freemartin is a sterile female individual of two-sexed twins in cattle, which externally appears like a female but internally has become so modified as to resemble a male. The trained farmer or breeder can readily distinguish these abnormal types, but for many years it was impossible to give the reasons which accounted for their production. It remained

one or the other of the sexes are present within the zygote from the very beginning of development. Occasionally something will happen to bring about expressions of both sexes, leading to the emergence of such individuals as sex-intergrades and hermaphrodites. Such phenomena have already been reviewed in Chapter VI, where the question of sex determination was considered. The freemartin is neither a sex-intergrade nor a hermaphrodite, for the reason that externally it seems to be a female, but internally the male tendencies have become the stronger. The explanation for its production is the one just given, that the gonads of the male twin develop faster and liberate a greater amount of hormones than those of the female twin, with the result that before the female reproductive organs have had a chance to establish themselves, they have been interfered with so much that they are prevented from developing to maturity. Concerning the question of whether the female of two-sexed twins in cattle ever develops normally, the answer is that this has been found to occur in about 6 per cent of the cases. Where such is the situation, the fetal membranes invariably remain distinctly separate, with no fusion, and normal individuals of both sexes are produced. In the other 94 per cent of the cases the development is abnormal, leading to the production of males and freemartins.

In regard to two-sexed human twins there exists no evidence to show that the female of such twins is sterile, in spite of the fact that there is a common belief to this effect, especially prevalent in agricultural communities where cattle-breeding is practiced. There is not a shred of scientific evidence to substantiate such a view, inasmuch as in human beings the membranes of the differently sexed individuals always remain separate and unfused throughout development, leading to the birth of normally fertile twins. It must be recalled that the freemartin occurs only in cattle. In the other mammals which have been studied, including wild and domesticated types, the fetal membranes of opposite twins seem to remain unfused, leading to the emergence of normal individuals.

Glands of Internal Secretion

The consideration of the freemartin brings up once more the question of the rôle played by the glandular secretions in normal and abnormal development. Those which are of special significance for our purpose are the products manufactured by the *glands of internal secretion,* or *endocrine glands.* During the last few years a large number of biologists have been studying these structures and have discovered that the secretions which these glands manufacture are of vital importance in the progressive unfolding of the organism. In those instances where a gland is modified so that the amount of its secretion is above or below normal, various malformations are apt to result, leading to the production of defective and abnormal types of organisms. Treatment of such individuals with appropriate amounts of prepared glandular extracts has often brought about such tremendous improvements in them that it has given many persons the impression that no matter how imperfect an individual's endocrine glands may be, he can be made normal by proper glandular treatment. Some investigators have been so optimistic in their claims as to what the prepared secretions of the endocrine glands will do that many distorted notions have been broadcast, often so inaccurate that they have developed a great number of misconceptions. Consequently the average person, misled by some of these views, has the firm conviction that it really does not matter what the heredity of a defective individual may be, for, since he can be treated by certain of the glandular extracts, he can be cured completely of his special defects or malformations.

While many startling transformations have been brought about through such treatment, nevertheless it must be remembered that, in large measure, the physical and mental nature of the individual organism is dependent on heredity. The kind of glands an organism possesses and the amount of their secretions depend mainly on the genes brought in by the germ cells that united to form the zygote that gave

origin to the particular individual. Whether a gland is large or small or is entirely lacking invariably depends on hereditary factors. Of course the environment is also important, but basically the formation of the glandular structure and the amount of its internal secretion are largely matters of the hereditary constitution of the zygote which gave origin to the individual.

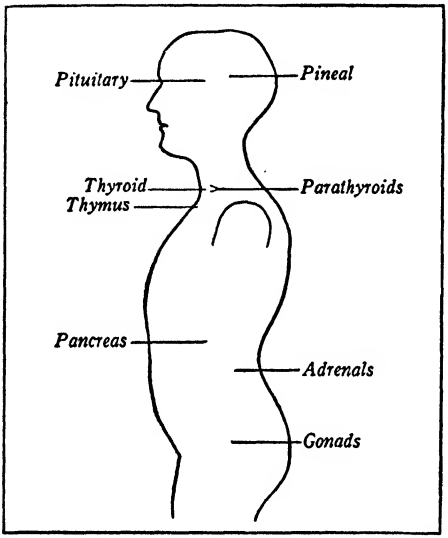

FIG. 47. Location of the Principal Endocrine Glands

As far as is known, the glands of internal secretion are confined almost exclusively to the higher animals, particularly the vertebrates. They are structures that manufacture secretions which are poured directly into the blood or lymph and are then carried by these circulating fluids to other portions of the body. They are rich in substances known as *hormones*, which, according to Hoskins, are "substances produced in one part of the body and distributed by the blood or lymph to other parts, the structure or functions of which are thereby modified." Biologists have recognized two general classes of glands: (1) those without a duct, commonly called the ductless glands, and (2) those possessing a duct. Belonging to the first group are such glands as the *thyroid*, *parathyroid*, *pituitary*, *adrenal*, *thymus*, and *pineal* glands and the *spleen*. In the second group may be placed structures like the *gonads* (testes or ovaries), *liver*, *pancreas*, *stomach*, *upper intestine*, and *kidneys*. Although these latter glands possess ducts, still the hormones which they manufacture are found to be absorbed directly into the blood or lymph in the same man-

ner as are other similar secretions of the ductless glands. The ducts have been developed chiefly for the purpose of conveying other products than the hormones. Fig. 47 is an outline drawing of the human body, indicating the location of the chief endocrine glands.

Although this field of investigation is still comparatively young and investigators are still groping in the dark regarding many of the functions of these glands, it has been shown definitely that hormones exist in the thyroid, parathyroid, and pituitary glands, the adrenals, the reproductive glands, and certain special areas of the pancreas. The other glands, such as the thymus, pineal, spleen, liver, stomach, upper intestine, and kidneys, have also been suspected of manufacturing hormones; but the evidence in favor of this has been so scanty that we shall do well to dismiss them and confine our attention exclusively to those glands which have been definitely proved to carry on endocrine functions and to manufacture hormones. Of necessity this account must be rather brief, but those who are interested in a fuller treatment are advised to read *The Tides of Life*, by R. G. Hoskins, of Harvard University (*Bi. 2, 68, 112, 113, 128*).

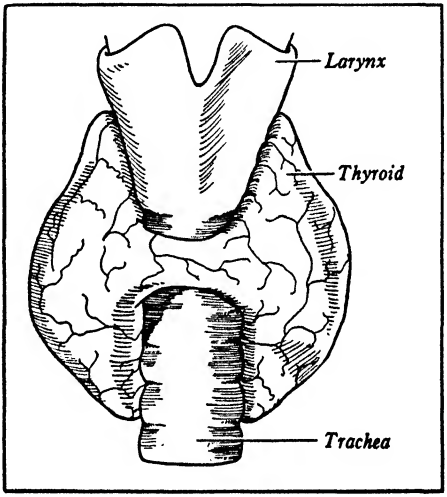

FIG. 48. The Thyroid Gland

Thyroid Gland

The thyroid gland (Fig. 48) is an organ lying in the throat region immediately in front of the trachea and below the larynx. It is composed of two oval bodies, one on either side of the trachea, joined by a slender ridge, the whole structure

resembling an H in appearance. The thyroid gland has been found to manufacture a complex hormone, *thyroxin*, which is rich in the element *iodine*. Experiments have shown that this hormone is extremely important in regulating the growth and metabolism of the body.

In those instances where the thyroid gland is deficient or fails to manufacture enough secretion, marked abnormalities may ensue, and these are invariably associated with a slowing up of the metabolism of the body. If the condition persists, it may lead to the production of a disease known as *myxedema* (Fig. 49, *A*), in which there is a marked disturbance in the normal metabolic rate, accompanied by a swelling of the hands and face, which soon assume a puffy appearance. Also the body temperature may be reduced as much as three and a half degrees, making the individual extremely sensitive to cold. At the same time various nervous disorders may manifest themselves, and these may greatly interfere not only with normal speech but also with the mental activities of the afflicted individuals. For some unexplained reason women are much more apt to have myxedema than are men. In fact the disease is rather rare in men. Persistent treatment with thyroid extract may bring about partial or complete recovery from myxedema (Fig. 49, *B*).

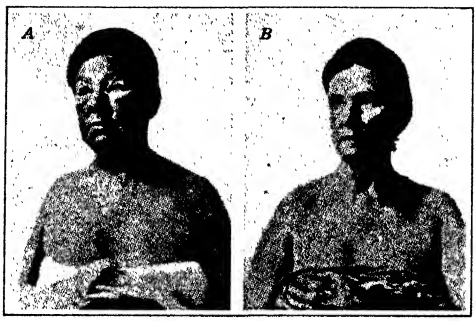

FIG. 49. Myxedema Patient[1]

A, patient before treatment with thyroxin; *B*, same patient after thyroxin treatment

In young children defects of the thyroid gland may be the means of impeding normal growth and may lead to the condition known as *cretinism*, or, as Hoskins calls it, *childhood*

[1] From Barker, L. F. (Ed.), *Endocrinology and Metabolism*. By permission of D. Appleton-Century Company, publishers.

myxedema, in which the bones of the skeleton may cease to grow in length, although they may increase considerably in thickness. The body itself becomes puffy and produces fatty tumors in various regions, especially over the collar bones in the neck. The skin and hair become dry and coarse. The sex organs also remain small and fail to function normally. Moreover, the mental development is so greatly retarded that these cretins are really little more than idiots, and although they may live on for many years, their intellectual

FIG. 50. Abnormalities Due to Thyroid Deficiency

A, patient before treatment; *B*, after three weeks of treatment with thyroxin; *C*, treatment discontinued for six months. (After Schlapp, courtesy of *Journal of Heredity*)

powers have been stunted to such a degree that they do not progress much beyond the mental age of a normal child of four or five (Fig. 50).

When there is an oversecretion of thyroxin, a disease known as *exophthalmic goiter* is produced, characterized by increased irritability, loss of weight, puffiness of the hands and face, increased heart rate, marked weakness, and a decided bulging of the eyes. In localities where the drinking water and soil are deficient in iodine content there is found an excessive amount of *goiter*, a disease of the thyroid gland which often reveals itself externally as a tumorous enlargement in the neck. Most investigators believe that this increase in the size of the gland is nature's method of attempting to increase

the iodine content of the blood necessary for the normal metabolism of the body. While it is true that a good share of this iodine is made available through the thyroxin manufactured by the thyroid gland, yet a considerable quantity of it must also be supplied to the body through the medium of the water and food which is consumed. When sufficient iodine is lacking in these latter substances, then nature attempts to compensate this deficiency through an enlargement of the gland, resulting in an increased number of cells for the purpose of manufacturing a larger amount of the hormone thyroxin. Naturally this produces abnormalities of various kinds, which undermine the health of the individual concerned.

Parathyroid Glands

The parathyroids consist of at least four small glands, which are located on the outer margins of the thyroid gland (two or more on each lobe) or have become embedded in the tissues of the gland itself. No hormone has as yet been isolated definitely from the parathyroids, but investigators believe these glands to be very important for normal development.

It has been learned that the absence of parathyroid secretions causes numerous nervous disturbances, invariably manifesting themselves as *tetany*, a condition in which there is violent spasmodic contraction of the voluntary muscles, accompanied by a rapid diminution of the calcium content of the blood.

Within recent years scientists have discovered that an oversecretion of the parathyroid hormone, known as *hyperparathyroidism*, gives origin to a definite disease characterized by weakness and pains in the bones. The condition gradually becomes aggravated, leading to a softening of the bones, accompanied by various skeletal deformities. The result is that the patient develops anemia, is forced to take to his bed, and soon becomes reduced to about half his former size. At the same time the calcium content of the blood is increased out of all proportion, and this is accompanied by a decrease in the

normal responsiveness of the muscles and nerves. Recently some relief has been afforded such patients through removal of portions of the parathyroids by means of surgical operations.

Pituitary Gland

The pituitary gland is a small structure attached to the base of the brain, weighing in man about .6 of a gram. It really consists of three divisions: the anterior, intermediate, and posterior lobes. Inasmuch as the intermediate region is usually associated functionally with the posterior lobe, it may be well for us to think of the gland as possessing just the two parts, the anterior and posterior sections (Fig. 51).

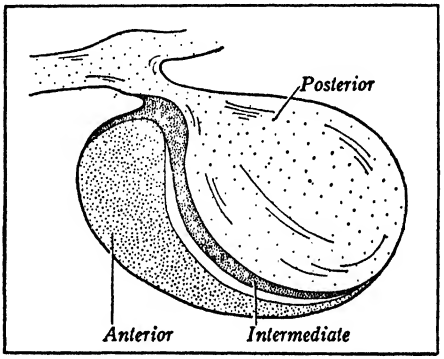

FIG. 51. Section through Pituitary Gland

An oversecretion of the anterior pituitary hormones, especially when this occurs during childhood, exerts an influence on the skeleton, chiefly on the bones of the limbs and the lower jaw, causing them to increase so tremendously in size as to bring about a condition known as *gigantism* (Fig. 52). A condition comparable to this, but occurring among adults, is known as *acromegaly*. On the other hand, an undersecretion in the anterior lobe causes a stunting in the growth of the individual, leading to a condition akin to *dwarfism* (Fig. 53). Here the organism remains infantile, puny, with an excessive amount of fatty tissue and little or no sexual development. As will be recalled, a lack of thyroid secretion also may be responsible for such a dwarfed condition. In fact, many investigators think that an intimate relationship exists between deficiencies of the thyroid and the anterior pituitary glands, and that abnormalities in both of these structures account for the stunted growth of the organism.

Aside from their effects on growth, the secretions of the anterior lobe of the pituitary have an effect on the basal metabolic rate of the body, on the proper functioning of the reproductive glands, on the amount of milk secreted by the mammary glands, and also on the thyroid and adrenal glands. Herbert M. Evans, of the University of California, in a recent paper in the *Journal of the American Medical Association* (*Bi. 68*), asserts that up to the present time five hormones have been found to exist in the anterior lobe of the pituitary. These are (1) the *growth* hormone, affecting the growth and size of the organism; (2) the *gonadotropic* hormone, which stimulates the gonads (testes and ovaries); (3) the *lactogenic* hormone, affecting the secretion of milk in the mammary glands; (4) the *thyrotropic* hormone, which affects the normal basal metabolic rate of the body and also exerts an influence on the normal state of the thyroid gland; (5) the *adrenalotropic* hormone, which has a decided influence on the proper functioning of the cortical region of the adrenal gland.

FIG. 52. Human Gigantism

Henry Mullins, in the center, is 17 years old, is 7 feet 6 inches tall, and is still growing. He weighs 285 pounds and wears a number 23 shoe

The secretions of the posterior lobe of the pituitary are found to be rich in the hormone *pituitrin*, and these have numerous effects on organisms. They may stimulate the smooth muscle cells of the uterus to undergo vigorous contractions; they may be the cause of sustained high blood pressure; they may regulate the water output of the body

and may be responsible for an increased or decreased secretion of urine. Sometimes they may cause increased pigmentation, resulting in a general darkening of the outer skin.

Recently the hormone pituitrin has been shown to consist of two components: (1) *oxytocin*, which stimulates the smooth muscles of the uterus, and (2) *vasopressin*, which causes the blood vessels to undergo contraction. Because of these functions, oxytocin has come to be used in obstetrics, to aid delivery and check hemorrhage; vasopressin is used after surgical operations and in diseases like pneumonia and diphtheria, to maintain the blood pressure.

FIG. 53. Dwarfism, or Infantilism

The dwarf girl is seven years old, weighs 20 pounds, and is 29 inches in height. She is standing beside a normal boy of the same age, who weighs 49 pounds and is 45 inches tall. (After Griffith, courtesy of *American Journal of Diseases of Children*)

Adrenal Glands

The adrenal glands, known as the *suprarenals* or *adrenals* (Fig. 54), consist, in mammals, of two small capsule-like structures situated above the upper margins of the kidneys. Each gland possesses two distinct zones: an outer one, the *cortex*, and an inner one, the *medulla* (Fig. 55). The secretions from these two regions seem to exert distinctly different influences on the body.

When the cortex fails to produce a sufficient amount of hormone material, *cortin*, it may lead to a malady known as Addison's disease, in which there is general prostration and extreme weakness of the body, accompanied by very low blood pressure, violent vomiting, severe aching of the

muscles, and bronzing of the skin. Invariably in the past this disease has proved to be fatal, but within recent years the prompt administration of cortin into the veins has produced remarkable recoveries. Not only is cortin a specific remedy in Addison's disease, but it has been found of great benefit in building up the body after the ravaging effects of numerous maladies.

When the cortex becomes diseased through the development of tumorous tissue, it may lead to peculiar expressions of the normal secondary sexual characters which accompany sex; for example, an adult human female may suddenly find herself developing such secondary sexual characters of the male as the beard, enlarged muscles, and masculine voice.

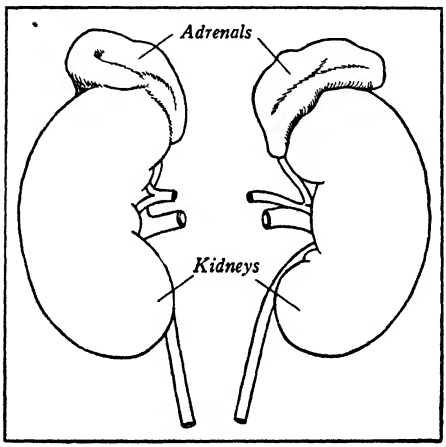

FIG. 54. Adrenal Glands

The medullary region of the adrenal glands has been shown to contain a hormone known as *adrenalin* (adrenin or epinephrin), and this is always found to be present in the blood stream. The reactions produced by adrenalin are quite similar to those resulting from the functioning of the *sympathetic*, or *autonomic*, nervous system. As most people know, this branch of the nervous system controls many of the activities going on in the body over which man has little or no conscious control, such as the circulation and pressure of the blood, the beating of the heart, and the functioning of the salivary and sweat glands. An increase or decrease of the adrenalin content of the circulating medium of the body increases or decreases the activities enumerated, leading to many serious disturbances in the organism. Specialists now believe that a lack of secretion of the medullary region may be one

of the important causes of the disease known as asthma. Because adrenalin possesses the power of contracting the smooth muscle cells within the walls of the blood vessels, it is often used as a means of stopping excessive bleeding.

Reproductive Glands

The reproductive glands, testes in the male and ovaries in the female, besides giving origin to the mature reproductive cells, also manufacture secretions which have a direct bearing on the normal development of the body. In large measure these secretions are responsible for the expression of many of the secondary sexual characters which the sexes normally develop. For example, when the testes are removed in the male, such characters as the beard, deep voice, and masculine musculature are suppressed or underdeveloped, and in their stead traits are produced which more nearly resemble those belonging to the female. Likewise the removal of the ovaries of the female leads to a suppression of the secondary characters that normally accompany this sex, and at the same time there is a tendency to take on characters which ordinarily express themselves only in the male. There is evidence also that the secretions produced by the ovary have to do with the sexual rhythm exhibited in the female of the higher animals, resulting in the regular and periodic manufacture of ripe eggs, the whole process being known in man as the *menstrual cycle* and in the other mammals as the *œstrous cycle*. Moreover, it is believed that hormones from the *corpus luteum*, a yellowish body composed of a mass of cells produced after

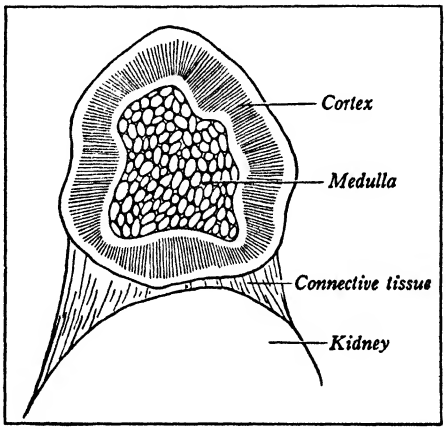

FIG. 55. Section through Adrenal Gland

the ovum has been discharged from the ovary, act on the walls of the uterus so as to prepare them for the implantation of the fertilized ovum, thereby making pregnancy possible. Recent evidence indicates that without the corpus luteum's acting on the uterus the retention of the fertilized ovum would become impossible (*Bi. 2*).

Pancreas

The pancreas is a gland whose cells are specialized chiefly for the purpose of manufacturing the digestive enzymes which aid in the breakdown of the complex organic foods taken in by the animal body. Although this is the main function of the pancreas, we also find, scattered among the predominating larger cells of the gland, numerous groups of smaller, clustered cells known as the *islands of Langerhans* (Fig. 56). The cells in each island manufacture a hormone known as *insulin*, which has the power of exerting a control over the utilization of sugar by the tissues.

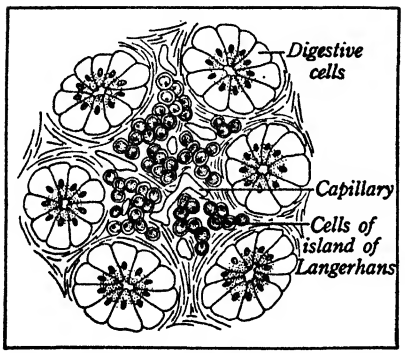

FIG. 56. Section through Pancreas, showing Cells of an Island of Langerhans

When these island cells are degenerate or missing, the amount of insulin manufactured and liberated into the blood stream is either greatly reduced or entirely lacking, with the result that the tissues cannot utilize the available sugar and an excessive amount accumulates in the blood and urine, giving origin to the disease known as *diabetes*. In recent years insulin has been isolated and manufactured from the pancreas of lower animals, and by the periodic injection of this material into the blood stream of patients suffering from diabetes, not only has their general health been greatly improved but likewise their span of life has been considerably prolonged.

An interesting connection appears to exist between adrenalin and insulin. The former hormone is instrumental in causing the liberation of sugar into the blood, whereas the latter makes it possible for the tissues to break down the sugar and utilize it, thereby decreasing the amount of this substance in the blood stream.

It is thus seen that the glands of internal secretion are exceedingly important in regulating and controlling the normal life processes of the organism. When these glands are deficient in one respect or another, they may lead to diseased and malformed individuals. In recent years many of these abnormalities have been successfully treated by the administration or injection of the necessary glandular extracts. Those who have been following recent developments in medicine know that experimental research has yielded much information along these lines, making it possible not only to extract and prepare some of the hormones which these glands manufacture but also, through the proper administration of the hormones themselves, to overcome many abnormalities and thus transform the afflicted individuals into as nearly normal types as the circumstances will permit. In many instances the treated individuals have recovered completely, but where abnormalities resulting from defective glands have progressed too far, such radical modifications in the organisms have been induced that full recovery has become impossible.

In this connection it must be emphasized that in cases of malformations arising from defective endocrine glands, treatment to overcome deficiencies must be persistent and prolonged. Quite often such treatment must be continued throughout the life of the patient. As far as the malformed glands themselves are concerned, they cannot be remedied because, as pointed out previously, in large measure they are dependent for their expression on hereditary genes. If these genes are normal, barring accident or poor environment they lead to normal glands; but if they chance to be deficient, then abnormal glands will result, leading to the development of a physically or mentally defective individual.

CHAPTER IX

The Immortal Germ Plasm

A FACT universally accepted among biologists is that life is handed on from generation to generation through the medium of the germ plasm. Because of this, the germ plasm is often spoken of as being immortal. Not only is life handed on in this manner but, as has been pointed out in Chapters II and III, if traits which originate in certain somatic structures are to be transmitted to following generations, they must be incorporated into those portions of the germ plasm which participate in reproduction. To pave the way for a clearer understanding of this concept, the cell, especially the germ cell, was considered in Chapters IV and V. It was discovered that within every cell there is a definitely specialized substance, the chromatin, which forms the chromosomes that are believed to bear the entities for the traits transmitted. Although all cells of an organism contain chromosomes, nevertheless in the higher forms it is only the germ cells which transmit the hereditary entities from parents to offspring. After germ cells unite and form the zygote, development proceeds until the organism is produced, with large numbers of cells. Most of these cells form the somatic, or bodily, structures, but a small number of them are set aside as the germinal glands for the purpose of carrying on the life and traits inherent in the particular individual of the species represented.

While it is true that all somatic cells contain full sets of chromosomes with entities for traits, nevertheless only those entities demanded by the particular tissues of which the cells are an actual part are expressed in representative characters. For example, take such an obvious character as the color of eyes. While it is true that the gene for eye color is present

in all somatic cells, yet it is not expressed in any other cells than those of the eye. In those cells where it does not assert itself, it remains dormant and some other genes are expressed.

In Chapter VI, where the character of sex was shown to depend upon specific chromosomes present in the uniting germ cells, attention was definitely focused on the germ plasm as the primary basis for heredity and development. The studies on twins and monsters, in Chapters VII and VIII, revealed that while the fundamental traits of organisms depend on the constitution of the germ cells, yet other factors also must be taken into consideration, such as the environment and the endocrine glands. Most of the evidence, however, indicates that the mechanism for the transfer of entities for traits lies within the chromosome complex of the germ plasm; in a word, the chromosomes are now believed to be the structures of greatest importance in heredity. Before any other phases of genetics are considered, especially the modern aspects of the experimental method of breeding known as Mendelism (Chapters X–XIII), it may be well to enumerate in the present chapter the chief reasons for regarding the chromosomes in this light.

In the first place, every species of plant and animal is found to possess a definite and constant number of chromosomes, by means of which the particular species may be recognized. This fact has already been mentioned in Chapter V, where the maturation of the germ cells was described. As was indicated there, the edible crab of the Pacific coast (*Cancer magister*) contains one hundred and twenty chromosomes in the somatic, or duplex, set, and half this number, sixty, in the germinal, or simplex, set. In man (*Homo sapiens*) the body cells, as well as the immature germ cells, possess a duplex set of forty-eight chromosomes, while the mature germ cells contain the simplex number, twenty-four. Other species of animals and plants likewise have a characteristic number of chromosomes. Since the number of chromosomes remains so definite and constant, biologists believe that they are the all-important elements for transmitting the distinctive

traits which crop out generation after generation in the organisms belonging to the same strain or species.

It has also been established that, aside from their constancy in number, the chromosomes may have an individuality of their own (Fig. 57), and carry the different factors for the traits of the adult organism. During the last twenty-five years a large number of geneticists, notably Thomas Hunt Morgan, Calvin B. Bridges, Hermann J. Muller, and A. H. Sturtevant, have studied over four hundred traits in the flies belonging to the *Drosophila* group; they have come to the conclusion that each chromosome is distinctive and individual, carrying many different genes all linked together like a series of beads in a chain, the entire group in each chromosome representing one distinct series of entities for different traits of the species (*Bi. 18, 140–146*). The vinegar, or fruit, fly (*Drosophila melanogaster*) (Fig. 58), in particular, has been studied from this standpoint. Since this species has only four pairs of chromosomes, of distinctive size and shape (Fig. 59), they can be recognized and studied very easily. Although in many of the lower

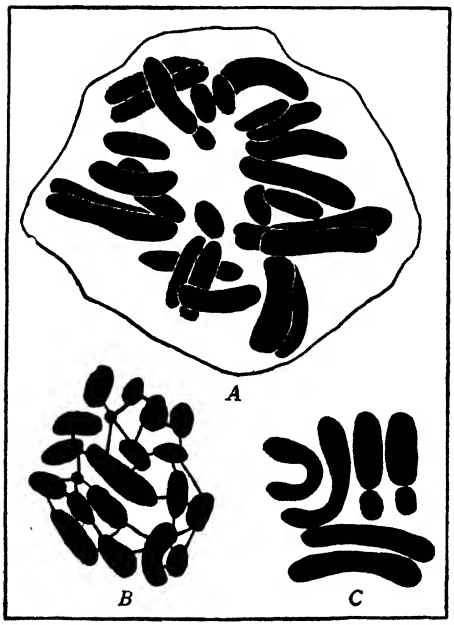

FIG. 57. Individuality of Chromosomes as seen in Immature Male Germ Cells[1]

A, the grasshopper *Brachystola magna* (after Sutton); *B*, the squash bug (*Anasa tristis*) (after Wilson); *C*, the *Culex* mosquito (after Stevens)

[1] From Fasten's *Origin through Evolution*. By permission of F. S. Crofts & Co., publishers.

animals the chromosomes do not show much individuality, still in a large number of other forms, particularly the higher ones, including man, it has been found that each chromosome has a definite individuality. This is exactly what has been shown for *Drosophila melanogaster*, — that every one of the chromosomes is distinctive not alone from the standpoints of size and shape but more particularly from the standpoint of the factors, or genes, which it carries.

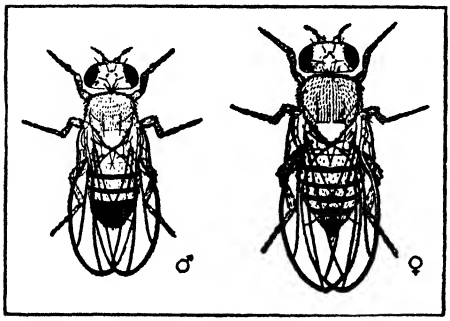

FIG. 58. Male (♂) and Female (♀) *Drosophila melanogaster*[1]

By means of a very large number of breeding experiments, the investigators working with fruit flies have been able to chart the precise location within the chromosomes of a great many of the genes responsible for the production of the actual characters.

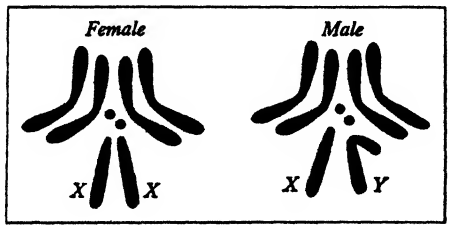

FIG. 59. The Four Pairs of Chromosomes in the Female and in the Male of *Drosophila melanogaster*[2]

The genes that hang together in the same chromosome are said to be *linked genes*; and if nothing happens to disturb their relationship, they become expressed simultaneously in offspring, accounting for the cases of so-called *linked heredity*. However, when the phenomenon of *crossing over* occurs (Figs. 25 and 26) during the synapsis stage of the maturation of the germ cells, as was pointed out in Chapter V, some of these linkages may be broken, thus

[1] From Morgan's *Evolution and Genetics*. By permission of Princeton University Press, publishers.

[2] Ibid.

accounting for many of the different expressions observed in progeny. The evidence at hand seems to indicate that the closer together genes lie within the same chromosome, the less opportunity there is for them to become separated when crossing over occurs; on the other hand, the farther apart they are, the greater becomes the possibility of the linkages between them being broken. These phases of genetics will be considered in greater detail in Chapter XIII.

In *Drosophila melanogaster* four linkage groups of genes have been established, corresponding to the four pairs of chromosomes possessed by the species (Fig. 60). In practically all other organisms, including man, cases of linked heredity have been discovered similar to those which have been indicated for the vinegar fly.

Recently Millislav Demerec (*Bi. 47*), geneticist of the Carnegie Institution of Washington, attempted to formulate the present conception of the gene. According to Demerec, genes are believed to be single organic molecules held together in groups, or gene strings, within the chromosomes. Each chromosome consists of a distinctive gene string, or group of molecules. Genes are capable of self-propagation and also of governing the life processes of the cells of which they are a part. Just as an organic molecule consists of various atoms, and any modification in any one of these atoms would bring about a change in the molecule, so, on a somewhat similar basis, may be explained the mutational changes which occur within the genes of organisms.

A third reason for regarding the chromosomes as the all-important structures in heredity is the establishment of the fact, within recent years, that sex is dependent on a special combination of chromosomes within the developing zygote. The facts in regard to sex determination have already been considered in Chapter VI. As was pointed out there, the actual entities which combine to produce the observed results are certain genes carried by the special sex chromosomes. It has been shown that these sex-producing genes are not the only ones carried within the sex chromosomes, there being

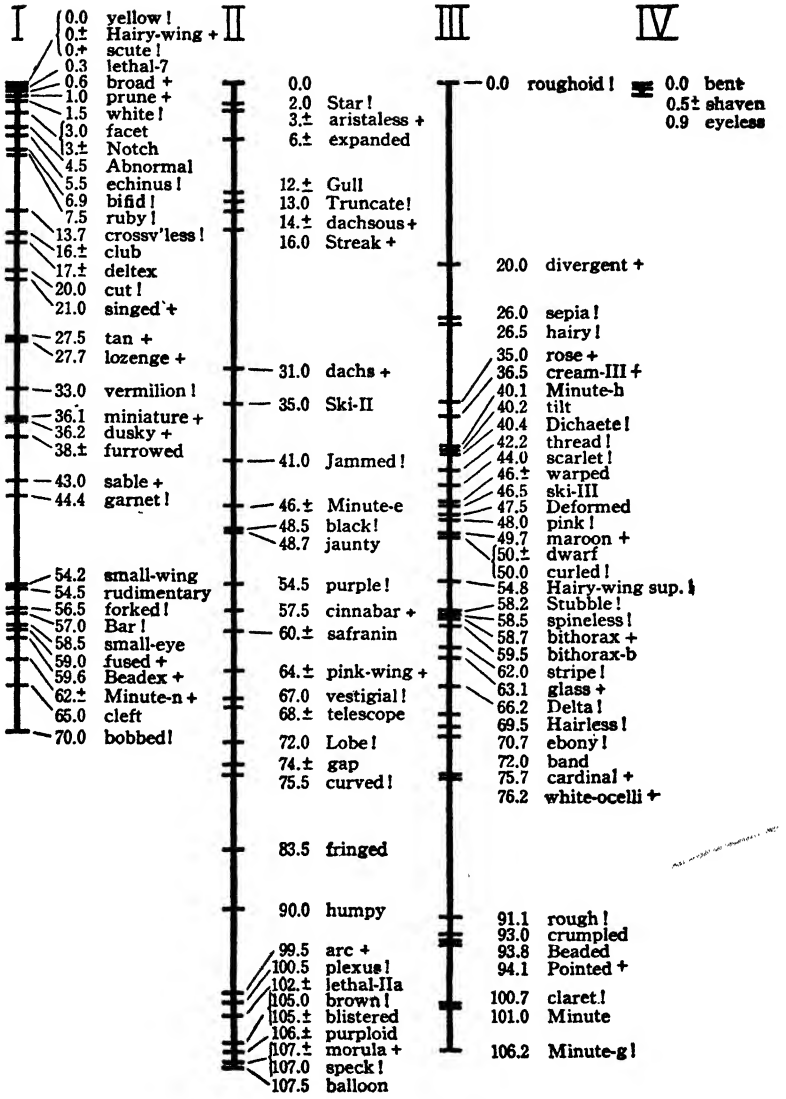

Fig. 60. Location of Genes in Chromosomes[1]

Chromosome maps showing the four linkage groups of *Drosophila melanogaster* (!, the most useful types; +, those nearly as good; unmarked, important only in special connections)

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[1] From Morgan's *The Theory of the Gene.* By permission of Yale University Press, publishers.

others, such as, for example, those producing color-blindness in man; and these usually behave as *sex-linked factors*, accounting for the transmission of the so-called sex-linked characters (Figs. 75 and 76). Instances of this sort of heredity are outlined fully in Chapter XII.

The discovery of the facts regarding sex determination gave biologists definite proof that one character, sex, was determined by genes. At the same time it immediately raised the question why it is not just as logical to assume that all other characters of the organism are determined similarly by genes within the chromosome complex of the mature germ cells. This is exactly what modern genetics has succeeded in establishing.

A fourth reason for regarding the chromosomes as all-important in hereditary transmission is the fact that during the maturation of the germ cells the homologous pairs of chromosomes undergo synapsis, and by means of the reduction division the pairs of entities for traits which they carry from the two parents become segregated in such a manner that only a single set finds its way into each mature germ cell. By referring to Chapter V, all the salient details of the maturation process may be reviewed. When fertilization occurs, each gamete brings in its single set of chromosomes, and these combine to restore the double set. The foundation is thus laid for the development and expression of the actual results in the organism arising from the combination.

In this connection it is of interest to note that when the *Mendelian principles* were rediscovered in 1900, they disclosed to geneticists an experimental method of breeding which enabled them to explain very nicely the facts revealed during the processes of the maturation and fertilization of the germ cells. Mendelism shows us concretely how the genes actually behave in crosses, and also indicates how they become segregated, reshuffled, and recombined in the formation of the mature germ cells that perpetuate the species. Mendelism, coupled with an understanding of the maturation and crossing-over phenomena, reveals the fundamental

importance of the genes within the chromosomes, indicating definitely that in crosses some genes are more potent than others and lead to the actual expression of the traits which they represent, completely dominating any other genes for similar traits which may have entered the cross. When this occurs, the genes which gained expression are called *dominant*, and those which did not are referred to as *recessive*. Sometimes a combination of genes leads to the emergence of a new trait, differing markedly in appearance, either quantitatively or qualitatively or both, from the expression of the similar trait in either of the respective parents. Such cases will be discussed more fully in Chapters X–XIII.

Finally, from the standpoint of experimental embryology there exists evidence to show clearly that the chromosomes are the carriers of the heritage. One of the most unique experiments ever performed was accomplished by the German biologist Theodor Boveri. He took the eggs of a certain species of sea urchin belonging to the genus *Sphærechinus*, from each one of which the nucleus had been removed, and fertilized them with the spermatozoa of another species of sea urchin, of the genus *Echinus*. The embryos which developed showed few of the traits of the female, resembling in practically all respects the *Echinus* species, from which the normal male gametes that participated in the crosses were derived. Later research by Boveri and others seemed to indicate that those *Sphærechinus* eggs that underwent considerable development were not entirely enucleated, but possessed a broken-down mass of nuclear material diffused throughout the cytoplasm. In reality, therefore, these larvæ were of the nature of hybrids, but revealed *Echinus* characters mainly because the genes brought in by the *Echinus* spermatozoa dominated those of the *Sphærechinus* ova.

Other experiments along the same line have been performed by a number of others investigating different species; these have yielded somewhat similar results, which seem to have a similar interpretation. Jacques Loeb, who, until his death in 1924, was head of experimental biology at the Rocke-

feller Institute for Medical Research, New York City, very early in his experiments on parthenogenesis crossed the eggs of a species of sea urchin with the spermatozoa of a distinct species of starfish; although these male germ cells entered the eggs, they were thrust out during early embryogeny, so that in reality they contributed nothing to the new individuals except that they were instrumental in initiating development. The embryos which were ultimately produced showed only those characteristics of the sea urchins from which the female gametes were derived. Still another investigator, Emil Godlewski, crossed the eggs of a number of species of sea urchins with the spermatozoa of a tube worm, and here also, as in the cases just cited, very shortly after the initiation of development the male elements were completely extruded, so that the resulting embryos showed only the characteristics carried by the female gametes, namely, those of the sea-urchin species. Many other experiments along similar lines may be mentioned, all pointing to the important rôle played by the chromosomes in development.

Occasionally abnormal fertilization occurs in which more than a single spermatozoön fertilizes an egg, giving rise to a condition where more than one full set of chromosomes for the species in question is found to exist within the zygote. Invariably this leads either to the disintegration of the embryo or to abnormal development resulting in the production of deficient or monstrous individuals. Fortunately, in most instances of such fertilization the developing zygote does not proceed very far but soon undergoes a rapid process of disintegration.

The recent experiments on the effects of radioactive emanations on the germ cells of organisms have indicated the great rôle played by the chromosomes in heredity. By exposing organisms to these emanations, particularly X rays, it has been possible for geneticists actually to bring about changes within the chromosomes of the germ cells, inducing either definite transformations in certain genes or distinct breaks within whole chromosomes, followed by a translocation

of the broken portions to other chromosomes. These latter phenomena are spoken of as *translocations* (Fig. 93, p. 255), and wherever they are found to occur they are responsible for the production of definite modifications in species. Painter and Muller (*Bi. 160*), of the University of Texas, have studied a number of such distinct transformations in *Drosophila melanogaster*, and have succeeded in showing that the changes were engendered by the method of translocation just described. As far as the genes themselves are concerned, no one has yet been able actually to demonstrate them; and because of this fact it has not been possible to recognize any modifications within them as clearly as the translocation of parts of chromosomes. However, by carefully studying the experimental results which have been obtained, it becomes obvious that the X ray has induced distinct modifications in the gene or genes for the specific character in question.

One other line of research which has indicated the relation of the chromosomes to heredity is that which has concerned itself with the products of crosses where both types of gametes from the respective parents have played equal and important rôles in the unions responsible for the resulting individuals. Sometimes, when different species are crossed, the result is that the offspring produced are sterile. This is the situation in a large number of the crosses between distinct species. Investigations of the germ cells of the parent species and those of the crosses have indicated the reasons why, in most instances, the products of crosses are sterile and develop no mature gametes. The case of the mule will serve to illustrate this point (*Bi. 209*). The mule is a cross between the horse and the jackass. When the germ cells of these parent species are examined microscopically, they are found to possess chromosomes that are distinctive from the standpoint of size and no doubt also from the standpoint of genes. When the immature germ cells of the mule are examined, they are found to contain a heterogeneous set of chromosomes rather than the harmonious double set found in all well-established species. Some chromosomes of the

mule seem to have mates, while others lack them. During growth, synapsis, and reduction the chromosomes attempt

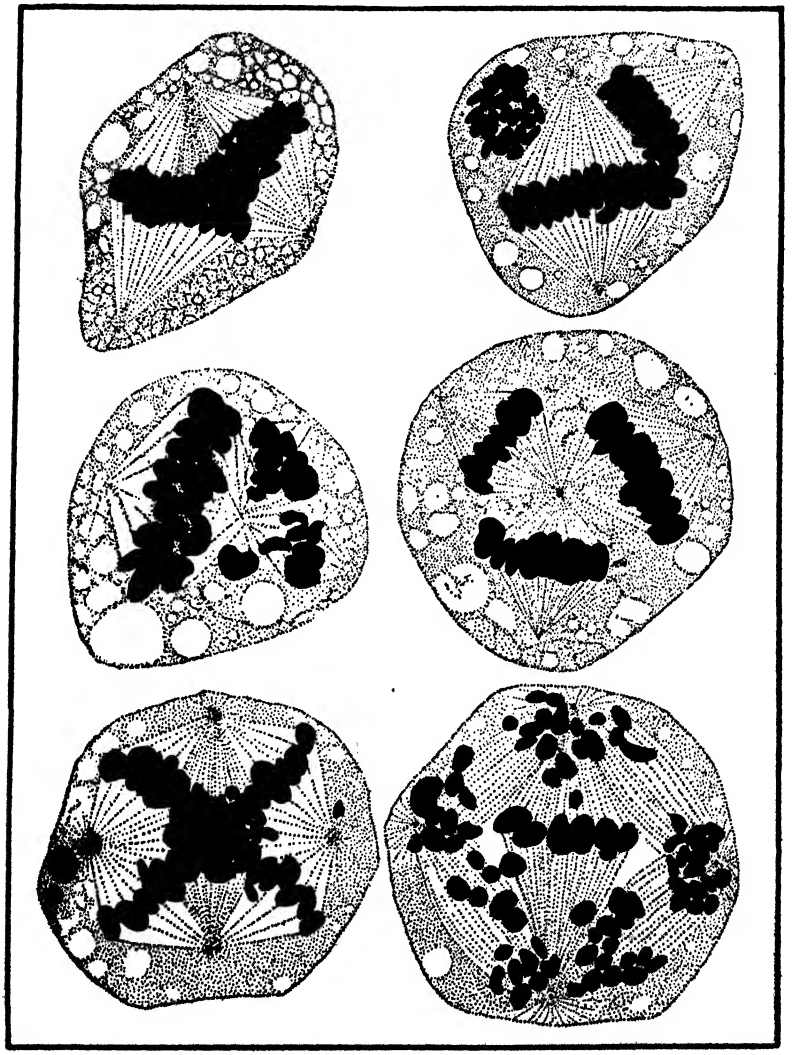


FIG. 61. Abnormal Mitosis in Primary Spermatocytes of the Mule[1]

[1] After Wodsedalek, courtesy of *Biological Bulletin*.

to line up in pairs; but inasmuch as each chromosome in such a pair is really different and distinct from the other one, having been derived from a different species, it soon becomes apparent that the process is a rather discordant one. The inevitable result is that instead of harmony's prevailing, as is customary where there is a logical alignment of pairs of homologous chromosomes, there exists disharmony because of the illogical arrangement which ensues. This soon leads to the disintegration and ultimate degeneration of the germ cells and their entire contents (Fig. 61). Inasmuch as no mature germ cells are produced, the mule, therefore, is sterile and incapable of engendering any progeny. Some investigators have published results to show that, in rare instances, some mules are fertile and capable of participating in the production of offspring. In such cases the difficulties encountered during maturation, which have been mentioned above, have apparently been ironed out; so that the process has become a harmonious one, leading to the production of fertile gametes.

All the evidence enumerated above points to the inevitable conclusion that the chromosomes are the most important carriers of the heritage. This will be noticed especially in the following chapter, where the modern method of experimental breeding, already alluded to as Mendelism, is described. This method not only shows how factors for characters enter and behave during crosses, but also reveals how they segregate out of crosses, during the formation of the germ cells, in accordance with rather definite and predictable ratios. It is remarkable how the purely scientific deductions, based on studies of the chromosomal components of the germ cells, have become linked with the most practical considerations of breeding, and have led to the establishment of innumerable varieties of organisms. Incidentally, facts such as these have helped to strengthen the conviction that in the final analysis heredity is largely a matter of the genes carried by the chromosomes of the germ cells that unite to produce the resultant organisms.

CHAPTER X

Mendelian Principles of Heredity

THOSE who are familiar with developments in biology will agree with the statement that since the year 1900 more has been accomplished in the field of genetics than in all the centuries preceding that date. This progress in genetics has been due, in large measure, to the fact that in the year 1900 there was a rediscovery of those principles of heredity first worked out by the Austrian monk Gregor Johann Mendel (Fig. 62), which gave us our first insight into the manner in which characters behave in crosses. These principles, which are now known under the familiar name of *Mendelism*, gave us a real conception of how the entities for characters, the genes, entered crosses to produce the results observed, and also how they segregated out of crosses during the formation of the germ cells. They made it possible to predict the ratios of types of individuals that would be produced when these gametes participated in reproduction.

Methods of Breeding

Before discussing the Mendelian principles at greater length, it may be well to familiarize ourselves with the practices of breeding in vogue before 1900. The oldest method utilized was the one of crossing organisms purely on the basis of directly observing their external characteristics. This may be spoken of as the method of *observation*, in which the eye was relied on as the exclusive guide in picking parents for desirable qualifications. Those organisms that possessed the traits which happened to strike the fancy of the breeder were the only ones chosen for mating purposes, and the others were disregarded. Of course such breeding was based

on the assumption that "like begets like,"— a conception that is as old as thinking itself and one which generally is borne out by the products obtained. There is no doubt that remarkable results have been accomplished by this means, but it must be stressed that the breeder, in pursuing such a method, had no real idea of the internal germinal make-up of the organisms with which he was dealing; therefore progress was slow and a large number of very costly mistakes were made. Often breeds which were supposed to be pure with respect to certain qualities were not actually pure but possessed hidden entities for traits which interfered radically with the expectations. Even at the present time there are many breeders who still rely on purely external observations as their sole guide in making crosses. Such breeders invariably are without any knowledge of modern genetics, — a science which reveals how it becomes entirely possible carefully to test breeds or strains of organisms before they are utilized in various crosses for stock-producing purposes.

FIG. 62. Gregor Johann Mendel[1]

The second method of breeding in vogue prior to the present century was the one that went under the name of the *statistical method*, which had for its chief aim the reduction of the principles of heredity and variation to some sort of mathematical expression, largely through the medium of an appropriate formula. Here, instead of separate individuals being considered, large numbers, constituting a *population*, were dealt with and an attempt was made to reduce the

[1] From Iltis's *Gregor Johann Mendel, Leben, Werk und Wirkung*. By permission of Julius Springer, Berlin, publisher.

resemblances and differences between them to a common denominator, applying alike to every one of the organisms included in the entire group. Francis Galton, in the nineteenth century, and Karl Pearson, in more modern times, have been the chief exponents of the statistical method of studying the various biological problems of heredity and variation. In recent years this method has been organized into a distinct branch of genetics known as *biometry*, and it is of real value in indicating the degree of resemblance or difference between the individuals of a large population. The statistical method, however, like the observational one, tells us nothing regarding the germinal constitution of the organisms with which it deals, and of course we now know that this is the factor of greatest significance in all genetical work.

The third, and modern, method of breeding is the experimental one known as *Mendelism*. This is a method based fundamentally on a thoroughgoing understanding of the factors which constitute the germinal material of the organisms utilized for breeding purposes. Wherever possible, both the observational and the statistical method are employed as accessory aids in Mendelian crosses; but for a real knowledge of the fundamental nature of the constitution of the individuals which enter crosses, the Mendelian method is the most reliable one that has as yet been devised. Since Mendelism is of such great importance in genetics, we shall now learn something of its discoverer, Gregor Johann Mendel, his life and the conditions under which he carried on the monumental breeding experiments that culminated in the discovery of his principles.

Gregor Johann Mendel

Mendel was born in Austria on July 22, 1822, and died there on January 6, 1884. His parents were poor peasants who could not possibly afford to give him much of an education. After attending the village school, where he made an excellent record, he entered the gymnasium (high school),

where his brilliancy was soon recognized. His parents, however, were too poor to continue his education after his graduation from the gymnasium. He realized that by enrolling in a theological school, not only would he be given an opportunity to prepare himself for the priesthood but, more particularly, he would obtain a general education, in which he was most vitally interested. Hugo Iltis, his biographer (*Bi. 120*), tells us that he was a sincere student, who, in spite of following a theological career, nevertheless was extremely liberal in his views. He pursued his theological course diligently, for he realized that in the country in which he lived this was the only way a person of his social position could ever hope to gain any education along advanced lines. He studied theology, philosophy, the arts, languages, and sciences, in the latter of which he was primarily interested.

After being ordained to the priesthood, he served in various minor positions until he was finally chosen as head abbot of the monastery in Brünn, Austria. While this position required certain administrative duties of him, which he executed efficiently even though they were distasteful to him, he was able to devote a good share of his time to the crossing and developing of various flowers, a work which he particularly loved. To gain greater proficiency in this branch of science he enrolled for special courses in botany at the University of Vienna, and soon developed into a highly trained worker in this field. In later years he interested himself exclusively in the flowering plants, particularly the garden pea (*Pisum sativum*).

Mendel's experiments were performed largely on garden peas, between the years 1857 and 1868, in the cloister gardens of his monastery in Brünn (Fig. 63). In 1866 he published a paper embodying the results of his work in the *Proceedings of the Natural History Society of Brünn* (*Bi. 11*), a purely local journal with an exceedingly limited circulation and not known to many scientists outside the immediate vicinity of Brünn. Because of this fact very few people ever saw the contribution, and therefore it remained unknown for a con-

siderable time. It is interesting to note that shortly before Mendel published his paper he sent it to the famous German botanist Karl Wilhelm von Nägeli, of the University of Munich, but for some unknown reason Nägeli did not recognize its merit or practical value. Either he was so busy with his own problems that he set Mendel's contribution aside for later examination and then forgot it entirely, or else he was

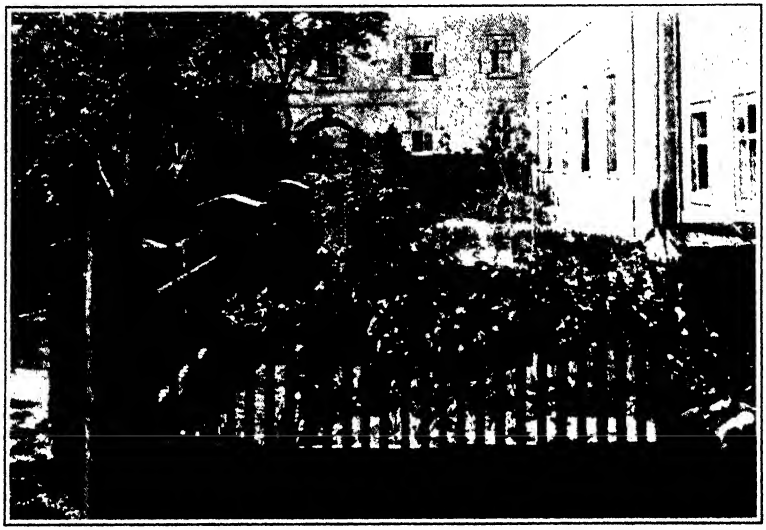


FIG. 63. Cloister Gardens in Brünn[1]

These are the gardens in which Mendel carried on his notable experiments

so engrossed in the evolutionary controversies of the times that nothing seemed important to him except the topic over which the controversy raged. It will be recalled that in 1858 the English scientists Alfred Russel Wallace and Charles Darwin had propounded, jointly, the theory of the origin of species through the agency of natural selection, and in the following year, 1859, Charles Darwin's monumental book *The Origin of Species* (*Bi. 38*) appeared, in which this evolutionary theory was elaborated more fully. At the present time it is

[1] From Iltis's *Gregor Johann Mendel, Leben, Werk und Wirkung*. By permission of Julius Springer, Berlin, publisher.

difficult to realize the revolution which Charles Darwin's book created in scientific circles. Following its publication, for a period of something like twenty years, *The Origin of Species* was the center of controversy in practically every civilized country of the globe. Scientists became divided into two camps, one upholding the Darwinian conception of evolution and the other stubbornly opposing it. Nägeli, who lived and worked during this same period, undoubtedly was too busy with this most important topic to have any spare time to examine the paper of an Austrian monk whose only claim on him was that at different times he had been in correspondence with him.

In the year 1900 three scientists, working independently in three different countries, happened to hit upon conceptions which were similar to those of Mendel. These were the botanists (1) Correns of Germany, (2) Tschermak of Austria, and (3) De Vries of Holland. In tracing back the previous literature on the subject, these biologists came across Mendel's paper and soon discovered that their conclusions were similar to those that Mendel had arrived at nearly forty years before their time. They also realized that inasmuch as Mendel's results had been accomplished and published so many years before their own, he had priority claims to recognition for the discovery, and so they named the principle for him. The term "Mendelism," therefore, refers to the principles and laws of heredity discovered and developed largely through the efforts of the Austrian monk Gregor Johann Mendel.

Mendelian Terminology

Before discussing Mendelism in greater detail and considering crosses, it may be well to familiarize ourselves with some current terminology used by the modern geneticist in dealing with the actual Mendelian crosses which he makes.

The individuals used as parents in a cross are indicated by the letter P, P_1 expressing the immediate parents, P_2 the

grandparents, and P_3 the great-grandparents. The offspring are designated by the letter F, F_1 representing the first filial generation of offspring, F_2 the second filial generation, and so on.

When crosses are made, distinct characters are dealt with, and these are designated by the breeder as *unit characters*. Ordinarily unit characters are traits of individuals which behave as units in heredity. The general term *hybrid* is used to express the progeny derived of parents which differ in distinct unit characters. When one unit character is involved in the cross, it is spoken of as a *monohybrid*; when two unit characters are involved, the cross is a *dihybrid*; when three unit characters are involved, a *trihybrid*, and so on.

Certain unit characters in crosses seem to dominate and cover over opposite traits. The former are therefore called *dominant* and are generally indicated by capital letters. In most instances the letter chosen is the first one of the word used to express the trait. For example, if the color black is the characteristic dealt with and it is dominant, then B would be the letter used by the breeder to indicate it. Those traits which, although present, do not appear in the cross, being covered over by the dominant characteristic, are spoken of as *recessive* and are indicated by corresponding small letters. Thus capitals indicate dominance and small letters recessiveness. To illustrate, if albino or white is the recessive character involved in the cross with the dominant black (B), then the letter b would be used to designate it. While this is a general rule, yet there are exceptions to it. Certain breeders, especially those dealing with corn, use the first letter of the recessive trait to designate the character. The dominant trait, therefore, would be indicated by the capital of the letter standing for the recessive. If this procedure were applied to the black and white traits mentioned above, then w would stand for the recessive white and W for the dominant black.

When a pair of traits or entities which enter crosses are opposite,— and this is usually the case where one is domi-

nant and the other recessive,— they are called *allelomorphs.* For instance, the color black is the allelomorph of white and vice versa. In like fashion, the genes for black and white are an *allelomorphic* pair, and when combined within a zygote they give rise to an organism which is hybrid for this color trait. When the zygote contains such a pair of factors, it is spoken of as a *heterozygote.* Where the factors are similar, we get a pure breed for the particular trait, and the zygote is spoken of as a *homozygote.*

In this connection it has been established by numerous geneticists who have intensively studied the traits of various species of organisms, notably *Drosophila melanogaster,* that there exists the condition of *multiple allelomorphism,* where a trait may be the allelomorph of a large number of other traits. In reality each one of these traits has been shown to be allelomorphic to all the others in the series. Also the genes responsible for the emergence of such allelomorphs occupy similar positions within the chromosomes. Needless to state, where a single cross is involved, only one pair of such an allelomorphic group is encountered.

In instances where neither of the traits which enter a cross dominates, but the two seem rather to interact to bring about a new expression of the character in question, then both traits are indicated by capital letters, the capital in each instance being the first letter of the word which describes the specific trait in question. For example, in the cross between the black (BB) and the white (WW) Andalusian fowls, to be more fully discussed later on (Fig. 66, page 193), the resultant progeny are all blue, BW. The blue character is produced by the combination of the entities for the white (W) and the black (B) traits which find their way into the same zygote to form BW.

When organisms are crossed, some of the individuals produced in the F_1 and other generations outwardly appear to be similar to one or the other of the respective parents; but when these are actually tested out through subsequent breeding experiments, it is discovered that some of them have a

different germinal constitution from that of the parents which they resemble. Individuals that appear alike externally, regardless of their germinal make-up, are said to belong to the same *phenotype*. When they are alike germinally, they are said to belong to the same *genotype*. As will be indicated in some of the actual crosses to be considered later on, organisms might belong to the same phenotype and yet, when tested out carefully through appropriate breeding experiments, be found to belong to a number of distinctly different genotypes. A simple example will be cited to help clarify the items under consideration. In crossing a pure-bred black guinea pig with a pure-bred white one, the resultant progeny are all black, resembling the pure-bred black parent to such a marked degree that the black offspring and the black parent cannot be distinguished. From an external standpoint they may be said to belong to the same phenotype — black; but actual breeding tests indicate clearly that they can be classified into two distinctive genotypes: (1) BB for the pure-bred black parent and (2) Bb for the hybrid offspring of the first generation. With the above explanations in mind, we can now consider the Mendelian principles of breeding a little more intelligently.

Mendelian Principles

Mendel dealt with simple hereditary phenomena, concentrating his attention on one or two obvious traits, whose behavior and inheritance in crosses he studied carefully. Fortunately these characters were true dominants and recessives and depended for their expression on the presence within the zygote of one or both of a single pair of factors for the specific traits in question. Furthermore, the inheritance of these characters could be studied and tested very easily. Had this not been the case, the discovery of the Mendelian principles would undoubtedly have been delayed considerably, probably until after Mendel's time.

Mendel's principles of breeding may be stated briefly as follows: When two organisms which differ in respect to one

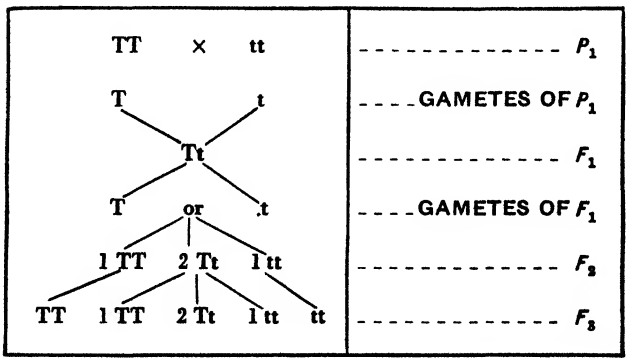
character are crossed, the offspring of the first generation will outwardly resemble one of the parents. The parent organism which thus impresses its character on these offspring is called the *dominant* parent, and the character which it impresses is likewise spoken of as dominant. The other parent, which enters the cross but seemingly does not leave its impression on the offspring, is referred to as the *recessive* parent, and the character which it contributes is spoken of as the recessive character. When, in turn, the hybrid male and female offspring of the first generation are crossed, the progeny of the second generation will then consist of 25 per cent dominant individuals, 50 per cent hybrid individuals that outwardly resemble the dominants, and 25 per cent recessive individuals. Since it is practically impossible to distinguish the hybrid offspring from the pure dominants, the ratio of individuals actually procured in the second, or F_2, generation is 75 per cent like the dominant parent and 25 per cent like the recessive parent,— a ratio of 3 : 1.

The essential features of Mendel's principles are based on the fact that hereditary traits are independent units which, although they enter crosses, nevertheless segregate out again as distinctive entities, independent of temporary dominance. Mendel's original experiments were conducted with peas, and they consisted of simple crosses in which one or two factors mainly were involved. After the rediscovery of Mendelism, crosses were made also in the animal kingdom, yielding results similar to those obtained by Mendel with plants.

Monohybrid Crosses

Monohybrid crosses are those in which single unit characters are involved. One of Mendel's earliest experiments was to cross a tall variety of pea with a dwarf one. Inasmuch as both of these plants were pure with respect to the character, the tall plants, when self-fertilized, gave only tall types; and likewise the dwarf plants yielded only dwarf individuals. On the other hand, when tall and dwarf plants were crossed,

the first-generation offspring, F_1, outwardly appeared tall, resembling the pure-bred tall parents. When the seeds of these plants were saved and planted in the following season, the progeny produced in the F_2 generation consisted of 75 per cent tall plants and 25 per cent dwarf ones, a ratio of 3 : 1. A more searching investigation and analysis of the 75 per cent tall plants soon revealed that 25 per cent of them were pure talls and the other 50 per cent hybrids, similar in every detail to the hybrid parents from which they were derived. Therefore, when all the results of this Mendelian cross were tabulated, the ratio of individuals produced was found to consist of 25 per cent pure talls, 50 per cent hybrid talls, and 25 per cent pure dwarfs. From a Mendelian standpoint, this cross is represented by the geneticist in the following manner:



Incidentally the above cross may be used as a convenient guide and illustration for representing other Mendelian crosses. The individuals, since they are produced by a combination of two gametes, contain a pair of determiners for each trait, and therefore they are represented by double letters: TT or tt or Tt. When the gametes are formed, the pair of entities for the traits become segregated during the reduction division of the maturation process, so that each mature gamete receives only a single letter, T or t.

One other item of interest in regard to Mendelian crosses is that geneticists have devised the convenient checkerboard

method of arriving at the different possible combinations which may be produced in the F_2 generation. Since the F_1 individuals are hybrid with respect to the trait in question, then each is capable of producing two types of gametes, one carrying the factor for tallness, T, and the other the factor for dwarfness, t. Males as well as females produce these different gametes in equal numbers. The checkerboard device outlined below affords a simple and accurate means of determining all the different possibilities which may be produced in the F_2 generation.

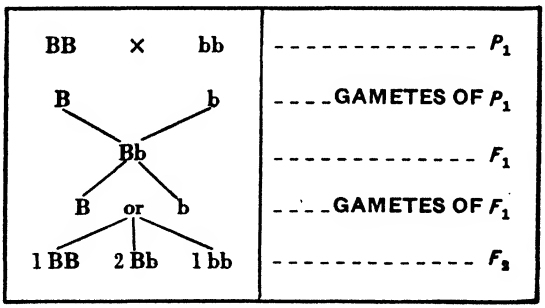
F_1 — MALE GAMETES \ F_1 — FEMALE GAMETES	T	t
T	TT pure tall	Tt hybrid tall
t	Tt hybrid tall	tt pure dwarf

When all the individuals produced are tabulated, it is seen that the F_2 generation consists of one fourth pure talls, TT; another fourth pure dwarfs, tt; and the rest, constituting one half of all the progeny, hybrid talls, Tt, which outwardly resemble the pure talls. This ratio is, of course, exactly the same as that expressed by the formula 1 TT : 2 Tt : 1 tt. These individuals outwardly belong to the two phenotypes, tall plants and dwarf plants; inwardly they consist of the three genotypes TT, Tt, and tt.

Mendel indicated a means of testing whether an individual was a pure tall or a hybrid tall. This consisted in making a *back cross* between the F_2 tall plants and the pure dwarf ones of P_1. If the tall individual was pure, TT, then the offspring would all be hybrid talls, Tt. If the tall individual was hybrid, Tt, then 50 per cent of the offspring would consist of tall hybrid individuals of constitution Tt, and the other 50 per cent would be pure dwarf of constitution tt.

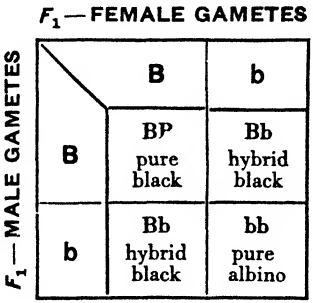
Mendel made crosses involving seven pairs of characters in peas, and his results were similar to those obtained in the cross illustrated above. The list of the actual crosses which Mendel made, with the dominant character in each instance mentioned first, is as follows: (1) tall plants and dwarf plants; (2) colored flowers and white flowers; (3) flowers axial (that is, arranged along the axis) and flowers terminal (or flowers bunched at the top); (4) green pods and yellow pods; (5) inflated pods and constricted pods; (6) cotyledons yellow and cotyledons green; and (7) rounded seeds and wrinkled seeds.

Following the rediscovery of Mendelism, animal-breeders succeeded in making crosses with animals similar to those made by Mendel with plants, and obtained like results, indicating the universality of the Mendelian principles. One such cross is that between a pure-bred black guinea pig (BB)



and a pure-bred albino, or white, guinea pig (bb). In the F_1 generation all the individuals are hybrid blacks (Bb). When these are mated, the progeny in the F_2 generation appear in typical Mendelian fashion as three fourths black and one fourth white. The latter are pure whites of constitution bb. The three fourths of the total number of individuals which appear outwardly as blacks, when carefully tested, show themselves to be one fourth pure blacks of constitution BB and the remaining two fourths are hybrid blacks of constitution Bb. The actual cross may be illustrated as per the above diagram.

All possible types of individuals produced in the F_2 generation may be derived by the convenient checkerboard method as shown below.



It can be seen clearly that the organisms belong to the two phenotypes (1) black (BB and Bb) and (2) albino (bb), and the three genotypes (1) BB, (2) Bb, and (3) bb.

Dihybrid Crosses

Dihybrid crosses are those in which two unit characters are involved. Mendel made such a cross between pea plants which seeds were round and yellow and those that had angular green seeds. Inasmuch as the round and yellow characters in each case have proved to be dominant over the angular and the green ones, the parent plants must be represented as RRYY and rryy. In the F_1 generation all the individuals obtained are round yellow, RrYy. When the seeds of this generation are planted, they produce an F_2 progeny consisting of a ratio of 9 round yellow : 3 round green : 3 angular yellow : 1 angular green.

This makes a ratio as between sixteen individuals, which is typical for a dihybrid. This number, sixteen, of individuals of the F_2 generation may be obtained by adding the F_2 types of a monohybrid, $3 + 1$, and squaring them. In reality, the sum of the components of the ratios of different types produced in the F_2 generation of a cross may be obtained easily through the formula $(3 + 1)^n$, in which n indicates the

number of unit characters involved; where one is involved, the sum would be $(3+1)^1=4$; where two characters are involved, as in a dihybrid cross, it would be $(3+1)^2=16$; where three unit characters are involved, the sum would be sixty-four, that is, $(3+1)^3=64$; and where four unit characters are considered, the sum of the ratios of the F_2 generation types would be $(3+1)^4=256$.

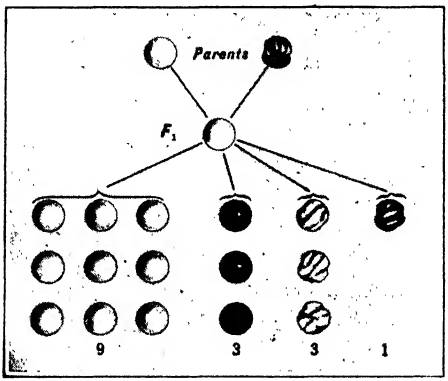


FIG. 64. Dihybrid Cross between Peas[1]

The types crossed are the round yellow (RRYY) peas and angular green (rryy) peas, giving the 9:3:3:1 ratio in the F_2 generation

Fig. 64 illustrates the above dihybrid cross with peas, and the zygotic constitution of the various individuals of the F_2 generation is shown more distinctly through the checkerboard method on the opposite page. This was discussed under the heading of "Monohybrid Crosses."

When the sixteen combinations of the F_2 generation are tabulated, it is noticed that they fall into four phenotypes and nine genotypes. These are listed in the table at the foot of page 177. In parentheses, following each genotype, are indicated the numbers of the squares in the checkerboard where the individuals are located.

When dihybrid crosses are examined carefully, they are found to bring out another feature of Mendelism which was not revealed by the monohybrid crosses, namely, the independent assortment of the genes, making possible new combinations of the genes found in different parents and thereby giving origin to new types, such as round green peas and angular yellow peas, which showed up in the above cross.

[1] From Morgan's *Evolution and Genetics*. By permission of Princeton University Press, publishers.

With the statement of this principle, we are now in a position to summarize the two cardinal laws which Mendel discovered.

F_1—FEMALE GAMETES

F_1—MALE GAMETES	RY	Ry	rY	ry
RY	1 RRYY round yellow	2 RRYy round yellow	3 RrYY round yellow	4 RrYy round yellow
Ry	5 RRYy round yellow	6 RRyy round green	7 RrYy round yellow	8 Rryy round green
rY	9 RrYY round yellow	10 RrYy round yellow	11 rrYY angular yellow	12 rrYy angular yellow
ry	13 RrYy round yellow	14 Rryy round green	15 rrYy angular yellow	16 rryy angular green

They are (1) that characters are independent units which segregate out from crosses regardless of dominance, and (2) that the allelomorphic pairs of characters of an organism

4 PHENOTYPES	9 GENOTYPES
9 round yellow	1 RRYY (1) 2 RRYy (2, 5) 2 RrYY (3, 9) 4 RrYy (4, 7, 10, 13)
3 round green	1 RRyy (6) 2 Rryy (8, 14)
3 angular yellow	1 rrYY (11) 2 rrYy (12, 15)
1 angular green	1 rryy (16)

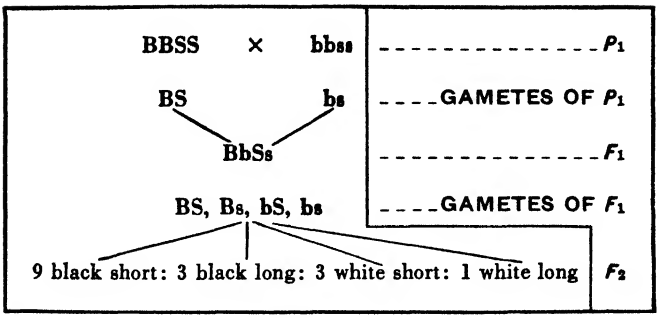
behave independently of each other in inheritance. Through proper matings these laws may be utilized to bring about an association of the genes into new combinations, giving origin to types which hitherto have not been in existence. This will become more apparent when the remainder of the crosses in the present chapter are analyzed carefully. Incidentally, knowledge of these laws is indispensable to an intelligent understanding of the more recent developments in genetics.

In reality, then, in Mendelian breeding the entities for characters which enter a cross segregate out again in the formation of the germ cells and recombine to form old as well as new combinations in the resultant offspring. William J. Spillman (*Bi. 193*), former agriculturist in charge of the Office of Farm Management of the United States Department of Agriculture, in commenting on this last-mentioned power, or law, of recombination says:

> Breeders have unconsciously used this law since breeding first became an art, but a knowledge of the principles involved now enables them to accomplish desired results much more quickly and surely than was formerly the case.[1]

A dihybrid cross in animals, similar to the one given in plants, which shows the Mendelian principles of segregation, independent assortment, and recombination of pairs of allelomorphic genes is the one made by Castle on guinea pigs. Castle crossed a pure-bred guinea pig possessing black fur and short hair with one that was an albino (that is, its fur was white) and possessed long hair. In the first generation all the individuals had black fur and short hair, indicating that the black ~~character~~ hair was dominant over the albino ~~character~~ and the short ~~fur~~ hair over the long ~~fur~~ hair. The parents involved in this cross are therefore of the constitution BBSS (black fur, short hair) and bbss (white fur, long hair). The results obtained may be indicated as in the chart at the top of the opposite page.

[1] W. J. Spillman, "Application of Some of the Principles of Heredity to Plant Breeding," *United States Department of Agriculture, Bureau of Plant Industry, Bulletin No. 165* (1911), p. 23.



By the checkerboard method given below the different individuals obtained in the F_2 generation from the crossing of all the possible gametes produced in the F_1 generation may be distinguished clearly. The sixteen individuals shown in the squares of the checkerboard are numbered in logical sequence. These numbers correspond to those given, in the parentheses, after the genotypes in the table on page 180.

F_1—FEMALE GAMETES

F_1—MALE GAMETES	BS	Bs	bS	bs
BS	1 BBSS black short	2 BBSs black short	3 BbSS black short	4 BbSs black short
Bs	5 BBSs black short	6 BBss black long	7 BbSs black short	8 Bbss black long
bS	9 BbSS black short	10 BbSs black short	11 bbSS white short	12 bbSs white short
bs	13 BbSs black short	14 Bbss black long	15 bbSs white short	16 bbss white long

As in the other dihybrid crosses, there were four phenotypes and nine genotypes, as shown in the following table, with the numbers of the squares indicated after each of the genotypes.

4 PHENOTYPES	9 GENOTYPES
9 black short	1 BBSS (1) 2 BBSs (2, 5) 2 BbSS (3, 9) 4 BbSs (4, 7, 10, 13)
3 black long	1 BBss (6) 2 Bbss (8, 14)
3 white short	1 bbSS (11) 2 bbSs (12, 15)
1 white long	1 bbss (16)

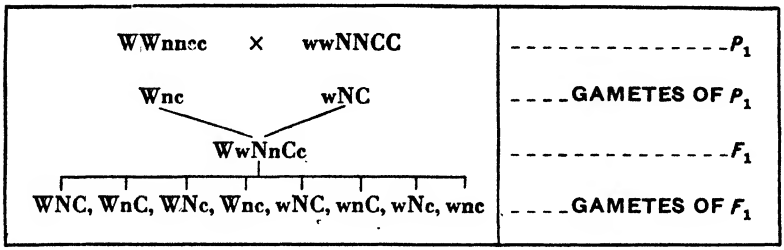
An examination of these results shows clearly that new types have been produced, namely, black long-haired individuals (BBss) and white short-haired individuals (bbSS). Mendelism thus makes it possible to eliminate certain undesirable traits and at the same time combine the desirable ones into a type that may then become the progenitor of improved forms, which may supplant the parent stocks. From an economic standpoint it is easy to see the tremendous importance of the benefits to be derived from such a procedure.

Trihybrid Crosses

A trihybrid cross is one in which three unit characters are involved. This means sixty-four possible combinations from the gametes of the F_1 hybrid, or $(3 + 1)^3 = 64$.

An interesting trihybrid cross in plants is the one made by Spillman at the Washington Agricultural Experiment Station, Pullman, Washington, involving two varieties of wheat for purposes of improvement. The cross was between a variety of winter wheat that lodged easily (that is, it had weak straw), with open chaff, so that its seed scattered readily when ripe (WWnncc), and a variety of spring wheat that did not lodge and had tightly closed chaff when ripe

(wwNNCC). In the cross the winter, nonlodging, and closed-chaff characters were dominant. If we let the following letters represent the various traits: W for winter and w for spring; N for nonlodging, or stiff, straw and n for lodging, or weak, straw; C for closed chaff and c for open chaff,—then the cross can be indicated as follows:



The sixty-four possible kinds of individuals which may be produced in F_2 are shown in this checkerboard:

F_1—FEMALE GAMETES

F_1—MALE GAMETES	WNC	WnC	WNc	Wnc	wNC	wnC	wNc	wnc
WNC	1 WWNNCC	2 WWNnCC	3 WWNNCc	4 WWNnCc	5 WwNNCC	6 WwNnCC	7 WwNNCc	8 WwNnCc
WnC	9 WWNnCC	10 WWnnCC	11 WWNnCc	12 WWnnCc	13 WwNnCC	14 WwnnCC	15 WwNnCc	16 WwnnCc
WNc	17 WWNNCc	18 WWNnCc	19 WWNNcc	20 WWNncc	21 WwNNCc	22 WwNnCc	23 WwNNcc	24 WwNncc
Wnc	25 WWNnCc	26 WWnnCc	27 WWNncc	28 WWnncc	29 WwNnCc	30 WwnnCc	31 WwNncc	32 Wwnncc
wNC	33 WwNNCC	34 WwNnCC	35 WwNNCc	36 WwNnCc	37 wwNNCC	38 wwNnCC	39 wwNNCc	40 wwNnCc
wnC	41 WwNnCC	42 WwnnCC	43 WwNnCc	44 WwnnCc	45 wwNnCC	46 wwnnCC	47 wwNnCc	48 wwnnCc
wNc	49 WwNNCc	50 WwNnCc	51 WwNNcc	52 WwNncc	53 wwNNCc	54 wwNnCc	55 wwNNcc	56 wwNncc
wnc	57 WwNnCc	58 WwnnCc	59 WwNncc	60 Wwnncc	61 wwNnCc	62 wwnnCc	63 wwNncc	64 wwnncc

Summarizing the results obtained through the checkerboard method, we get the following types in the F_2 generation: 27 winter, stiff, closed-chaff; 9 winter, lodging, closed-chaff; 9 winter, stiff, open-chaff; 9 spring, stiff, closed-chaff; 3 winter, lodging, open-chaff; 3 spring, lodging, closed-chaff; 3 spring, stiff, open-chaff; 1 spring, lodging, open-chaff. This is the typical trihybrid ratio derived from the formula

8 PHENOTYPES	27 GENOTYPES
27 winter, stiff, closed-chaff	1 WWNNCC (1) 2 WWNnCC (2, 9) 2 WWNNCc (3, 17) 4 WWNnCc (4, 11, 18, 25) 2 WwNNCC (5, 33) 4 WwNnCC (6, 13, 34, 41) 4 WwNNCc (7, 21, 35, 49) 8 WwNnCc (8, 15, 22, 29, 36, 43, 50, 57)
9 winter, lodging, closed-chaff	1 WWnnCC (10) 2 WWnnCc (12, 26) 2 WwnnCC (14, 42) 4 WwnnCc (16, 30, 44, 58)
9 winter, stiff, open-chaff	1 WWNNcc (19) 2 WWNncc (20, 27) 2 WwNNcc (23, 51) 4 WwNncc (24, 31, 52, 59)
9 spring, stiff, closed-chaff	1 wwNNCC (37) 2 wwNnCC (38, 45) 2 wwNNCc (39, 53) 4 wwNnCc (40, 47, 54, 61)
3 winter, lodging, open-chaff	1 WWnncc (28) 2 Wwnncc (32, 60)
3 spring, lodging, closed-chaff	1 wwnnCC (46) 2 wwnnCc (48, 62)
3 spring, stiff, open-chaff	1 wwNNcc (55) 2 wwNncc (56, 63)
1 spring, lodging, open-chaff	1 wwnncc (64)

$(3 + 1)^3$. There are eight phenotypes and twenty-seven genotypes enumerated in the table at bottom of page 182. As in the previous tables, the numbers in the parentheses after the genotypes represent the squares in the checkerboard where the individuals are found.

The type which Spillman desired was that represented by the genotype WWNNCC, that is, a pure wheat with respect to the *winter*, *nonlodging*, and *closed-chaff* characters. It is seen that this type of wheat presented itself only once in the F_2 generation, and the question which naturally arises is How can this be isolated from the other mixed types which resemble it, in order that it may be fixed permanently for future generations? Spillman says this can be done in plants as follows:

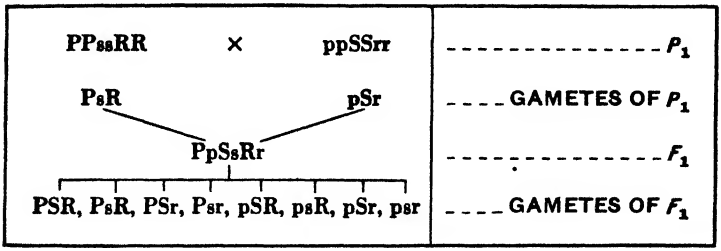
> One way to overcome this difficulty in a self-pollinated species is to save the seed of each second-generation plant separately. If the species is one that is not self-fertilized, but one which can be artificially self-fertilized, we can accomplish the segregation of the desired type by artificial self-fertilization of all the second generation individuals that appear to be of the type desired and by planting their seed separately. When the next generation matures it will be seen which of them have reproduced true to type. The seed of these may be saved, and thus form the basis of a new and fixed variety in self-fertilized species and in such open-fertilized species as will endure such self-fertilization.[1]

Of course, types which can be propagated vegetatively through cuttings and the like are easily fixed. In those reproduced through cross-fertilization, the procedure is as follows:

> In cross-fertilized species, if the desired combination is not at hand, we can get it by crossing but cannot be sure of keeping it unless it is a form that can be propagated vegetatively, such as berries, tree fruits and potatoes. The best we can do in cross-fertilized species which are propagated from seed is to make a cross with a view to getting a certain desired combination of characters and then select the desired type until we get a fairly constant strain of it.[2]

[1] W. J. Spillman, "Application of Some of the Principles of Heredity to Plant Breeding," *United States Department of Agriculture, Bureau of Plant Industry, Bulletin No. 165* (1911), p. 22. [2] *Ibid.* p. 54.

In a manner similar to Spillman's experiments, Castle made crosses of guinea pigs involving three characters. For



example, he crossed a pure-bred pigmented, long-haired, and rough-coated guinea pig with an albino, short-haired, and smooth-coated guinea pig and obtained, in the first generation, individuals all of whom were pigmented, with short

F_1—FEMALE GAMETES

F_1—MALE GAMETES	PSR	PsR	PSr	Psr	pSR	psR	pSr	psr
PSR	1 PPSSRR	2 PPSsRR	3 PPSSRr	4 PPSsRr	5 PpSSRR	6 PpSsRR	7 PpSSRr	8 PpSsRr
PsR	9 PPSsRR	10 PPssRR	11 PPSsRr	12 PPssRr	13 PpSsRR	14 PpssRR	15 PpSsRr	16 PpssRr
PSr	17 PPSSRr	18 PPSsRr	19 PPSSrr	20 PPSsrr	21 PpSSRr	22 PpSsRr	23 PpSSrr	24 PpSsrr
Psr	25 PPSsRr	26 PPssRr	27 PPSsrr	28 PPssrr	29 PpSsRr	30 PpssRr	31 PpSsrr	32 Ppssrr
pSR	33 PpSSRR	34 PpSsRR	35 PpSSRr	36 PpSsRr	37 ppSSRR	38 ppSsRR	39 ppSSRr	40 ppSsRr
psR	41 PpSsRR	42 PpssRR	43 PpSsRr	44 PpssRr	45 ppSsRR	46 ppssRR	47 ppSsRr	48 ppssRr
pSr	49 PpSSRr	50 PpSsRr	51 PpSSrr	52 PpSsrr	53 ppSSRr	54 ppSsRr	55 ppSSrr	56 ppSsrr
psr	57 PpSsRr	58 PpssRr	59 PpSsrr	60 Ppssrr	61 ppSsRr	62 ppssRr	63 ppSsrr	64 ppssrr

hair, and rough coats. It is thus seen that pigment is dominant over albinism, short hair is dominant over long hair, and rough coat is dominant over smooth coat. The parents, therefore, are of constitution PPssRR and ppSSrr, whereas the F_1 individuals are all of constitution PpSsRr. The cross may thus be shown as in the chart at the top of the opposite page.

By the checkerboard method shown at the foot of the opposite page, the F_2 generation reveals the following ratio of individuals: 27 pigmented, short hair, rough coat; 9 pigmented, long hair, rough coat; 9 pigmented, short hair, smooth coat; 9 albino, short hair, rough coat; 3 pigmented, long hair, smooth coat; 3 albino, long hair, rough coat; 3 albino, short hair, smooth coat; 1 albino, long hair, smooth coat.

Fig. 65 shows the results of the cross carried out to the F_2 generation. The eight phenotypes and twenty-seven different genotypes are indicated in the table on page 187. After each genotype, in parentheses, are listed the numbers of the squares in the checkerboard, on page 184, where the individuals are found.

Here, as in plants, new types presented themselves showing new combinations of genes found originally in different parents. The breeder is constantly on the lookout for these, and if they happen to be more desirable than his old types he is anxious to fix them in order that they may breed true in future generations. Castle (*Bi. 22*) discusses this problem and asserts the following:

> Now the breeder who by means of crosses has produced a new type of animal wishes, of course, to "fix" it,— that is, to obtain it in a condition which will breed true. He must, therefore, obtain homozygous individuals. If he is dealing with a combination which contains only recessive characters, this will be easy enough, for such combinations are invariably homozygous. His task will become increasingly difficult, the more dominant characters there are included in the combination which he desires to fix.
>
> The most direct method for him to follow is to test by suitable matings the unit-character constitution of each individual which shows the desired combination of characters, and to reject all

which are not homozygous. In this way a pure race may be built up from individuals proved to be pure. Such a method, however,

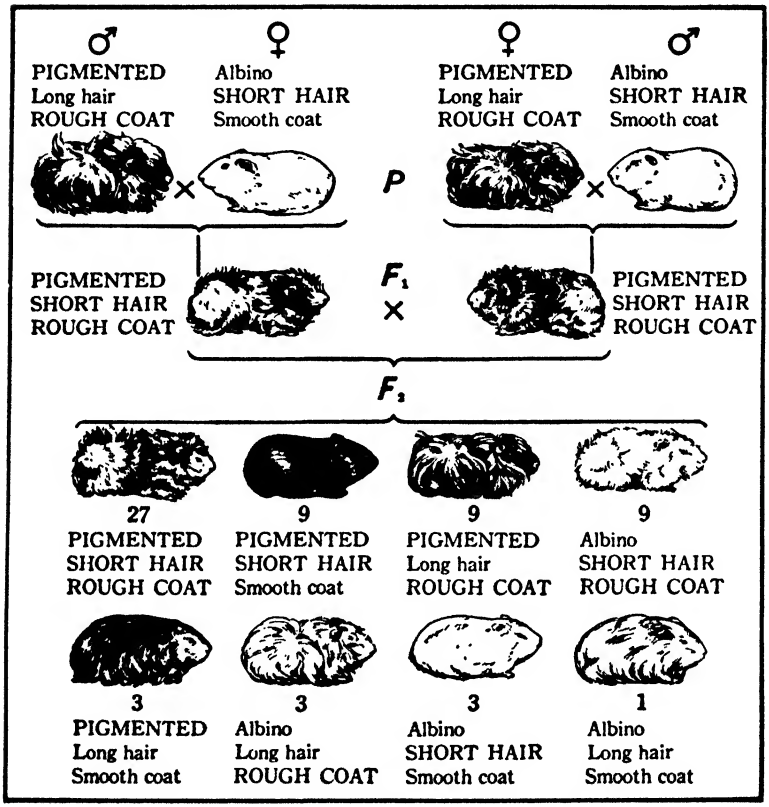


FIG. 65. Trihybrid Cross between Guinea Pigs[1]

The diagram shows the combinations produced in the F_2 generation when guinea pigs possessing pigment, long hair, and rough coats are crossed with individuals that are albinos, with short hair and smooth coats. Words in capitals indicate dominant traits; those in small letters, recessive traits

though sure, is slow in cases where the desired combination includes two or more dominant unit-characters, for it involves the application of a breeding test to many dominant individuals, most of which

[1] From *Being Well Born*, by Michael F. Guyer, Copyright 1916 and 1927. Used by special permission of the publishers, The Bobbs-Merrill Company.

must then be rejected. It is, therefore, often better in practice to breed from all individuals which show the desired combination, and

8 PHENOTYPES	27 GENOTYPES
27 pigmented, short hair, rough coat	1 PPSSRR (1) 2 PPSsRR (2, 9) 2 PPSSRr (3, 17) 4 PPSsRr (4, 11, 18, 25) 2 PpSSRR (5, 33) 4 PpSsRR (6, 13, 34, 41) 4 PpSSRr (7, 21, 35, 49) 8 PpSsRr (8, 15, 22, 29, 36, 43, 50, 57)
9 pigmented, long hair, rough coat	1 PPssRR (10) 2 PPssRr (12, 26) 2 PpssRR (14, 42) 4 PpssRr (16, 30, 44, 58)
9 pigmented, short hair, smooth coat	1 PPSSrr (19) 2 PPSsrr (20, 27) 2 PpSSrr (23, 51) 4 PpSsrr (24, 31, 52, 59)
9 albino, short hair, rough coat	1 ppSSRR (37) 2 ppSsRR (38, 45) 2 ppSSRr (39, 53) 4 ppSsRr (40, 47, 54, 61)
3 pigmented, long hair, smooth coat	1 PPssrr (28) 2 Ppssrr (32, 60)
3 albino, long hair, rough coat	1 ppssRR (46) 2 ppssRr (48, 62)
3 albino, short hair, smooth coat	1 ppSSrr (55) 2 ppSsrr (56, 63)
1 albino, long hair, smooth coat	1 ppssrr (64)

eliminate from their offspring merely such individuals as do not show that combination. The race will thus be only gradually purified, but a large stock can be built up much more quickly.[1]

[1] W. E. Castle, *Genetics and Eugenics* (Fourth Edition), pp. 141–142. Harvard University Press, Cambridge, 1930.

Post-Mendelian Developments

When the Mendelian principles were rediscovered, geneticists immediately recognized their value. Moreover, they believed that all characters were as simple as those which Mendel dealt with and that the offspring of a cross showed resemblances to their parents in the exact ratio indicated by Mendel for his original crosses. It must be remembered that Mendel thought that each trait depended for its expression on a pair of entities, one dominating over the other, the dominating one really determining the expression of the trait which made its appearance in the cross. To Mendel, therefore, heredity was a very simple thing; but since his time it has been discovered that while, in the main, there are many traits which behave in a fashion similar to those which Mendel dealt with, nevertheless there are others which are more complicated and do not follow such definite lines.

Although crosses involving such traits proved to be a source of grave concern to geneticists, especially during the early years following the rediscovery of the Mendelian principles, and at times made them even question the validity of the Mendelian contentions, a more careful analysis has indicated that the peculiar ratio of individuals obtained was due to the fact that certain characters depend for their expression on more than just one or two factors within the zygote responsible for the origin of the new organism. In fact, in many instances it has been shown that characters are dependent on a rather large number of factors being combined together within the same individual. This, instead of weakening Mendelism, has lent additional strength to it and also has clearly indicated that fundamentally heredity depends on the entities for traits carried within the germ cells that combine to produce the offspring.

In reality, the new developments since the rediscovery of Mendelism have been along three main lines: First, an advance has been made through the elaboration and extension of the *gene hypothesis* for the expression of traits. Second,

there have been developments in the study of the so-called *sex linkage* and *nondisjunction* phenomena. Sex linkage is a special type of Mendelian inheritance in which the genes for traits are located within the sex chromosomes, whereas in nondisjunction homologous chromosomes, instead of separating during synapsis, remain together and pass over into one of the germ cells. Finally, the third line of advance has come through the elaboration of the theory of so-called *linkage* and *crossing-over* phenomena. Linkage studies have indicated that factors for traits are not absolutely independent units segregating out of crosses separately, as Mendel thought, but may remain combined or linked so as to come out together in offspring. When crossing over occurs, certain of the linked genes within a chromosome may become separated so as to make possible new expressions.[1] In Chapters XI–XIII these developments will be considered in greater detail. For additional reading connected with the items dealt with in these chapters, the student is referred to the bibliography as follows: *Bi. 3, 7, 11, 13, 18, 22, 27, 28, 53, 58, 96, 118, 123, 133, 140–146, 153, 174, 188, 203, 204.*

CHAPTER XI

The Gene Hypothesis

WHEN the geneticist deals with crosses, he must always be conscious of the fact that what actually cross are the germ cells of the organisms in question and, as indicated under our discussion of the germ plasm, the things carried by the germ cells that ultimately gain expression as the recognizable unit characters are definite entities for traits within the chromosomes and are designated by various names, such as *genes, factors,* or *determiners.* What they actually are is difficult to answer, inasmuch as no one has ever been able to isolate and examine them physically, chemically, or otherwise. However, attempts to visualize the constitution and action of genes have been made, as has been described in Chapter IX. Most geneticists feel certain that they are present within the chromosomes, and that they are the entities responsible for the development of the adult traits which characterize the existing organisms.

Mendel thought that each trait depended for its expression on a pair of entities,— one, the dominant, dominating over the other, the recessive, the former really determining the expression of the trait which appeared. In practically all the crosses made by Mendel, and also in numerous others like them which have been made since his time, the dominance of one character over another has proved to be absolute, so that it has not been possible to distinguish the F_1 hybrids from the dominant parent. While these have all proved to be instances of *total dominance,* nevertheless there are numerous other examples in which the dominance of one character over the other is seldom absolute, varying considerably in its expression, so that oftentimes the recessive character also may easily be detected.

Types and Degrees of Dominance

Since the rediscovery of Mendelism good examples have been found to show that dominance may vary from the condition where it is absolute to that where it is nonexistent. Crosses showing the latter condition reveal that each gene really participates and coöperates with others to bring about a different expression of the character in question. Many geneticists treat this topic under the general heading of *interaction of genes.* Let us now consider typical cases illustrating the different types and degrees of dominance.

Total Dominance

Cases where the dominance of one character over another is absolute have been amply discussed in the previous chapter. In fact, in all the crosses made by Mendel and in numerous others made since his time such total, or complete, dominance was observed.

Partial Dominance

There are other crosses, however, and a large number of them, in which dominance has proved to be partial, so that the F_1 hybrids, while in large measure resembling the dominant parent, may also show traces of the recessive character, making it possible to distinguish the hybrids rather easily. For example, when horned cattle are crossed with polled, or hornless, ones, they produce polled progeny, in many of which traces of horns, or scurs, may be recognized. Many other examples similar to those cited have been recorded by geneticists. Inasmuch as the hybrids can be distinguished from the parents, it becomes a relatively simple matter to illustrate the ratios in Mendelian crosses.

Delayed Dominance

In connection with dominance, geneticists have also found that certain characters, and of course the factors which account for them, remain dormant and do not assert themselves

until the organism has continued to exist for some time independently. When they do assert themselves, they dominate and so reveal the real nature of these genes. Such instances have been called cases of delayed dominance. A good example is the cross which Davenport made between white and black Leghorn fowls. They produce offspring which, although chiefly white, are nevertheless speckled with black; later on, however, the white color asserts itself and becomes the dominating one.

Even in man numerous cases of delayed dominance have been discovered. For instance, the color of the eyes and of the hair do not assert themselves definitely until late in childhood or even, in some cases, not until the period of adolescence. Almost everyone recalls the experience of watching the color of the eyes and of the hair of a child change as he progresses from childhood to youth.

Nondominance

It has already been mentioned that the geneticist has discovered a good many crosses in which the hybrids are altogether different from their parents and may be distinguished easily from them. All instances of this sort are cases of the nondominance of either of the allelomorphic factors. Instead these factors coöperate and interact to produce the observed expression. Good examples are at hand to show that instead of one factor's dominating the other, both contribute to produce a character intermediate between the ones utilized for crossing purposes. It must not be inferred that the factors responsible for the intermediate expression actually merge so as to lose their identity; rather, they produce a reciprocal effect on each other, so as to give origin to an expression of the particular trait which is halfway between the appearance of the characters as they are found in the parents. An excellent illustration of such a cross is the one involving the black and the white Andalusian fowls (Fig. 66). Here, instead of one character's dominating the other, both are effective in producing a hybrid which is bluish in color. When the F_1 in-

dividuals are mated, the independence and segregation of the black and the white factors can be readily distinguished in the F_2 offspring, which show a ratio of 25 per cent blacks, 50 per cent blues, and 25 per cent whites. The blacks are pure, or homozygous, for the black factor; the whites are homozygous for the white factor; while the blues, on the other hand, are heterozygous for the color factor, so that it is impossible to obtain a pure strain of these individuals. Because both the factor for black and that for white are neither dominant nor recessive, but are of equal importance in their contribution to the origin of the blue hybrids, geneticists represent their genes by capital letters, B and W. Likewise, the constitution of the parents of such a cross would be BB for the blacks and WW for the whites, whereas that of the hybrid would be BW.

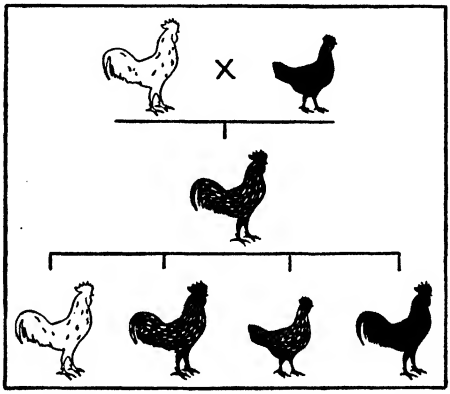


FIG. 66. Cross between White and Black Andalusian Fowls[1]

The blues are represented by black figures with white splotches

Still another cross made in recent years that has yielded results similar to those obtained in Andalusian fowls is the one in which red Shorthorn cattle (RR) have been mated with white Shorthorns (WW). The resulting F_1 progeny appear neither red nor white but of a color intermediate between the two, known as reddish roan, of constitution RW. As in the case of the Andalusian fowls, when the roans are mated together the F_2 progeny consist of 25 per cent red, 50 per cent roan, and 25 per cent white. In reality, the roan individuals are hybrids that do not breed true to type.

[1] From Fasten's *Origin through Evolution*. By permission of F. S. Crofts & Co., publishers.

Multiple-Gene Effects

In the crosses used as illustrations thus far, the traits that appeared depended for their expression on a pair of allelomorphic factors, one of which either completely or partially dominated the other or, in those cases where a new expression appeared, both of which coöperated to bring about the observed result. Of course these were all examples of exceedingly simple Mendelian phenomena. Since the rediscovery of the Mendelian principles, competent observers have shown that things are not nearly so simple in all instances, for often many characters of plants and animals depend for their expression on the coming together and interaction of a number of genes which belong to different allelomorphic pairs. In some cases two such different factors may be responsible for the result, whereas in others three or more must coöperate before any effect is produced. Inasmuch as geneticists have discussed these *multiple-gene effects* under such headings as supplementary genes, complementary genes, atavism and reversion, modifying genes, lethal genes, epistasis, and cumulative genes, it may be well for us to consider them similarly, in logical sequence.

Supplementary Genes

In the crosses used to illustrate nondominance, the factors which united to produce the F_1 generation really belonged to the same pair of allelomorphs. Geneticists have found, however, that certain characters depend for their expression on the coming together into one zygote of genes which really belong to different allelomorphic pairs, each one of which is independently effective in producing its distinctive type of character. A very good example of the interaction of *supplementary genes* is revealed in the interesting cross which Bateson and Punnett made involving the combs of fowls. When the combs of fowls are examined, four main types may be found: the single comb, the rose comb, the pea comb, and the walnut comb, all of which are shown in

Fig. 67, illustrating the cross in question. When pure-bred, single-combed individuals are mated, nothing but single-combed offspring result. The same is true with the rose-combed and pea-combed individuals,— when they are mated with types like themselves, nothing but rose-combed or pea-combed fowls result. It has been discovered also that the

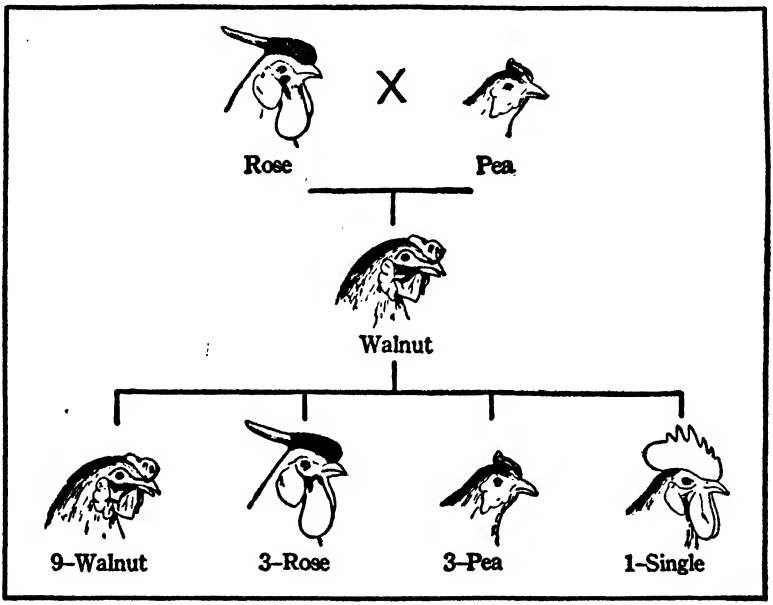


FIG. 67. Cross between Rose-Combed and Pea-Combed Fowls[1]

rose-combed factor dominates over the single-combed factor, so that in a cross involving these two types only rose-combed individuals develop in F_1. The same is true of the pea-combed types, — when crossed with the single-combed birds, only pea-combed fowls result in F_1. When the rose-combed and the pea-combed fowls are mated, however, instead of one's dominating the other, a new type is produced, namely, the walnut-combed individual. When these F_1 individuals are mated together, they give origin to the typical

[1] From Fasten's *Origin through Evolution*. By permission of F. S. Crofts & Co., publishers.

dihybrid ratio of 9 walnut : 3 rose : 3 pea : 1 single. Bateson and Punnett were able to solve this cross by representing the rose-combed factor as R and the pea-combed as P. The constitution of the rose-combed parent would therefore be RRpp and that of the pea-combed one, rrPP. When these parents were mated together, both the factor R and the factor P were introduced into the F_1 individuals, so as to produce a constitution of formula RrPp, accounting for the development of the walnut combs. The types of fowls produced in the F_2 generation, as well as their germinal make-up, will be more easily observed in the checkerboard figure given below.

F_1—FEMALE GAMETES

F_1—MALE GAMETES	RP	Rp	rP	rp
RP	1 RRPP walnut	2 RRPp walnut	3 RrPP walnut	4 RrPp walnut
Rp	5 RRPp walnut	6 RRpp rose	7 RrPp walnut	8 Rrpp rose
rP	9 RrPP walnut	10 RrPp walnut	11 rrPP pea	12 rrPp pea
rp	13 RrPp walnut	14 Rrpp rose	15 rrPp pea	16 rrpp single

Complementary Genes

These are factors found in different individuals, which when alone remain ineffective and unexpressed. They gain expression only when, through appropriate crossings, they are combined within the same zygote. An example which

will make this clear is Bateson's cross involving different varieties of white sweet peas. Bateson artificially crossed two strains of white sweet peas of the genus *Lathyrus*; when the F_1 generation was produced, they all possessed purple flowers, like the wild ancestral Sicilian type, from which the different varieties of sweet peas have been derived. On the other hand, when the F_1 purple individuals were crossed, the F_2 generation yielded a ratio of 9 purple-flowered individuals to 7 white ones.

For some time this peculiar ratio puzzled geneticists, but Bateson worked out the cross and showed that it was really a dihybrid cross involving *complementary genes*, each pair of which happened to be found in opposite parents. When separate and alone, these complementary factors do not gain expression; but when they happen to be combined in one zygote, they become expressed and the purple color makes its appearance. Bateson arrived at his results by assuming that the color purple is dependent for its expression on two

F_1—FEMALE GAMETES

F_1—MALE GAMETES	CP	Cp	cP	cp
CP	1 CCPP purple	2 CCPp purple	3 CcPP purple	4 CcPp purple
Cp	5 CCPp purple	6 CCpp white	7 CcPp purple	8 Ccpp white
cP	9 CcPP purple	10 CcPp purple	11 ccPP white	12 ccPp white
cp	13 CcPp purple	14 Ccpp white	15 ccPp white	16 ccpp white

factors, — (1) a color factor, C, and (2) a purple factor, P. Each parent therefore lacked one or the other of these factors, being of constitution CCpp or ccPP. When these white parents were crossed, the F_1 individuals possessed the constitution CcPp and were all purple. The F_2 ratio of 9 purple to 7 white may be observed easily in the checkerboard diagram at the bottom of page 197.

Atavism and Reversion

Often, in breeding, a type appears which resembles one of the grandparents rather than either of the immediate parents; where this happens to be the case the phenomenon is spoken of as *atavism.* A common example of atavism is the production of a blue-eyed child from two brown-eyed parents. Sometimes a character appears which, although present in a remote ancestor, has not put in an appearance for a number of generations, and where this occurs, it is referred to as a *reversion.* Bateson's cross between the white strains of sweet peas, yielding the purple Sicilian type, may be taken as a good illustration of reversion, in which certain hidden factors happen to come together so as to produce the ancestral type from which the parents originated. For many years breeders noticed that every now and then in crosses there was a throwback to the original, or ancestral, type from which the independent strains or varieties had arisen. For instance, when different types of rabbits are allowed to run loose in a pen, sooner or later the offspring revert back to the wild gray-coated, or agouti, types (Fig. 68). This same thing happens when different types of pigeons are allowed to cross, for often individuals are produced that show the characteristic bluish plumage and black-barred or black-checked wings of the wild rock pigeon (*Columba livia*), which is considered to be ancestral to all the various breeds of domestic pigeons. If space permitted, numerous other examples could be cited, all illustrating the same phenomenon. Before the Mendelian principles were known, these cases could not be explained satisfactorily; but

now they are considered to be typical Mendelian phenomena, explainable on the basis of the separation and segregation of the numerous factors of the ancestral type into different individuals, where they remain latent and unexpressed until, through the medium of appropriate crosses, they again become combined in one individual and so produce the original ancestral type.

Sometimes reversion to the ancestral type depends on the interaction of a rather large number of these latent factors. Some of the best studies along this line have been made on the coat color patterns in rodents such as rabbits, guinea pigs, squirrels, rats, and mice.

In the house mouse it has been established that the wild grayish-brown, or agouti, pattern depends for its expression on something like a dozen or more factors. The genes which are here involved are C for color, without which (c) no pigmentation is possible and albinos result; A for the agouti pattern, the lack of which (a) allows the actual color pigment to express itself; B for black pigmentation, which,

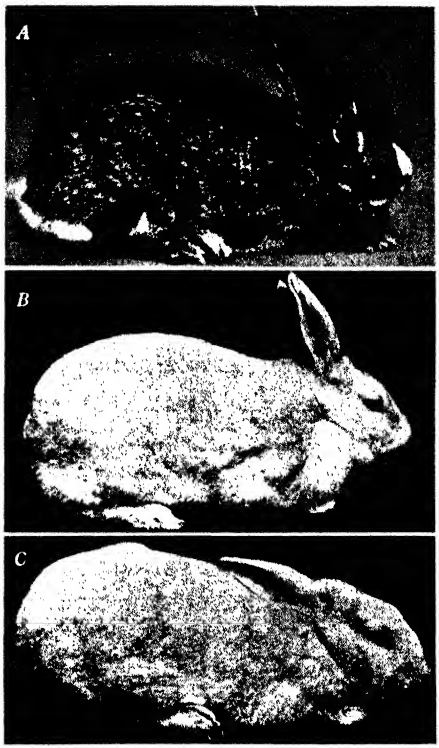


FIG. 68. Reversion in Rabbits[1]

A, the wild gray-colored agouti rabbit produced when the two true-breeding albino rabbits, *B* and *C*, were crossed

[1] From Castle's *Genetics and Eugenics*, fourth revised edition. By permission of Harvard University Press, publishers.

being dominant over b, results in brown or chocolate; D for dense color, making possible a completely pigmented condition rather than the faded condition caused by the recessive (d); S for solid color, as against spotted or white condition indicated by the recessive (s); P for dark eye, which is normal for the wild types as against the pink-eyed condition (p) accompanying animals whose fur lacks intense amounts of the black and brown pigments and therefore appears faded; and nonyellow, y.

The wild type, as indicated by the agouti pattern, appears only when the factors C, A, B, D, S, P, and y are combined in one mouse in either the homozygous or heterozygous condition. The constitution of such an individual in the former state would be AABBCCDDPPSSyy, whereas that of an individual in the latter state would be AaBbCcDdPpSsyy.

Modifying Genes

In connection with the studies on coat colors of animals, the spotted condition has been of especial interest, for it has been observed that various degrees of expression of this condition become possible, and these have all resulted from the effects of so-called *modifying genes*, which have influenced the production of the quantity and the extent of pigmentation. These modifying factors can assert themselves only when certain other factors are present, — for instance, in the case of spotting in mice, when the factor for white spotting (s) happens to be present. Modifying factors have been discovered in a large number of plants and animals. When they coöperate with other factors, they bring about distinct differences in the quantitative expression of certain characters in either a plus or a minus direction. As will be shown later, these effects are similar to those produced by *cumulative genes*, and, like them, help to explain many complicated conditions observed in organisms.

Lethal Genes

Geneticists have found that not only may certain factors interact with, interfere with, or modify the expression of other factors, but in certain instances factors may lead to the destruction of either the germ cells themselves or of the organisms to which these germ cells have given origin. Such factors are known as *lethal genes,* and invariably they are recessives, so that they are able to produce fatal effects only when they are found to be present in the homozygous condition. When present in the heterozygous condition, although they are incapable of producing fatal effects, they may lead in some instances, to be indicated later, to structural modifications of one sort or another.

One of the classic examples of the action of lethal factors is the cross made by Cuénot between yellow house mice. When yellow house mice are crossed, they always produce yellow individuals and different-colored ones (either black, gray, or brown) in the ratio of two thirds yellow to one third of the other color. This ratio comes out so regularly and differs so consistently from the typical Mendelian ratio of three fourths dominant to one fourth recessive for a monohybrid cross that it was regarded as rather exceptional and peculiar. Cuénot solved the problem by suggesting that aside from the yellow color's being carried by the Y factor, this also was a lethal factor capable of affecting the life of the individual. If the dominant yellow is represented by Y and it is assumed that this also acts as a lethal factor, then the recessive, y, or the lack of yellow (making possible the expression of coloration), would be minus the lethal effect. Inasmuch as the yellow parents are alive, they are unquestionably heterozygotes of constitution Yy. When they are crossed, their progeny consist of a ratio of one fourth YY : two fourths Yy : one fourth yy. Those of constitution YY would never appear, as they are killed off before they are born, leaving the others to develop normally; when they appear, two thirds of them are yellow and the remaining third black,

gray, or brown. Thus it is seen that while visibly the ratio differs from the typical Mendelian one for a monohybrid, nevertheless this is not actually the case, because those forms that are homozygous for the yellow factor (YY) also have a double dose of the lethal factor and die before they are born.

Lethal factors have been discovered in a large number of plants and animals. In *Drosophila melanogaster* various workers have discovered over forty lethal factors, the effects of which have been studied most extensively. Geneticists have succeeded in showing that lethal genes are recessive and produce their fatal physiological effects only when they are found combined in the homozygous condition. It thus becomes obvious that the only way certain types of organisms which possess recessive lethal genes can be saved from extinction is to prevent them from crossing with other types possessing similar lethal genes.

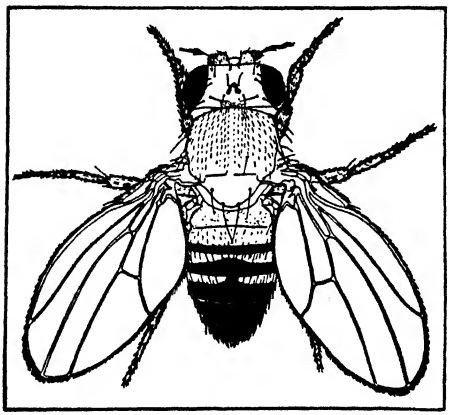


FIG. 69. Dichæte Type of *Drosophila melanogaster*[1]

Aside from exerting a fatal effect on organisms, the lethal genes may also influence the expression of various other structures. In the vinegar fly it has been shown definitely that some of the lethal genes may have a double effect, being recessive for the physiological lethal effect and dominant for producing structural changes in various portions of the body. In the homozygous condition these lethal genes lead to the death of the organism, whereas in the heterozygous condition the single lethal factor affects certain portions of the body so as to produce distinct modifications.

[1] Courtesy of *Carnegie Institution*.

One such interesting variation in the vinegar fly is the "dichæte" type (Fig. 69), in which the wings are spread wide apart and uplifted and also a number of the long spines on the body are missing. It has been shown conclusively that such dichæte flies are heterozygous for the lethal factor. In those instances where they are homozygous for the lethal gene the individuals are prevented from developing very far and are soon killed off. Just as in the case of the yellow mice, when a pair of dichæte flies are crossed, the resultant progeny consist of approximately two thirds dichætes and one third normal flies. This of course is not the typical Mendelian ratio for a monohybrid, but the results can be explained easily on the basis that all the offspring possessing the lethal factor in homozygous fashion are killed off, leaving only the heterozygotes (the dichætes) and those that are minus any of the lethal genes (the normal wild-type flies).

Epistasis

Sometimes in the case of two factors that are not allelomorphs but exert an influence on the same structure, it happens that one of them gains expression and at the same time covers over, masks, or inhibits the appearance of the other one. The factor which thus asserts itself is said to be *epistatic* and the one which is prevented from expression is said to be *hypostatic*. This entire phenomenon of one distinct factor for a structure being covered over and masked by a different one affecting the same structure is called *epistasis*. In instances of complete dominance, where the results are the same as in epistasis, the factors involved are those of an allelomorphic pair rather than different, or non-allelomorphic, ones, as in epistasis. A good illustration will serve to clarify this phenomenon.

Epistasis is shown in the cross between white Leghorn and white Wyandotte fowls. It has been shown quite conclusively that the white plumage of the white Leghorns is dominant over colored plumage. On the other hand, the white plumage

of such varieties as white Wyandottes and white Plymouth Rocks is recessive to colored plumage. Moreover, the white plumage of the Leghorns has been shown to be due to a color factor, C, which is prevented from becoming expressed by an inhibiting factor, I, whereas the white of such varieties as the white Wyandottes or white Plymouth Rocks is the result of the lack of the color factor, c, as well as the inhibiting factor, i. When white Leghorns (CCII) and white Wyandottes (ccii) are mated together, the F_1 generation offspring are all white (CcIi), with small black markings similar to those produced when white Leghorns are crossed with colored ones. On the other hand, when the whites of the F_1 generation are crossed, the offspring are in the peculiar ratio of thirteen sixteenths white to three sixteenths colored. The results are easily shown by the checkerboard method, where it will be noticed that white is produced in every instance where the color factor C and the inhibitor factor I are found in the same individual (1–5, 7, 9, 10, and 13). This is also

F_1 — FEMALE GAMETES

F_1 — MALE GAMETES	CI	Ci	cI	ci
CI	1 CCII white	2 CCIi white	3 CcII white	4 CcIi white
Ci	5 CCIi white	6 CCii colored	7 CcIi white	8 Ccii colored
cI	9 CcII white	10 CcIi white	11 ccII white	12 ccIi white
ci	13 CcIi white	14 Ccii colored	15 ccIi white	16 ccii white

true where both color and inhibitor factors are lacking, as in the case of individuals of constitution ccii (16), or where the color factor alone is missing, as in individuals 11, 12, and 15 (one ccII and two ccIi). In all the other individuals, 6, 8, and 14 (one CCii and two Ccii) the color factor makes its appearance. It is thus seen that the inhibiting factor I is epistatic to the hypostatic color factor C and prevents its expression.

Cumulative Genes

A *cumulative gene* is one which, if added to another similar gene, invariably affects the intensity, or degree, of expression of a character. Such genes, in large measure, may be said to influence the quantitative development of traits. Although many geneticists still further classify cumulative genes into such categories as intensifying genes, duplicate genes, diluting genes, distribution genes, and the like, the action of all these is more or less similar and introduces nothing especially new in Mendelism beyond that which is revealed by crosses showing cumulative gene effects.

Some of the crosses showing best such gene effects were made by the Swedish geneticist Nilsson-Ehle, who crossed various strains of wheat differing from each other in the possession of either reddish or whitish kernels. In one cross between a red and a white strain of wheat, the F_1 individuals all possessed light reddish kernels of a hue not quite so red as the kernels of the red parent but of a shade between the red and the white colors of the kernels of the two parents. This at first suggested an explanation similar to that given for the roan offspring of the cross between red and white Shorthorn cattle. However, when the F_1 hybrids were crossed, the F_2 individuals obtained showed a ratio of 15 reds to 1 white. These red individuals were not all of the same color, but varied considerably in their degree of redness from pure red to different gradations of pink. This 15 : 1 ratio suggested to Nilsson-Ehle a dihybrid cross in which two similar factors were involved for the character in question. Inas-

much as the character red, instead of the character white, makes its appearance in the F_1 generation, it must be looked upon as the dominant trait, and accordingly its factor should be represented as R. Likewise, the recessive factor for white should be represented as r. On the assumption that two factors for redness are involved, these can be represented as R_1 and R_2. The red parent would then be of constitution

F_1—FEMALE GAMETES

F_1—MALE GAMETES	R_1R_2	R_1r_2	r_1R_2	r_1r_2
R_1R_2	1 $R_1R_1R_2R_2$ red	2 $R_1R_1R_2r_2$ red	3 $R_1r_1R_2R_2$ red	4 $R_1r_1R_2r_2$ red
R_1r_2	5 $R_1R_1R_2r_2$ red	6 $R_1R_1r_2r_2$ red	7 $R_1r_1R_2r_2$ red	8 $R_1r_1r_2r_2$ red
r_1R_2	9 $R_1r_1R_2R_2$ red	10 $R_1r_1R_2r_2$ red	11 $r_1r_1R_2R_2$ red	12 $r_1r_1R_2r_2$ red
r_1r_2	13 $R_1r_1R_2r_2$ red	14 $R_1r_1r_2r_2$ red	15 $r_1r_1R_2r_2$ red	16 $r_1r_1r_2r_2$ white

$R_1R_1R_2R_2$, and the white parent of constitution $r_1r_1r_2r_2$. The F_1 cross would consist of $R_1r_1R_2r_2$ individuals, of a lighter red than the red parents. The F_2 progeny may be shown clearly by the checkerboard device above, and when this is examined it becomes apparent that only when both dominant factors are missing does a white individual make its appearance. In all other cases where R_1 or R_2 or both are present, the individuals are red, being of a lighter or darker shade, depending entirely on the number of red factors present.

In another similar cross which Nilsson-Ehle made involving red-kerneled and white-kerneled wheat, the F_2 generation revealed a ratio of 63 reddish individuals to 1 white. As in the previous cross, the reds were of different shades and degrees of expression. This suggested a trihybrid cross in which three similar factors were involved, and if these be represented as R_1, R_2, and R_3 for the dominants and r_1, r_2, and r_3 for the recessives, then the red parent would be indicated as $R_1R_1R_2R_2R_3R_3$ and the white one as $r_1r_1r_2r_2r_3r_3$. It is not necessary to go into the various details of actually figuring out the individuals of the F_1 and F_2 generations of this cross. Anyone can carry them to the F_2 generation by the checkerboard method and tabulate the results. Fig. 70 is a diagrammatic representation of the various types of F_2 individuals. In the figure the black dots represent the dominant red factors, and the number of these that are present determine the degree of redness of the individuals. In a similar manner, a figure may also be devised to illustrate Nilsson-Ehle's previous cross, in which two factors were involved.

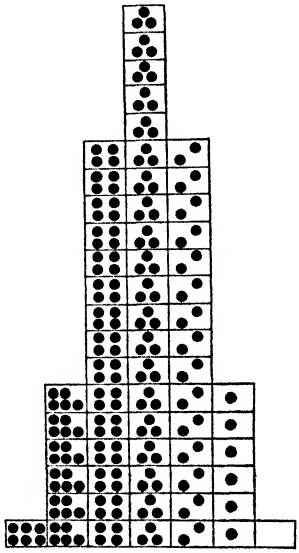


FIG. 70. Diagram showing Cumulative Factors of Nilsson-Ehle's Cross[1]

The types of the 63 reddish individuals and the number in each type and also the single white one obtained in the F_2 generation can be determined clearly. The black dots indicate the number of color factors each individual possesses, and the squares indicate the number of individuals belonging to each class

This discovery by Nilsson-Ehle of quantitative effects produced through the medium of cumulative factors has been instrumental in explaining many of the phenomena observed in plants and animals. Even in man such an explanation accounts for many of the character

[1] From Coulter's *Outlines of Genetics*. By permission of University of Chicago Press, publishers.

expressions which make their appearance. One striking illustration of this sort is the gradation to be noticed in the skin color of mulattoes (Fig. 71). Investigators who have studied this question are of the opinion that the pure-blooded Negro possesses two pairs of cumulative genes for black pigmentation, which are separately heritable and quantitative in their effect. If these factors are represented by the letters B_1 and B_2, then the constitution of the Negro in regard to color is

FIG. 71. Gradation of Offspring from Mulatto Parents[1]

$B_1B_1B_2B_2$, and likewise that of the white man is $b_1b_1b_2b_2$. The crossing of such individuals results in the production of mulattoes of constitution $B_1b_1B_2b_2$. When, in turn, there is a mating of such F_1 mulattoes, the F_2 generation of individuals consists of a ratio of 15 mulattoes to 1 white. An examination of these F_2 mulatto individuals, as indicated in the diagram of Fig. 72, reveals that they vary considerably in color, grading all the way from light brown through deeper shades to intense black. Of course this result is exactly similar to that which Nilsson-Ehle obtained in the F_2 generation of his wheat hybrids, in which two cumulative factors were involved.

[1] From Davenport's "Heredity of Skin Color in Negro-White Crosses." Courtesy of Carnegie Institution.

By observing the F_2 generation resulting from the crossing of the F_1 mulattoes, it is noticed that one sixteenth of the total number of individuals produced are white in color. This does not mean that in other respects such persons will have the characters of the white race, because all the other traits of the parents also participate in the cross. When this is borne in mind, it becomes obvious that even though an F_2 individual is white in color, appearing like the white race, still in many of the other characters such a person may resemble the Negro race. In studying heredity, however, one must concentrate on a few characters. Fig. 73 shows the white offspring of a mulatto mother and a white father.

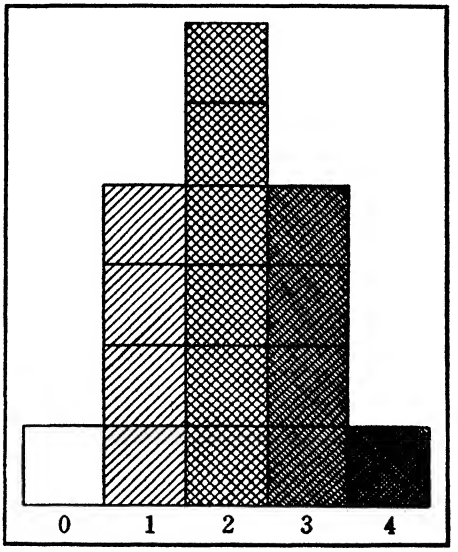


FIG. 72. Diagram of Possible Types of F_2 Individuals resulting from Mulatto Crosses

The numbers indicate the number of genes for black pigmentation which are present in the respective types, and the squares represent the number of individuals belonging to each type

When species in general are examined, it is found that each one of them shows individual variations of a quantitative kind in either a plus or a minus direction. Charles Darwin, although not knowing the exact nature of these minute, visible modifications, nevertheless relegated them to a place of greatest importance in his scheme of the evolution of species. At the present time, however, such variations are considered to be Mendelian phenomena dependent for their expression on the shuffling, segregation, and recombination of definite factors for the traits in question. In reality, then, they are products of the effects of the interaction of multiple genes of a cumulative kind.

Galton's Views on Heredity

Many cases of inheritance discussed in the present chapter have, until the last few years, been considered instances of *blending inheritance.* Francis Galton (*Bi. 81*) first designated them as such in 1889, and until recently they were so regarded and described in genetic literature. In addition Galton recognized *alternative inheritance.* He considered as examples of alternative inheritance those cases where one character completely dominated another one. Blending inheritance was the name given to cases where the trait which put in an appearance was intermediate in its expression between the characters present in both of the parents.

FIG. 73. Mulatto Mother and her White Child[1]

When Mendelism was discovered, it was soon recognized that alternative inheritance was typical Mendelian inheritance, but for a long time blending inheritance was considered different. However, it is now known, as is evident from the discussions in the present chapter, that all instances of blending inheritance conform to the multiple-gene conception and are therefore Mendelian in nature.

It is also of interest that Galton, after studying cases of inheritance, especially in human beings, formulated in 1897 his famous *law of ancestral heredity,* or, as it is more com-

[1] From Lotsy and Goddijn. Courtesy of *Genetica,* published by Martinus Nijhoff.

monly known at the present time, the *law of filial regression* (*Bi. 77*). This is a general law which attempts to reveal in mathematical terms the degree, or ratio, of resemblance between an individual and his ancestors. Galton was of the opinion that, from a hereditary standpoint, the influence of each generation of ancestors became less as the remoteness increased. He believed that the immediate parents contributed, on the average, one half; the four grandparents, one fourth; the eight great-grandparents, one eighth, and so on. Moreover, he believed that by adding these degrees of resemblance one could get a picture of pretty nearly the entire heritage of an individual. Galton expressed this apparent gradual gradation in resemblance from the immediate parents to the remote ancestors as "regression," or, to put it another way, "reversion to the general average of the race."

On the surface the law of filial regression seems to hold good in those cases that Galton assumed to be real instances of blending, but where alternative heredity is involved, the law breaks down completely. It must be emphasized that at the present time Galton's views on heredity are of interest largely from a historical standpoint and that since the beginning of the present century they have been replaced by newer concepts. Modern genetics opposes the conception of blending inheritance and, in general, opposes the law of filial regression.

Single-Gene Effects

In the various crosses which have been cited to illustrate different aspects of Mendelism, it has been indicated that in certain instances a single factor by itself may be responsible for the expression of a character, whereas in others many factors must combine before a character appears. Then again good examples are at hand to show that a single factor may influence or be responsible for the expression of more than one character. In the case of the yellow mice discussed under "Lethal Genes," it was shown that a single factor not only

determines the yellow character but also exerts a lethal effect, leading to the death of the individual.

Many single genes are now known, each of which produces a simultaneous effect on many different characters of an organism. Muller has shown this clearly in the vinegar fly, where a single gene has been shown to be responsible for such characters as abnormally shaped abdomen, infertility, shape and size of wings, the disarrangement of the bristles, and the like. Other investigators have shown similar effects, all leading to the conclusion that genes of an organism not only produce primary effects, leading to the definite expression of certain traits, but each gene may also produce secondary effects, affecting the expression of numerous other characters.

Environment and Gene Expression

While the basic traits of an organism depend on the factorial organization of the zygote responsible for the organism's development, nevertheless the external and internal environments determine, to a large extent, not only which genes will gain expression but also their degrees of expression. Practically everyone is familiar with the striking effects produced on organisms by such obvious external factors as soil, moisture, food, and light. Good examples of such effects were given in Chapter III, where inheritance of acquired characters was considered. Even though it is by no means proved that somatic characters acquired through environmental influences are inherited, still such stimuli certainly may be instrumental in altering structures of individual organisms. Where conditions are good, the genes have an opportunity to gain their fullest expression; where conditions are not good, there is apt to be interference with the expression of the genes, so that often the best results are not obtained. Fig. 74 shows two Norway maple trees derived from the same stock and of exactly the same age. The smaller tree (Fig. 74, *A*) received no care, while the larger one (Fig. 74, *B*) was fertilized and watered regularly.

As far as the internal environment is concerned, the effects of certain internal agencies have already been considered in previous portions of this book. Mention of only one or two will bring them to mind. The discussion of hormones in Chapter VIII showed how far-reaching may be the effects produced through the lack or superabundance of the hormone

FIG. 74. Effects of Environment on Growth of Trees

Two Norway maples, eight years old, of the same stock. *A* received no care, but *B* received care

secretions within the circulating medium of an organism. Many instances of abnormal development may be accounted for on this basis. Although an abundance of genes may be present for normal development, their expression becomes dependent largely on the presence of normal amounts of hormones within the blood stream; if these are not present in such quantities, it may lead to the development of various kinds of abnormalities.

CHAPTER XII

Sex Linkage and Nondisjunction

PHENOMENA of *sex linkage* and *nondisjunction* of chromosomes were first worked out in connection with studies on the sex chromosomes and the rôles which they play in the production of the sexes. Especially helpful has been the genetic research on such problems in the vinegar fly (*Drosophila melanogaster*), because it has enabled geneticists to explain similar conditions in other organisms. Moreover, such investigations have afforded some of the strongest proofs for the chromosomal basis of heredity, and at the same time they have been largely instrumental in the elaboration of the linkage and crossing-over principles to be considered in the next chapter.

Sex Linkage in Man

Cases of linkage were first noticed in connection with the character of sex and were called sex-linked inheritance. For instance, in man such characters as color-blindness, night blindness, hemophilia (or free bleeding), and the like were common in males and of rare occurrence in females. It was noticed that when a normal woman married a color-blind man, all the children were apparently normal. The daughters, however, carried the color-blind factor, and if any of them married a normal male, 50 per cent of the sons produced were color-blind and the remaining 50 per cent normal. Of the daughters produced, 50 per cent were normal, being minus the color-blind factor, and the other 50 per cent were carriers of the factor for the trait. Outwardly, however, all the daughters appeared alike and apparently were minus the color-blind trait.

Color-blind females are produced when a female who is a carrier for color-blindness marries a male who is color-blind. Of the male offspring produced, 50 per cent will be color-blind, while the other 50 per cent will be normal. Among the females, 50 per cent will be color-blind and the remaining 50 per cent will be carriers. Fig. 75 is a diagrammatic representation of crosses, showing the sex-linked nature and inheritance of color-blindness. Fig. 76 also shows the sex-linked nature of such color-blindness in man and the rôle of the X-chromosome in transmitting it. In a similar fashion a chart could be developed showing the production of color-blind human females from a cross between a color-blind male with a female carrier of the trait. It thus becomes evident that in the male only a single gene for color-blindness is necessary to produce the condition, whereas in the female two genes for the trait are essential before color-blindness puts in an appearance. The reasons for this situation will become apparent when cases of sex linkage among vinegar flies, the first ones to be studied, are described and analyzed on pages 216 and 217.

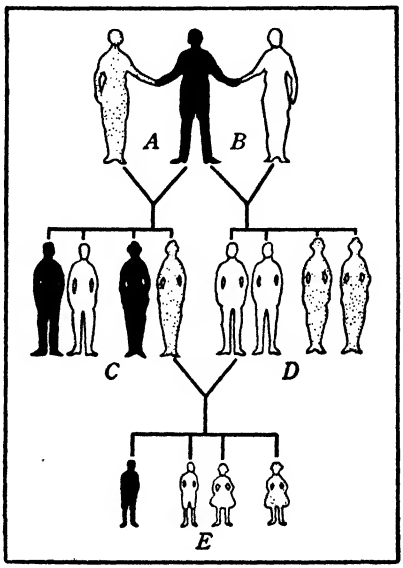


FIG. 75. Sex-Linked Inheritance of Color-Blindness[1]

The black figures represent individuals who are color-blind; the shaded figures represent "carriers," those in whom the trait is covered over; the white figures represent normal individuals. *A* represents a cross between a color-blind male and a carrier female, with the resultant progeny seen in *C*. *E* represents the union of a color-blind male and a normal female, with the offspring indicated in *D*. *E* represents the progeny of the mating of a normal male with a carrier female

[1] From Fasten's *Origin through Evolution*. By permission of F. S. Crofts & Co., publishers.

Sex Linkage in the Vinegar Fly

The reason for the linkage of this character chiefly with the male sex was not apparent until Morgan explained similar phenomena in the vinegar fly. Soon after work began on this fly, which is normally red-eyed, a white-eyed male made its appearance in one of the cultures. In order to test whether the trait was a heritable one, Morgan mated this white-eyed male with a normal red-eyed female (Fig. 77). In the F_1 generation all the individuals possessed red eyes. When these were carefully tested, the males proved to be pure with respect to the red color, and the females were carriers of the gene for the white trait, which was covered over. When one of these females was mated to a normal male, half of the F_2 males were found to be white-eyed, while the other half were red-eyed. Although the F_2 females were all red-eyed, tests showed that half of them were pure with respect to the trait, whereas the other half were carriers for the white-eyed condition. An examination of Fig. 77 shows all these individuals. In a manner similar to the production of color-blindness among human females, white-eyed female fruit flies resulted when a red-eyed female carrier was mated to a white-eyed male, as shown in the F_2 generation of the reciprocal cross, Fig. 78.

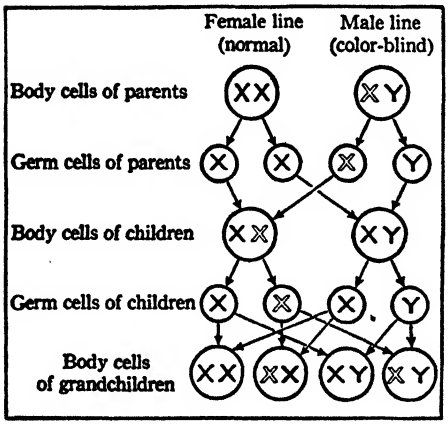


FIG. 76. Rôle of X-chromosome in Transmitting Human Color-Blindness[1]

The black X represents the normal chromosome; the white X represents the chromosome carrying the factor for color-blindness

[1] From *Being Well Born*, by Michael F. Guyer, Copyright 1916 and 1927. Used by special permission of the publishers, The Bobbs-Merrill Company.

Morgan, after studying his results, came to the conclusion that the white-eyed character was governed by a sex-linked gene carried in the sex chromosome, X. In the male a single dose made it appear; in the female two doses were necessary for it to crop out. When one of the X-chromosomes in the female contained the gene for the white-eyed character and the other X-chromosome did not, then this character acted in a manner similar to a recessive, being covered over by the gene for red eye, and the red-eyed character made its appearance. While the females in this case were all red-eyed, still they were carriers of the genes for the white-eyed character. On a similar basis it became possible to explain the peculiar behavior of color-blindness in the human species, as described on pages 214 and 215. Moreover, Morgan's explanation for sex linkage in the vinegar fly immediately gave the clue to the answer for similar phenomena among many of the other animals used in genetic studies.

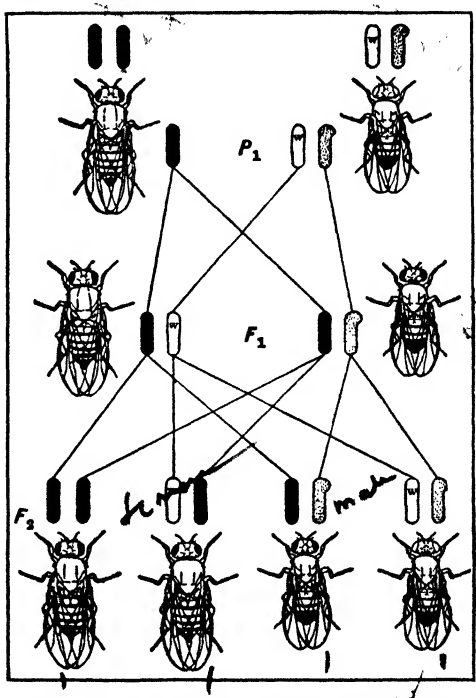


FIG. 77. Sex-Linked Inheritance of White Eyes in *Drosophila melanogaster*[1]

The cross indicated is between a red-eyed female and a white-eyed male. The X-chromosome which carries the gene for red eye is represented by the black rod; the X-chromosome carrying the gene for white eyes is represented by the open rod with a small w within it. The Y-chromosome is stippled

[1] From Morgan's *Theory of the Gene*. By permission of Yale University Press, publishers.

Sex Linkage in Poultry

In those cases where sex determination is the reverse of that indicated for most animals, as, for example, in moths or fowls, instances of sex linkage have also been found, and these likewise follow the reverse order — being rare in males and abundant in females. Fowls present good illustrations of such types of inheritance. As pointed out in Chapter VI, dealing with sex and its determination, the male gametes of the fowl are all of one type, all possessing the sex chromosome Z (which corresponds to X). The female produces two types of gametes, one possessing the sex chromosome Z and the other being without it and containing the accessory chromosome W (corresponding to Y). Fig. 34 on page 103 show the male and female groups of chromosomes in the fowl, ZZ indicating the male and ZW indicating the female. A good example of such sex-linked inheritance is to be noticed when a barred Plymouth Rock cock is mated to a black Langshan hen.

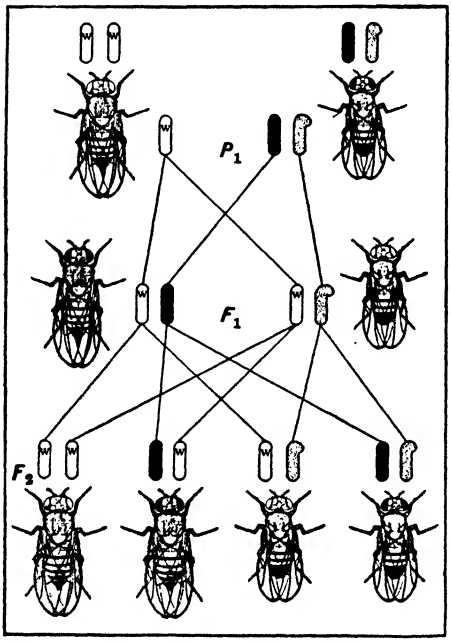


FIG. 78. Reciprocal Cross, Inheritance of White Eyes in *Drosophila melanogaster*[1]

The cross is between a white-eyed female and a red-eyed male. The gene for white eye is carried by the X-chromosome as an open rod with a small w, whereas the gene for red eye is carried by the X-chromosome represented by the black rod. The Y-chromosome is stippled

[1] From Morgan's *Theory of the Gene*. By permission of Yale University Press, publishers.

When such a cross is made (Fig. 79), the F_1-generation individuals are all barred, being similar to the Plymouth Rock male parent. When the F_1 males and females are interbred, the F_2 generation which results shows all the males barred in character; but of the females produced half are barred and the other half are black, like the black Langshan female grandparent. Further analysis of the F_2 males reveals that half of them are carriers of genes for the black Langshan character, but inasmuch as these genes are covered over by the dominant genes for the barred trait of the Plymouth Rock, the black character does not make its appearance.

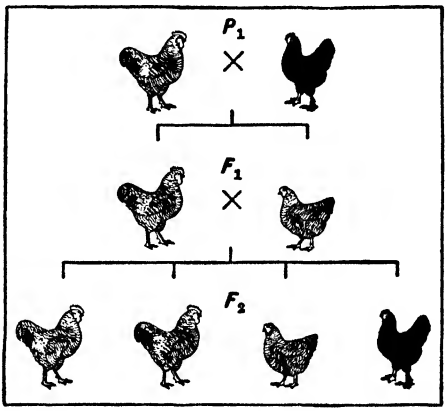


FIG. 79. Cross between Barred Plymouth Rock Cock and Black Langshan Hen

In the F_1 generation the males and females are all barred. Of the F_2 offspring, the males are all barred; but of the females, half are barred and the other half are unbarred, like the black Langshan type

In the reciprocal cross, illustrated by Fig. 80, in which a black Langshan cock was mated to a barred Plymouth Rock hen, the F_1 generation consisted of male individuals that were all barred and female individuals that were all black. When these F_1 individuals (males and females) were crossed, the F_2 generation consisted of the following progeny: of the males produced, half were black and the remaining half were barred carriers for blackness; of the females, half were black and the remainder were barred.

Sex-Limited Traits

It is well to distinguish sex-linked characters from those which are *sex limited.* Sex-linked traits are due to genes located within the sex chromosomes, the heredity of which has

already been indicated in the previous portions of this chapter. Sex-limited traits, on the other hand, are those secondary sexual characters accompanying one or the other of the sexes, manifesting themselves as definite somatic expressions. In many instances they may appear in both sexes, but in one of them they may become more intensified than in the other. The genes responsible for the appearance of such sex-limited traits are undoubtedly borne by the autosomes rather than the sex chromosomes. As will be recalled from the discussion of the endocrine glands, many sex-limited traits are also dependent on the normal functioning of these structures.

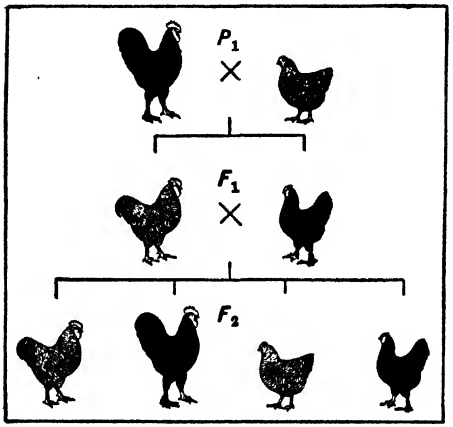


FIG. 80. Reciprocal Cross, Black Langshan Cock and Barred Plymouth Rock Hen

In the F_1 generation the males are like the barred parent and the females like the black Langshan parent. In the F_2 generation half of the offspring are barred Plymouth Rock and the other half are black Langshan

Sex-limited characters are prevalent throughout the animal kingdom; hence it is necessary to indicate only a few of the more obvious illustrations in order that these traits may be recognized easily. For instance, among human beings appear the beard in males and the mammary glands in females. As is noted in a later portion of this book where certain human traits are discussed (Chapter XVII), baldness in man is now considered to be a sex-limited character generally appearing in adult males. Among birds equally good examples are at hand, such as the heavier spurs, gaudier plumage, and lustier voices which distinguish the males from the females.

Nondisjunction

By *nondisjunction* is meant the nonseparation of pairs of homologous chromosomes during the synapsis stage of the maturation of the germ cells. Cases of nondisjunction were first revealed by Bridges in 1913, in connection with studies on sex-linked inheritance in the vinegar fly. When white-eyed females were bred to red-eyed males, the females produced were all red-eyed and the males all white-eyed. In some instances, however, Bridges found that when the above cross was made (white-eyed females and red-eyed males), although most of the offspring ran true to the common expectation of red-eyed females and white-eyed males, still in about 5 per cent of the cases the reverse results were obtained, namely, red-eyed males and white-eyed females. The percentages were approximately 47.5 per cent red-eyed females, 47.5 per cent white-eyed males, 2.5 per cent white-eyed females, and 2.5 per cent red-eyed males. These figures reveal that 95 per cent of the forms obtained were normally expected individuals and the remaining 5 per cent were unusual ones, deviating from the normal expectancy. These exceptions were explained by Bridges as instances where the X-chromosomes of the immature germ cells of the female failed to separate during maturation to produce the eggs. While in most instances the separation is complete, giving origin to eggs in each of which there is one X-chromosome, yet in those few cases where no such separation occurs the result is the formation of two additional types of eggs, one with two X-chromosomes and the other with none. In reality, then, three types of eggs come into existence in such a female: one with a single X-chromosome, the other with two X-chromosomes, and the third without any X-chromosome. The first type, with the single X-chromosome, which is the normally expected condition, is produced in greatest abundance, predominating over the other two types.

When these ordinary eggs of a white-eyed female belonging to the first type (each with a single X-chromosome,

carrying the gene for white eye) are fertilized by the two kinds of spermatozoa from a red-eyed male, two kinds of offspring are produced, namely, red-eyed females and white-eyed males. When the eggs that contain the two X-chromosomes (with linked genes for white eyes) are fertilized by the spermatozoa with Y, they give origin to white-eyed females of constitution XXY. On the other hand, when the eggs that are minus the X-chromosomes are fertilized by the spermatozoa with X-chromosomes (carrying genes for the red character), they give origin to zygotes with a single X which develop into red-eyed males. While it is logical to assume that eggs with the two X-chromosomes (carrying factors for white eyes) may be fertilized by spermatozoa with X (carrying red-eyed factors) and also that eggs minus the X-chromosomes may be fertilized by Y-containing spermatozoa, giving rise to individuals whose sex-chromosomal constitution is either XXX or Y, nevertheless none of these show up in the offspring. Undoubtedly the reason for their not being present is because they die soon after fertilization.

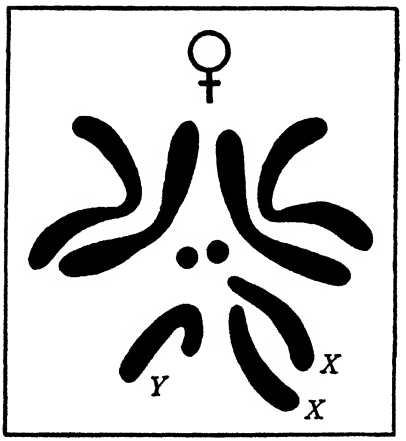


FIG. 81. Chromosomes of a White-Eyed, Nondisjunction Female of *Drosophila melanogaster*[1]

After Bridges suggested this explanation, careful breeding tests, coupled with cytological examinations of the germ cells of parents and their offspring, confirmed these contentions. Fig. 81 shows the chromosomal constitution of one of these white-eyed, nondisjunction females. Futhermore these XXY white-eyed females also show nondisjunction of the X-chro-

[1] From Morgan's *A Critique of the Theory of Evolution*. By permission of Princeton University Press, publishers.

mosomes in about 4 per cent of the cases. The maturation of the germ cells of such females leads to the production of four types of ova with respect to the distribution of the X- and Y-chromosomes, 46 per cent of them having XY, another 46 per cent containing X, 4 per cent possessing XX, and the remaining 4 per cent having just Y. On crossing these white-eyed nondisjunction females with normal red-eyed males, the different kinds of individuals obtained are those indicated in Fig. 82. In this diagram the black X carries the dominant gene for red color of eyes, and the open X the recessive gene for white eyes. Of the eight types shown, the YY individuals die, and therefore do not appear among the offspring. Two exceptional kinds of individuals also put in an appearance: number 4, a red-eyed male (XY), and number 7, a white-eyed female (XXY). As will be recalled, these individuals (numbers 4 and 7) do not appear when an ordinary white-eyed female possessing two X-chromosomes is crossed with a normal red-eyed male.

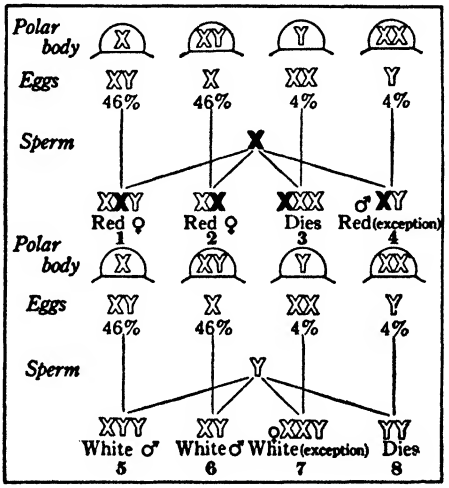


FIG. 82. Fertilization of the Eggs of a White-Eyed, Nondisjunction Female of *Drosophila melanogaster*[1]

The diagram shows the four classes of eggs produced by an XXY type of female and the results obtained when these eggs are fertilized by the two types of spermatozoa of a normal red-eyed male

Since Bridges's work, nondisjunction has been discovered in chromosomes of the vinegar fly other than the sex chromosome. Comparable phenomena have also been shown to exist in various other plants and animals. Wherever these

[1] From Morgan's *Theory of the Gene*. By permission of Yale University Press, publishers.

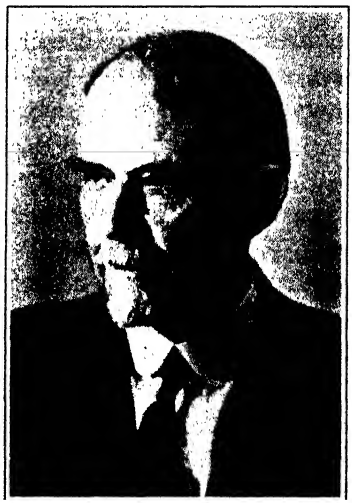
cases have been studied carefully they have been found to yield results similar to those encountered in the vinegar fly, leading to distinct modifications in type.

Instances are at hand where, because of nondisjunction, the chromosome number of a species has been trebled (*triploidy*), quadrupled (*tetraploidy*), or still further increased. That such modifications in the chromosome number must have been responsible for quantitative as well as qualitative differences in species seems certain from the research results obtained by numerous geneticists and cytologists during the last twenty-five years. As a general rule, where the distribution of the chromosomes is regular, the normal inheritance of genes is expected and obtained; on the other hand, where the distribution of the chromosomes is irregular, the probability is that the inheritance of the genes is abnormal, leading to the appearance of differences. Hence heredity must be regarded as a matter of the separation and distribution of the groups of genes found within the chromosomes during the stages of the maturation of the germ cells. By knowing the gene constitution of the germ cells of the species utilized in crossing, the modern geneticist is able to plan experiments and predict results similar to those which he has already obtained in vinegar flies, peas, guinea pigs, and the like.

CHAPTER XIII

Linkage and Crossing Over

THE newer developments in genetics have been woven not only around the gene hypothesis, sex linkage, and nondisjunction of chromosomes, as elaborated in the last two chapters, but also around the so-called *linkage* and *crossing-over* phenomena. Since the vast majority of the work along these lines has been done on the fruit, or vinegar, fly (*Drosophila melanogaster*), most of the examples used to illustrate the principles of linkage and crossing over will be chosen from this interesting organism. The vinegar fly has proved to be a veritable mine of information along the lines of heredity and variation. This organism has played a most important rôle in the development of the newer phases of genetics, being especially helpful in affording convenient material for the elaboration of the principles of linkage and crossing over. Since 1907, when Thomas Hunt Morgan (Fig. 83) and his students began working with vinegar flies, such a mass of reliable data has been accumulated in genetics that this special field has come to be regarded as one of the most important branches of biology. Although linkage and crossing over have been touched upon briefly in previous portions of this volume, it may be well to consider them at greater length in the present chapter.



Trevor Teele Photo

FIG. 83. Thomas Hunt Morgan

Linkage Phenomena

Geneticists now believe that the chromosomes of the germ cells carry the hereditary entities which determine, in large measure, the traits of the individual. The reasons for regarding the chromosomes in this light have already been summarized. Furthermore, it has been indicated that the number of chromosomes within the germ cells is small compared with the number of traits found in the individual. For example, such a species as the vinegar fly is found to possess four chromosomes within its germ cells; the human species contains twenty-four; and all the other species of organisms likewise are found to contain a definite number of chromosomes. On the other hand, the traits of these forms may be extremely numerous, and in such a complex species as man they may number many thousands. It stands to reason that the germinal entities for such a multitude of characters, if carried by the chromosomes, as most modern biologists believe, must be carried in groups linked together within the small number of chromosomes that characterize the specific species. On such a basis every chromosome must be looked upon as a sort of container for a large number of different genes, the entire complex representing one linkage group. There are as many linkage groups as there are chromosomes. As a rule, the genes of one chromosome represent different traits from those of the genes of every other chromosome. In the work with the vinegar fly it soon became apparent that the entities for traits cling together or are linked within the chromosomes, and in many instances these are bound together so completely that they are inherited together generation after generation.

Since the idea of linkage was first conceived, such phenomena have been shown to exist in a great many plants and animals. At first this conception was regarded as theoretical and fanciful by many biologists, but so many examples of linkage have appeared within the last twenty-five years that at the present time the conception is of practically universal

acceptance. In some forms, especially in *Drosophila melanogaster*, work has progressed to the point where the genes linked within the chromosomes have been definitely charted and plotted with respect to their specific positions within each of the four chromosomes of the species. Since the number of chromosomes is so small in this species, it has proved to be especially favorable for the working out of the linkages of genes.

Linkage Groups of Drosophila melanogaster

As indicated in the last chapter, the first work on linkage was that associated with sex, and up to the present time about one hundred and fifty such sex-linked characters have been studied and logically attributed to the sex-determining chromosome, X, of *Drosophila melanogaster*. Other linked characters also have been studied in the vinegar fly, and the positions of the genes which determine them have been assigned to each of the three other chromosomes of the germ cells. Since two of these chromosomes are the longest within the germ cell, being of approximately the same size, and since also two large linkage groups have been found to exist that are not associated with sex, these groups have been assigned to these large chromosomes. Geneticists have labeled them the second and third linkage groups respectively. Soon after the discovery of these three linkage groups, corresponding to the sex chromosome and the two large autosomes of practically equal size, there began to appear variations which could not be linked to or placed in any one of these groups; consequently they were all assigned to the third autosome, which in reality is the fourth chromosome of the germ cell. This fourth chromosome, which is much smaller than any of the other chromosomes, has been found to be the seat of three characters, and these have been grouped together as the fourth linkage group. Up to the present time over four hundred such new types of character variation have been revealed in the vinegar fly. A partial list of the genes which

account for them, as well as their positions on the four chromosomes, is shown in Fig. 60, on page 155.

Thomas Hunt Morgan, in his volume *The Theory of the Gene* (*Bi. 145*), summarizes the four linkage groups in *Drosophila melanogaster* as follows:

> One of these groups of characters of Drosophila is said to be sex-linked, because in inheritance the characters show certain relations to sex. There are about 150 of these sex-linked mutant characters. Several of them are modifications of the color of the eye, others relate to its shape or its size, or to the regularity of the distribution of its facets. Other characters involve the body color; others the shape of the wings, or the distribution of its veins; others the spines and hairs that cover the body.
>
> A second group of about 120 linked characters includes changes in all parts of the body. None of the effects are identical with those of the first group.
>
> A third group of about 130 characters also involves all parts of the body. None of these characters are the same as those of the other two groups.
>
> There is a small fourth group of only three characters: one involves the size of the eyes, leading in extreme cases to their total absence; one involves the mode of carriage of the wings; and the third relates to the reduction in size of the hairs.[1]

Good examples of linkage may be considered under the headings "Total Linkage" and "Crossing Over," where partial linkage is discussed.

Total Linkage

A cross showing total linkage is one involving four characters belonging to the second linkage group. Such a cross takes place when a male vinegar fly possessing the four recessive characters of black body, purple eyes, small (or vestigial) wings, and black speck at the base of the wings is mated with a female of the wild type having the dominant traits of gray body, red eyes, long wings, and no speck at the

[1] T. H. Morgan, *The Theory of the Gene*, pp. 11–12. Yale University Press, New Haven, 1928.

base of the wings. All the F_1 individuals appear like the wild type, having gray body, red eyes, long wings, with no black speck at their base. When one of these F_1 males is crossed with a recessive-type female, these independent characters, instead of assorting separately and distinctly to give origin to new types, hang together so that the F_2 offspring are exactly like the two grandparents, 50 per cent of them being like the recessive grandparent, possessing black body, purple eyes, vestigial wings, with black specks at their base, and the other 50 per cent being like the dominant wild-type grandparent, showing gray body, red eyes, and long wings, with no black specks at their base. Fig. 84 shows this cross revealing complete, or *total, linkage*. Such complete linkage occurs only in the case of the F_1 males, for when the F_1 females are mated with the recessive types of males, a certain small percentage of crossing over occurs, resulting in offspring that possess some of the characters present in both parents.

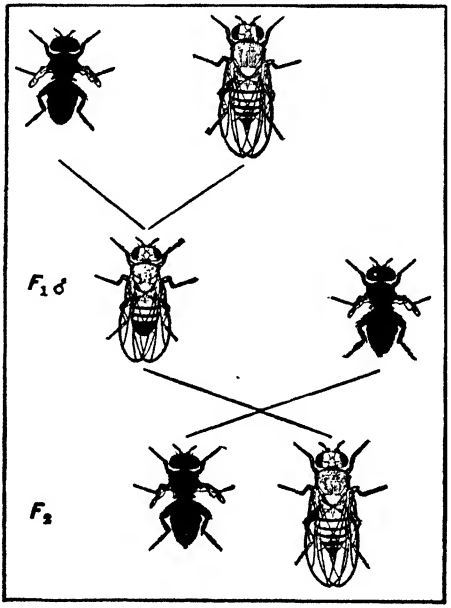


FIG. 84. Cross showing Total Linkage of Four Characters in *Drosophila melanogaster*[1]

When a fly possessing the four linked recessive characters of black body, purple eyes, vestigial wings, and speck is crossed with a wild-type fly with the linked dominant characters of gray body, red eyes, long wings, and no speck, all the F_1 individuals resemble the wild type of parent. When these F_1 males are back-crossed to recessive types of females, two kinds of second-generation offspring are produced, 50 per cent being like the recessive grandparent and the other 50 per cent like the dominant grandparent

[1] From Morgan's *Theory of the Gene*. By permission of Yale University Press, publishers.

There are other cases of linkage in the vinegar fly, as well as in other organisms, which do not show such complete hanging together of the genes for traits, indicating that at times some of them may become separated and be combined with genes brought in by the chromosomes of the opposite parent, thereby yielding some individuals that show a new combination of the traits. In all such instances the percentages of these latter types invariably is less than 50 per cent, so that most of the organisms produced resemble the parental types utilized in the cross. These are all instances of *partial linkage*, which may be explained more adequately under the heading "Crossing Over." The study of such crossing-over phenomena has made it possible to determine more accurately the position of the linked genes within the chromosomes of the species.

Crossing Over

Before dealing with examples of crossing over we must recall certain general facts already alluded to in previous discussions. In our analysis of the germ cell it was pointed out that during the synapsis stage of maturation the homologous chromosomes come together and line up in pairs in order to undergo reduction and segregation into distinct gametes. Since each of these chromosomes represents a linkage group of genes for certain of the traits of one of the immediate parents, a great deal depends on how these homologous pairs combine and separate during the synapsis stage of maturation. In those cases where they merely come together, touch, and separate without any exchange of chromatin between them nothing happens to break the linkage of the genes, so that all of them remain as they were originally within the separate chromosomes before synapsis. When these chromosomes find themselves in germ cells which participate in reproduction, they then lead to the development of offspring possessing the same linked traits as the parents. On the other hand, when the homologous chromosomes come together in a manner such that an exchange of chromatin

occurs between them, we find that, on separation of the pair, each chromosome, instead of being the same structure that it was originally, really is a combination consisting of some genes contributed by the maternal chromosome and the remainder by its paternal mate.

In recent years it has been shown that this realignment of genes between homologous pairs of chromosomes is made possible by the device of crossing over, whereby the two chromosomes of each pair that participate in synapsis twist around and cross over each other. Of course the amount of crossing over determines the gene constitution of each of the separate chromosomes after synapsis. Where little crossing over has occurred, most of the genes in each of the pairs are the same as those in the original chromosomes contributed by the respective parents, and when these participate in the production of offspring, the largest percentage of the young resemble the parents in all the linked characters. The percentage of offspring that are different indicates the amount of crossing over which has occurred. Where much crossing over has taken place between the homologous pairs of chromosomes, the expectation is that a larger percentage of the offspring will be different, and the experimental results actually bear out this fact.

By very careful studies of certain crosses, involving linked genes within the four linkage groups of the vinegar fly (*Drosophila melanogaster*), it has been possible to locate the positions of the genes within each of the respective chromosomes, and also to determine their exact amount of crossing over to yield new combinations. A reëxamination of the chromosome maps shown in Fig. 60, on page 155, reveals what modern genetics has been able to accomplish along these lines. Since work on the chromosomes of the vinegar fly began, similar chromosome maps have been worked out for corn, barley, peas, tomatoes, and other organisms.

With this explanation in mind, let us now consider a few typical illustrations of crossing over. Although such phenomena are known in numerous plants and animals, we shall

be concerned chiefly with type crosses in *Drosophila melanogaster*, where such phenomena have been studied most extensively. One case of crossing over involving sex-linked characters located in the X-chromosome is that between a female vinegar fly having white eyes and yellow wings and a male of the wild type, with red eyes and gray wings. In the F_1 generation the daughters possess red eyes and gray wings like the male parent, and the sons white eyes and yellow wings like the female parent. When these F_1 males are mated with the F_1 females, four classes of flies are produced in the F_2 generation: one having white eyes and yellow wings; the second having the characteristics of the wild type, red eyes and gray wings; the third class showing red eyes and yellow wings; and the fourth, white eyes and gray wings. Upon calculating the percentages of these classes it is discovered that the first two are exactly like the grandparents and constitute 98.5 per cent of the F_2 individuals, whereas the last two classes comprise only 1.5 per cent of this F_2 generation. Fig. 85 shows this cross with the genes for the dominant char-

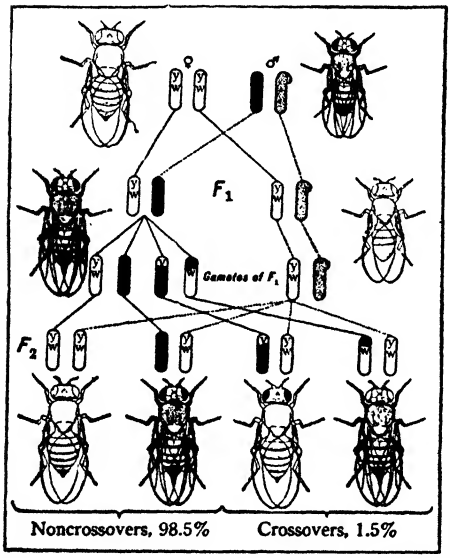


FIG. 85. Drosophila Cross showing Crossing Over in Sex-Linked Genes[1]

Cross between a white-eyed, yellow-winged female and a male of the wild type possessing red eyes and gray wings. The black rods represent the X-chromosome with the red eyes and gray wings; the light rod with y and w indicates the X-chromosome carrying genes for yellow wings and white eyes. The rods with white and dark portions are those where crossing over has occurred. The Y-chromosome is stippled

[1] From Morgan's *Evolution and Genetics*. By permission of Princeton University Press, publishers.

acters of red eyes and gray wings carried in the dark X-chromosome of the male and the genes for recessive white eyes and yellow wings in the light X-chromosomes of the female.

Another cross, showing crossing over of genes linked in chromosomes other than the X-chromosome, is one with flies, involving body color and size of wings carried by the second linkage group. When a male fly possessing a black body and vestigial wings is mated to a female fly having a gray body and long wings, the F_1 offspring all show the characters of the wild type, that is, gray body and long wings. When one of these females is mated to a male possessing the recessive characters of black body and vestigial wings, the F_2 offspring are of four types: the first two of these types, constituting 83 per cent of the individuals, are like the grandparents, having either black body and vestigial wings or gray body and long wings; the last two types, constituting 17 per cent of the F_2 generation, consist of flies with either gray body and vestigial wings or black body and long wings. Fig. 86 shows this cross.

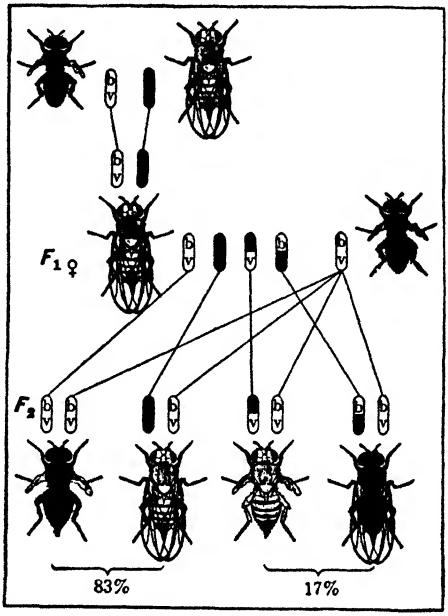


FIG. 86. Drosophila Cross showing Crossing Over of Genes in Second Linkage Group[1]

Here a male possessing black body and vestigial wings is crossed with a female having gray body and long wings. The F_1 offspring all have gray bodies and long wings. When these F_1 females are backcrossed to the recessive males with black bodies and vestigial wings, four classes of flies are produced in the proportions indicated

[1] From Morgan's *Evolution and Genetics*. By permission of Princeton University Press, publishers.

Chromosome Maps

By the aid of linkage and crossing-over studies such as have been described, it has been possible to get an insight into the constitution of the chromosomes of the germ cell. At the present time geneticists consider the chromosomes as structures that carry the genes for traits of the adult organism linked together in a linear series arranged in a manner similar to a large number of beads in a chain. Each chromosome thus represents a group of genes logically arranged, one after the other throughout the length of the chromosome, and the entire structure is referred to as a linkage group. Wherever these hereditary phenomena have been studied it has been found that there are as many linkage groups as the haploid number of chromosomes which characterize a species — in man there are twenty-four; in the vinegar fly, four; in corn, ten; in the garden pea, seven; and so on. Moreover, these studies have enabled us to locate not only the position of many of the genes within the chromosomes but also their relative distances from each other. The positions of the genes are referred to as their *loci*, each one being at a definite *locus*. It is evident that genes at different loci invariably are distinct in character.

Such chromosome-mapping has been pursued most ardently in *Drosophila melanogaster* and, as before stated, over four hundred genes, constituting four linkage groups, have already been studied and located in the four chromosomes of this interesting species. Although this appears to be a rather large number, nevertheless Morgan believes that the sum total of all the genes present in this insect is at least ten times as great, that is, four thousand. The location and plotting of these genes have been accomplished largely through mating experiments involving crossing over, by means of which linked genes in each chromosome of a homologous pair have become separated and attached to the remaining genes of its mate. On such a basis we can account for the differences which make their appearance in the offspring, revealing a link-

age of traits other than that found in the respective parents. The percentage of such differences, in most instances, is an index of the amount of crossing over which occurs between the linked genes of homologous pairs of chromosomes. It has been found that when genes are close together within a chromosome, the chances of their crossing over and becoming separated are very much smaller than when they are farther apart. When the percentage of individuals showing differences is small, it indicates that very little crossing over has occurred and that the genes themselves are located close to each other; on the other hand, when the percentage is large, it is an indication that much crossing over has occurred and that the genes are widely separated from each other. So specific have results of this sort been that geneticists have come to the conclusion that the amount of crossing over is in direct proportion to the distance between the genes of a linkage group.

In order to clarify and really understand the above statements it might be well for us to consider some concrete illustrations. Suppose that we take the two genes, A and B, that are on the same chromosome and find that the percentage of crossing over is small, say 10 per cent. This would indicate that the genes lie close to each other in the chromosome. On the other hand, if the percentage of crossing over between gene A and another gene C in this same chromosome is relatively high, approximately 35 per cent, then this would indicate that the distance between A and C is rather great, making it possible for frequent crossings over to take place. By subtracting the percentage of crossing over between A and B (10), from that between A and C (35), the percentage of crossing over between B and C is found to be 25. Moreover, by knowing the percentages of crossing over between A and B, and B and C, it becomes possible to predict the relative amount of crossing over between genes A and C. By adding the 10 per cent of crossing over between genes A and B, and the 25 per cent between genes B and C, one would get the amount of crossing over between A and C,

which, as indicated, is 35 per cent. This is not all theory, for it has actually been found to work out in various species, particularly in the vinegar fly. Take, for example, three such linear sex-linked genes, within the first linkage group of the vinegar fly, as yellow wings, white eyes, and bifid wings. Crossing over between yellow wings and white eyes takes place in 1.2 per cent of the cases. When white eyes are tested with bifid wings, the result shows 3.5 per cent of crossing over. If the gene for yellow wing is on one side of the gene for white eye, then the amount of crossing over with the bifid-wing gene should be 4.7 per cent. On the other hand, if the yellow-wing gene is on the other side of the gene for white eye, then the percentage of crossing over with the bifid-wing gene should be 2.3 per cent. When the actual experimental results are analyzed, it is found that the percentage of crossing over between yellow wings and bifid wings is approximately 4.7 per cent. This result is, of course, the same as that obtained by adding the percentages of 1.2, between yellow wings and white eyes, and 3.5, between white eyes and bifid wings. It must be emphasized that the unit of measure used in plotting the distance between the genes is that indicated by 1 per cent of crossing over. If the amount of crossing over between two genes is 1 per cent and that between two others is 10 per cent, it means that the distance between the latter genes is ten times as great as that between the former ones.

In spite of the fact that the above general rule holds good for the linear arrangement and distances of the genes as determined by the percentage of crossing over which occurs, nevertheless modifications have presented themselves in the form of *double crossing over* and *interference* in crossing over of genes by neighboring ones which have already crossed over.

Double Crossing Over

By double crossing over is meant that distant genes in homologous chromosomes cross over in two places instead of in one, as indicated in Fig. 25, on page 85. When the percent-

age of such crossing over is studied, it is found to be less than the sum of the percentages of the single crossovers between the genes involved, thus giving the impression that these distant genes are closer to each other than is actually the case.

An example, involving three linear genes of the first linkage group of *Drosophila melanogaster*, will help to clarify this statement. When white-eyed, miniature-winged, and bar-eyed vinegar flies are crossed with wild-type individuals (those possessing red eyes, long wings, and normally shaped eyes), about 33 per cent of the offspring will show crossing over betwen the white-eyed and miniature-winged conditions. The amount of crossing over between the gene for miniature wing and the gene for bar eye is 22 per cent. Adding these two percentages together, we get a sum of 55 (33 + 22) which, while it represents the actual distance between the genes for the white-eyed and bar-eyed characters, none the less is not a true indication of the actual percentage of crossing over obtained between those characters. The experiments reveal that the amount of crossing over is 44 per cent, and this deviation from the expected amount of 55 per cent has been explained as due to the phenomenon of double crossing over between the genes for white eyes, miniature wings, and bar eyes.

Interference

Another phenomenon which has complicated chromosome-mapping is that of *interference*, which means simply that often when crossing over occurs between genes in certain regions of homologous chromosomes, it at the same time interferes with and prevents crossing over in neighboring genes closely adjacent to them. The greater the distance between the genes, the more possible does it become for them to cross over; likewise, the shorter the distance between the genes, the greater becomes the probability that the crossing over of a pair at one place will not only interfere with, but also prevent, the crossing over of neighboring pairs in their immediate vicinity.

Significance of Modern Genetics

Now that we have considered Mendelian principles in their old and new implications, it may be well to summarize the importance of this newer genetics. In the first place, such knowledge has made it possible for the breeder to gain a clear insight into the genetic constitution of the individuals with which he is dealing. Every newly formed organism comes from a combination of two germ cells, each one of which is the carrier of the representative chromosomes of the parent from which it was derived. The chromosomes, in turn, are the bearers of the genes which account for the heredity of the species in question. Then again, the newer genetics has revealed to us the manner in which genes enter and behave in crosses, accounting for the actual results obtained.

The discovery in recent years that the salivary-gland chromosomes of various *Drosophila* are veritable giants as compared with the germinal chromosomes has made it possible to study the structural organization of the chromosomes in much greater detail. By appropriate staining methods it has been shown that the salivary chromosomes possess transverse dark and light bands, arranged in such an orderly manner that they are believed to be the regions in or near which the distinctive genes are located. So consistent is this band arrangement within each of the respective chromosomes that it has made gene-mapping a much more accurate process than it formerly was. When certain chromosome transformations take place in the germ cells that produce the new individuals, such changes become expressed in the chromosomes of the somatic cells, including those of the salivary glands. For a fuller treatment of this newer genetic research, the reader is referred to various recent papers in the *Journal of Heredity*, especially that in the December, 1934, issue (Vol. 25, pp. 465–476) by Theophilus S. Painter, entitled "Salivary Chromosomes and the Attack on the Gene."

CHAPTER XIV

Variation and Species Formation

THE last chapter was concluded with a general appraisal of the newer genetics and, as was indicated there, this field is now regarded as a potent experimental means of bringing about modifications in organisms leading to the establishment of new varieties. Mention of the subject of modifications in type brings immediately to mind the question of *variation*, and, as pointed out in the beginning of this volume, variation is one of the chief topics of discussion in genetics. Every trait that one encounters is, in reality, a variation which made its first appearance in the immediate generation of offspring or else appeared in a previous one and was handed on to future generations of individuals through the medium of heredity. Therefore every organism must be looked upon as a unified bundle of traits, or a bundle of variations. The geneticist and breeder are interested in those variations which are real,— those which, when once induced in an organism, later become transmitted through the medium of the germ cells to the generations of offspring that follow.

The creation of new varieties is very closely linked with the origin and development of species. It is one of the important topics not only in genetics but also in *organic evolution*, a study which has for its sphere the discovery of the facts and principles responsible for the emergence of the different types of organisms which have existed in the past, or those which are found to be in existence now, or those which will emerge in the future. In dealing with variation, we are striking at the very heart of the subject of evolution. While geneticists have made progress in analyzing variations, nevertheless they still are greatly puzzled concerning the factors which initiate them. Those who are familiar with the history

of biology know that, while it is true that the fact of evolution is firmly established among scientists, nevertheless there are numerous differences of opinion regarding the causal factors which have been responsible for bringing about the necessary variations that are important in the evolution of species. Bearing this preliminary explanation in mind, it may be well for us to concern ourselves with the topic of variation at greater length and consider chiefly its importance in genetics.

Kinds of Variation

With respect to their future, variations are of two kinds, being either *transitory* or *permanent.* The transitory variations are modifications which appear during the lifetime of an organism and pass out of existence at the time of its death. They are the changes which usually are referred to as acquired, or somatic, characters. The permanent variations are germinal and, as is especially significant from a genetic standpoint, come out in later breeding tests. In other words, they are inherited. A somatic, or transitory, change is one which may express itself because of a peculiar stimulus in the environment, and it apparently remains only so long as the stimulus which induced it lasts. On the other hand, the germinal modifications are permanent, irrespective of whether the original stimuli which accounted for their appearance in the germ cell remain present or not. As students of genetics we are interested not only in the permanent germinal variations but also in the transitory ones, especially for the purpose of discovering whether any of them ever can become permanently fixed in the structure of the germ cells so as to be inherited.

In regard to amount and character of variations, the types that are most important from the standpoint of evolution are (1) *continuous,* or *fluctuating,* and (2) *discontinuous,* or *nonfluctuating.* The continuous variations are those which appear regularly in a plus and a minus direction, each change being a little more or a little less prominent than the previous one.

These variations are extremely small modifications, and in large populations they are statistically distributed along a normal distribution curve. On the other hand, the discontinuous, or nonfluctuating, variations may be either large or small (mostly small); but when they are examined it is found that they do not follow any normal distribution. In reality, they crop out haphazardly rather than regularly. They are what De Vries has called *mutations* or *saltations*, because they are sudden jumps from the normal.

Historically it is an interesting fact that the older biologists emphasized continuous variations as of greatest significance in evolution, and these were the ones that Charles Darwin (Fig. 6, page 21) made the foundation for his famous theory of evolution. Darwin also recognized mutations as factors in evolution but regarded them as rather large, prominent modifications, of rare occurrence and of secondary importance.

The Darwinian Hypothesis

The Darwinian conception of the evolution of species is of such vital importance in genetics that we must consider the significant points in this hypothesis. In spite of the fact that many people are of the opinion that the idea of evolution started with Charles Darwin, nevertheless it must be emphasized that the evolution conception is very old, dating back to the time of the ancient Greeks. Although most of these ideas were vague and erroneous, yet they may be discerned clearly in the writings of these ancient philosophers and scientists. Henry Fairfield Osborn, in his monumental volume *From the Greeks to Darwin* (*Bi. 158*), gives a splendid account of the historical development of the various evolutionary conceptions from the time of the ancient Greeks to the period of Charles Darwin in the nineteenth century. Before the advent of Darwin, facts to substantiate the theory of evolution were meager and fragmentary. With the coming of Darwin, however, all this was changed, for during his lifetime he accumulated more factual material in support of evolution than has

ever been gathered together by any one person before or since his time.

Darwin as a young man was appointed naturalist on the *Beagle*, which made a cruise of exploration around the world for something like five years, stopping mainly along the western coast of South America. While on this trip he conceived his ideas on evolution. Instead of immediately rushing into print and publishing them, Darwin worked patiently for another twenty years, collecting a vast amount of factual material in support of his contentions. Even so, he probably would not have published them as soon as he did had it not been for the fact that ideas similar to his own occurred to the naturalist Alfred Russel Wallace, who sent Darwin a preliminary draft of his theory. When Darwin realized that Wallace's conceptions were similar to his, he was tempted to suppress his own efforts completely and give Wallace the entire credit for the contentions. Urged by their many mutual friends, however, Wallace and Darwin were induced to present brief papers embodying their ideas on evolution before the meeting of the British Association for the Advancement of Science, held in the year 1858. To commemorate this event, in 1908, fifty years after it happened, the Linnean Society of London had a special medal made known as the Darwin-Wallace Medal (Fig. 87).

In 1859, the year after Wallace and Darwin presented their short papers on evolution before the British Association, Charles Darwin's monumental work entitled *The Origin of Species* (*Bi. 38*) was published, and this gives a splendid account of his evolutionary conceptions. It is hard to realize what a revolution this volume created in intellectual circles. Immediately the thinking world was divided into two camps, one condemning Darwinian evolution and the other vigorously supporting it.[1] Through the efforts of a large number of scientists in various countries, Darwin's evolutionary con-

[1] For a discussion of the controversy which followed the publication of Darwin's views on evolution, the reader is referred to Nathan Fasten's *Origin through Evolution*. F. S. Crofts & Co., New York, 1929.

tentions were soon established and were accepted by most of the thinking world.

Inasmuch as the central idea of Darwinian evolution is built around the conception of *natural selection*, the Darwinian hypothesis is often referred to as the *theory of natural selection*. Most people, however, fail to realize that coupled with this factor of natural selection are numerous others which, though they may be somewhat subsidiary to it, are

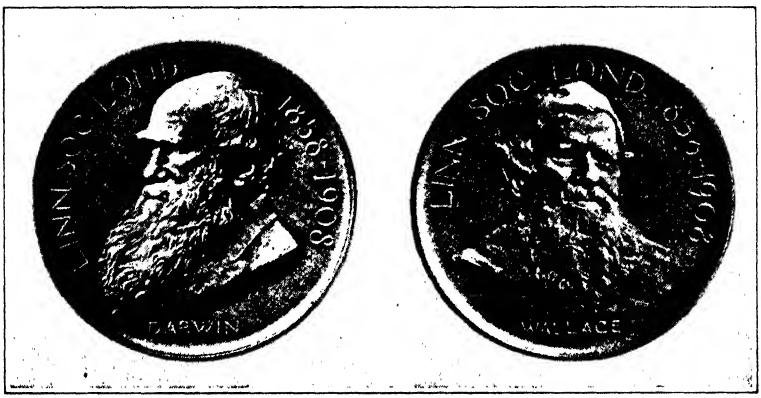


FIG. 87. The Darwin-Wallace Medal of the Linnean Society[1]

just as important as that of natural selection. The chief points in Charles Darwin's hypothesis are as follows:

1. The Fertility of the Organic World

The fertility of the organic world is well known to biologists. Generally speaking, organisms are very prolific in a state of nature and more of them come into existence than can possibly develop to maturity. Large numbers of individuals are destroyed soon after the beginning of development, only a very few of them ever completing their entire life cycle. Were this not the case, then certain regions of our globe would be so completely dominated by one particular species that everything else would be wiped out of existence. An ex-

[1] Courtesy of *Popular Science Monthly*.

ample will clarify the point: A female mountain trout may deposit as many as three thousand eggs during the breeding season. If all of these eggs were fertilized and developed to maturity, then it would not take more than a few generations for so many mountain trout to be developed that they would crowd out everything else in their environment. They would become the sole masters of all the available room, food, and oxygen, with the result that all other organisms would be deprived of these necessities and would soon perish. As everyone knows, this does not happen, for only enough of the fertilized trout eggs mature to insure the perpetuation of the species.

2. The Operation of Heredity and Variation

Through the factor of heredity the characteristics of species are handed on from one generation to the next, insuring the perpetuation of those permanent traits present in the parent species. We know, however, that variations or differences are constantly cropping out; when these are permanent in character, they make possible the development of new traits which, through the medium of heredity, may be passed on to the offspring, thus leading to the establishment of new varieties, types, or species. As previously mentioned, Darwin emphasized chiefly the small fluctuating variations as the ones of greatest significance in the establishment of species. While he recognized mutations, he considered them as large variations appearing rather infrequently and of lesser importance in his evolutionary scheme.

3. The Limitations of the Environment

Inasmuch as our planet is definitely limited in size, nature's supplies of food, water, oxygen, sunshine, and the like are limited likewise, being capable of supporting, from year to year, only a fixed number of organisms within certain ranges. Consequently the agencies of the environment may be regarded as efficient checks on any sudden and rapid increase in the number of organisms that populate the earth.

4. The Struggle for Existence

Organisms are constantly competing among themselves for the possession of those factors in the environment which enable them to maintain life. The larger the number of organisms in a certain region, the fiercer becomes the struggle for existence among them.

5. The Survival of the Fittest through Selection

During the struggle for existence those organisms which possess the best variations to cope with the conditions in the environment survive, whereas the others soon pass out of existence. Those that have survived because of their superior characteristics are the ones which become the parents of the next generation. Since this is the case, the offspring may be said to have inherited the superior variations present in their parents. Concerning the selective process which determines the survival of the organisms, Darwin emphasized three agencies, namely, (1) *natural selection,* (2) *artificial selection,* and (3) *sexual selection.*

Natural selection was considered of greatest importance by Darwin. This is a blind force existing in nature which automatically chooses the best-fitted organisms that present themselves for survival. Often the variations which fit an organism in nature to survive are not the ones which man himself would select if the choice depended on him.

Where man selects those traits for perpetuation which happen to strike his fancy, the method is referred to as artificial selection. Those who are familiar with breeds of animals and plants know that for centuries man has selected types for perpetuation, with the result that numerous distinct varieties and species of organisms have been established. It is quite certain that unless many of these are nurtured and cared for constantly, they soon revert to the wild natural type from which they were derived. Therefore it seems safe to assert that in a state of nature most of these different kinds of organisms would not have come into existence, for the reason that the variations responsible for them could not survive.

Darwin pointed out the rôle that sexual selection plays in determining which types of individuals shall perpetuate the species. During the mating season there is a constant struggle going on between the males for the possession of the females. Often the victorious male, who has either killed off or chased off many of his adversaries, becomes the possessor of one or more females, so that he becomes the sire of all the offspring to which these females give birth. Sexual selection has thus played its part in allowing certain variations to gain expression.

6. The Origin of Species

Through the operation of all the above factors, especially survival of the fittest through natural selection, new varieties and types make their appearance, leading ultimately to the production of new species.

Throughout Darwin's evolutionary hypothesis the emphasis was placed chiefly on the small, continuous, fluctuating variations exhibited by species. These are the ones which he considered of greatest value in the emergence of new types of plants and animals. As before stated, mutations he regarded as large, prominent modifications of rare occurrence in nature and of rather minor importance in evolution.

Selection and Improvement

The central idea in Charles Darwin's evolutionary hypothesis was that, through the selection of the chance, fluctuating variations which presented themselves, it was possible to make types of organisms vary in one direction or another, so that eventually there would result the establishment of new varieties and species. As proof of the validity of these contentions, Darwin and others pointed to the numerous accomplishments of different practical breeders, whereby, through methods of rigid selection, they were able to establish distinctly different breeds of plants and animals. Everybody accepted such views, never even questioning or critically examining them. It was not until some time after Hugo

De Vries enunciated his mutation conception, especially during the first part of the twentieth century, that biologists undertook a critical examination of the continuous, fluctuating variations as effective agents leading to the establishment of permanent new types in organisms.

Before such work is discussed more fully, it may be well for us to understand clearly the chief contention of the Darwinians in regard to the production of new types through selection. These scientists assert that when one examines all the offspring of certain parents, one finds that the different traits express themselves either more or less markedly in them than in their parents. By rigid selection, for breeding purposes, of those individuals which show the greatest increase in the expression of a certain trait, more and more of the progeny will show a larger degree of the character, with the eventual result that a distinct change in type will be established. The same facts will hold true for individuals showing a smaller expression of the character than the normal, — gradually more and more individuals will be produced showing a decrease in the trait, with the result that eventually a type will be established showing such a marked deviation in the character as to be considered a new variety, of the nature of a new species.

FIG. 88. Wilhelm Ludwig Johannsen[1]

Critical experimentation to find out whether these contentions were correct was begun during the early portion of our present century, particularly by the Danish botanist Johannsen (Fig. 88) on so-called *pure lines* in beans. The

[1] Courtesy of *Genetics*.

term "pure line" is used in genetics to denote that the progeny are all pure or identical, from the standpoint of their germinal constitution, with respect to traits considered. In those cases where organisms reproduce by *self-fertilization*, or through the vegetative processes of *cutting*, *fragmentation*, or *splitting*, or by means of *parthenogenesis* (that is, where the eggs develop without the agency of fertilization), the pure-line condition is easily established. Where *cross-fertilization* occurs, a pure-line condition similar to the above is established when the genes for the traits in question derived from both the parents are identical. Generally speaking, organisms as they exist in nature are members of what is known as a *population*, really consisting of a mixture or combination of a number of pure lines. Through the medium of rigid selection a breeder is enabled to segregate the numerous pure-line strains which comprise the population. Individuals belonging to the same pure lines may therefore be said to possess the same germinal determiners and to have been derived from the same parental source. When a pure line is studied from the standpoint of a single variation, it is soon found that most of the offspring adhere closely to the average degree of expression of this particular trait. Others show varying degrees of the expression of the trait, either slightly above or slightly below the average. A few show the largest deviation from the average in a positive direction, and a like number show the greatest deviation in the negative direction.

When all the progeny are studied statistically and a curve is plotted, it is seen that the variations may be arranged in a regular curve similar to that shown in Fig. 89. This is the *curve of normal variation*, indicating that most individuals are around the average of the group, known in statistical language as the *mean* of variation. The other individuals show either more or less variation from the mean, and these are indicated on either one or the other side of the mean of the curve. Those individuals which show the most marked variation from the mean in either a plus or a minus direction comprise the fewest number.

The advocates of the Darwinian conception of evolution were of the opinion that continued selection of those individuals showing the greatest degree of variation from the mean operated to produce a permanently modified type in either a plus or a minus direction. As will be pointed out when the experiments on pure lines are discussed, such has not proved to be the case. When those progeny of a pure line which show the greatest degree of variation are propagated, and the curve of the variation of their offspring is then plotted, it becomes apparent that this new mean of variation is practically identical with that of the old mean for the curve of the pure line to which their parents belonged. Moreover, if the curve of the entire population is compared with the curves for the respective pure lines, it is noticed that while each pure line may have its own curve with its distinctive mean, no one of these falls outside the general curve and mean for the entire population. Therefore modern biologists believe that selection merely sorts out the distinctive pure lines of which a population is composed. In most instances selection is necessary to keep the pure lines distinctive; for the moment it ceases to operate, the pure lines revert to the general type of the population. With this preliminary explanation, let us now consider Johannsen's famous experiments along this line.

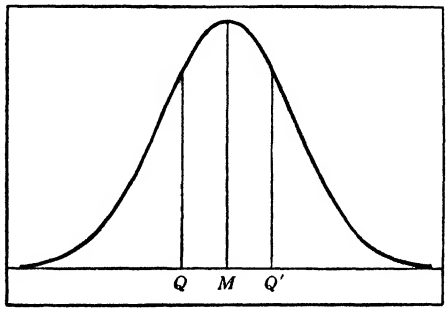


FIG. 89. Curve of Normal Variation[1]

M denotes the mean, while *Q* and *Q'* represent quartiles. The lines drawn from *M*, *Q*, and *Q'* divide the area of the curve into four equal portions so far as numbers of individuals are concerned

In the year 1909 this Danish botanist undertook experiments to prove whether continued selection of fluctuating

[1] From Lock's *Recent Progress in the Study of Variation, Heredity, and Evolution.* By permission of John Murray, publisher.

variations operated to produce new varieties and species, as Charles Darwin had contended. Johannsen took for his material a population of the common garden variety of bean known as the princess bean (*Phaseolus vulgaris*), which ordinarily propagates by self-fertilization, and plotted a curve of the variation of the size of the beans in his various plants. The result was that he obtained a curve of normal variation, indicating that most of the beans are around the average size as represented by the mean of the curve of variation. He then selected from his population beans of different sizes, the largest as well as the smallest and also others in between these two limits. He selected nineteen such beans in all, planted them carefully in separate plots, and saved the seeds of the different plants produced. In each instance he selected for further experimentation those beans which showed the most marked variation in size, in the hope that eventually he would get individuals that would show a definite and permanent modification in the size of the beans in either a plus or a minus direction. The most rigid selection on the part of Johannsen failed to yield any such results. While his beans gave origin to pure lines that possessed distinctive differences in each case, nevertheless the mean of each pure line adhered very closely to the general mean for the entire popula-

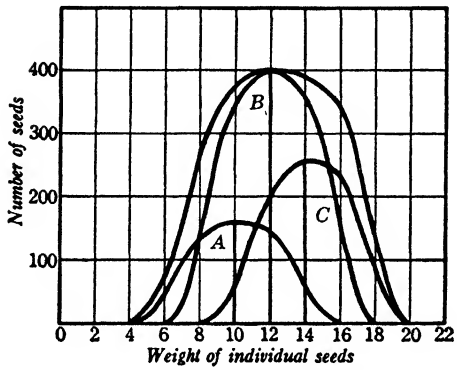


FIG. 90. Curves of Variation in a Population of Beans[1]

A is a curve for seeds varying between 4 and 16 centigrams in size, with a mean of about 10 centigrams; *B*, curve for seeds between 6 and 18 centigrams, with a mean of about 12 centigrams; *C*, curve for seeds between 8 and 20 centigrams, with a mean of about 14 centigrams. The curve for the whole population is the outer one, which incloses those for the pure lines

[1] From Goodrich's *Living Organisms*. By permission of Oxford University Press, publishers.

tion. Although the nineteen beans became pure lines with respect to the character for which the selection was made, still when their progeny were examined carefully, it was discovered that the largest beans produced were no larger in size than the largest ones in the general population. Likewise, the smallest beans yielded no smaller types than those present in the original population. This is graphically shown in Fig. 90, which indicates the curve of variation of the beans in the general population and a few of the curves of some of the extracted

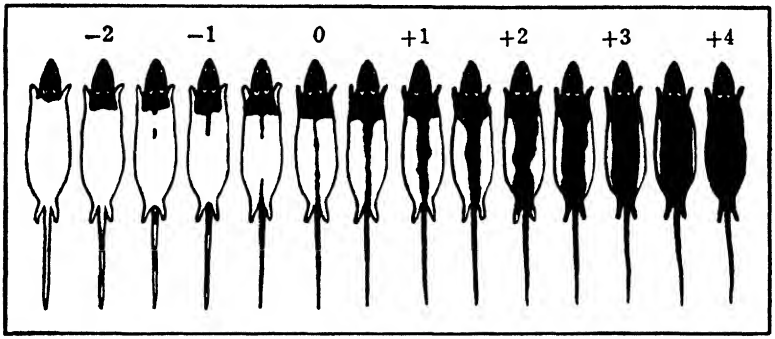


FIG. 91. Variation among Hooded Rats[1]

Plus and minus variations of the white spotting pattern of the hooded rat, obtained through the medium of selection, beginning with the type indicated at 0

pure lines. Following his experiments, Johannsen came to the conclusion that although rigid selection of fluctuating variations sorted out the various hereditary possibilities inherent in the germinal constitution of a species, it was wholly incapable of yielding anything new, by either adding to or detracting from the species.

In line with Johannsen's experiments, Castle's work on the hooded rat might be cited. The hooded rat is one which shows varying degrees of black on the dorsal side of the body, particularly in the regions of the head, shoulders, and middle of the back, while the rest of the body is white. Castle found that when hooded rats were studied, they could be arranged

[1] From Castle's *Genetics and Eugenics*, fourth revised edition. By permission of Harvard University Press, publishers.

in a series, similar to a curve of normal variation, showing various expressions of the hooded pattern (Fig. 91). By continued selection of those having a marked degree of the hooded pattern, Castle was able to establish a type in which the dark pigment covered a more extensive area than in any of the individuals found in his original stock. Also, by rigid selection of individuals showing the least hooded pattern, this character gradually became less and less marked until an almost entirely white individual was produced. At first Castle was most enthusiastic regarding his results and claimed that they substantiated Darwin's contentions in regard to the selection of fluctuating variations. Later genetic work, however, revealed that the hooded-pattern expression of these rats was the result of a combination of modifying factors and that the intensification or diminution of the trait was due to the presence or absence of more or less of these numerous factors within the individual. In this species selection has been the means — a rather unconscious one — of bringing together more or less of the complex factors involved in the production of the results obtained. In this connection we might refer back to somewhat similar results obtained by Nilsson-Ehle and others as discussed in Chapter XI, on the gene hypothesis.

The experimental work on pure lines has led most modern biologists to the conviction that selection has no effect on the genes responsible for the production of the unit characters. Both the quantitative and the qualitative expressions of the genes are due, in large measure, to a number of coöperating agencies. In certain instances these are environmental; in others they are internal, due either to the effects of glandular secretions or to other genes that bring about a modification, intensification, diminution, or temporary suppression in the expression of the unit characters in question. Permanent modification can come only when the gene itself is definitely changed, and, as far as is known at the present time, this occurs only when a mutation takes place.

The Mutation Conception

Although Darwin recognized mutations, he considered them as rather prominent variations secondary in importance in evolution to the minute, fluctuating kinds. The Dutch botanist Hugo De Vries (Fig. 92) was really one of the first to call attention to discontinuous variations or mutations as the primary agents responsible for evolution. In the year 1886, while De Vries was roaming around in an abandoned potato field, a short distance from his laboratory in the city of Amsterdam, he noticed a number of discontinuous variations among evening primroses, belonging to the species *Œnothera lamarckiana*. As these variations were growing in the same environment as the ordinary types and it seemed certain that no selection could have taken place, De Vries came to the conclusion that they originated spontaneously as mutations. In order to check his conclusions a little more carefully, he transplanted these new primroses to his experimental gardens, and there they have continued to give off numerous new varieties, which have led to the establishment of new species. Approximately a dozen new evening primroses, known technically as *mutant* types, which had never been seen or described before, have thereby been discovered by De Vries.

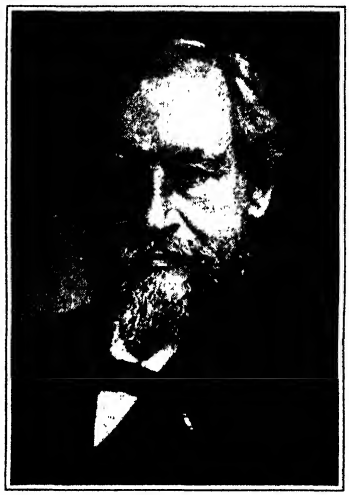


FIG. 92. Hugo De Vries[1]

In his volume *The Mutation Theory* (*Bi. 51*), De Vries discusses the whole question of the origin of species through mutations. When De Vries first called attention to mutations, biologists considered such variations as rather prom-

[1] Courtesy of *Scientific Monthly*.

inent modifications easily distinguishable from the type which gave origin to them. However, as research along these lines progressed, it became apparent that most mutations are small modifications rather than large ones, in many instances being as minute as the fluctuating variations of Darwin. But it must be remembered that mutations are germinal in origin and therefore breed true. At the present time this is the way mutations are regarded by most geneticists. After Johannsen's experiments on pure lines, attention was concentrated especially on mutations, or discontinuous variations, as factors in the production of species. In particular, the workers on the vinegar fly have discovered a large number of permanent variations, some four hundred of them, coming into existence through the medium of small mutations. These affect all parts of the body and comprise four linkage groups corresponding to the four chromosomes within each of the germ cells of this species. Other investigators also have shown the existence of numerous mutations in other plants and animals. In fact, so many mutations have been described up to the present time that one must conclude that such modifications are constantly making their appearance spontaneously in organisms.

Mutations are extremely interesting from various standpoints. In the first place, they are changes that really breed true to type. In the second place, they are of much more frequent occurrence than is generally supposed to be the case. In fact, they are constantly cropping out in species. In the third place, most of the mutations which develop are of no particular benefit to the species, really unfitting the individuals for survival in the struggle for existence, and these types are quickly eliminated in nature. A few mutations, however, are of distinct advantage to the organisms, making them better fitted to cope with conditions in the environment, and therefore giving them a better chance for survival. These are the ones that succeed in establishing new types and varieties of organisms. Finally, when types arising by means of mutations are examined, many of them are found to possess

alterations in their germinal constitutions, often expressed either through a change in the number of chromosomes common to the species or through a realignment in the gene constitution of the chromosomes themselves. Where the former transformation takes place, the chromosome count may be either increased or diminished from that which is normal for the species. Where the latter takes place, portions of certain chromosomes are often broken off and transferred to other chromosomes of the germ cells (Fig. 93). Biologists

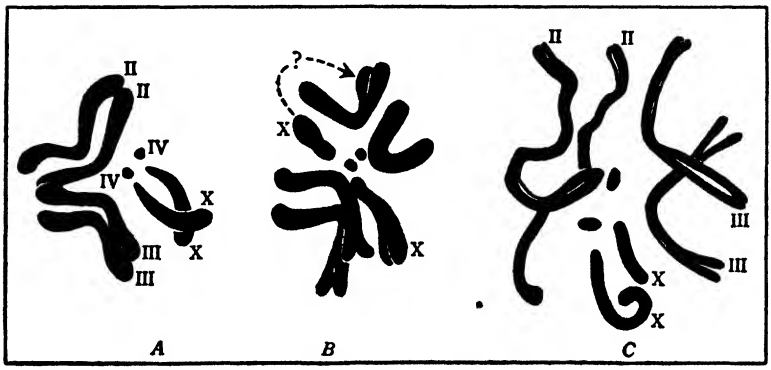


FIG. 93. Translocation in Chromosomes of *Drosophila melanogaster*

A, the four pairs of normal chromosomes in the female, showing size of X-chromosomes; *B* and *C* show reduction in the size of one of the X-chromosomes following a translocation. (After Muller and Painter, courtesy of *Journal of Heredity*)

who have examined the cells of types arising through mutations have succeeded in establishing the phenomena which have been indicated.

Still another interesting thing concerning mutations is that during the last few years geneticists have succeeded in inducing them in various species through the use of X rays and similar radiations. It is believed that such stimuli engender modifications within the gene constitution of the chromosomes of the germ cells that lead to the establishment of mutations. Reference has already been made to the work of Muller, where he induced vinegar flies to mutate at a tremendously increased rate of speed by exposing them to powerful X rays.

In recent experiments Patterson and Muller (*Bi. 162*) have induced *progressive* and even *reverse mutations* (Fig. 94) by irradiation. In this connection the work of Babcock and Collins (*Bi. 8*), of California, and of Hanson and Heys (*Bi. 103*), of Missouri, is also of significance. As will be recalled, these geneticists exposed vinegar flies in natural locations, where the rate of radiation was about two and one-half times as great as in the normal environment, and this condition induced the fruit flies to mutate at about two and one-half times their normal rate. The biologists who have studied the question believe that these powerful rays in some manner seek out certain of the genes within the chromosomes so as to bring about permanent changes in them, and these express themselves later as mutations.

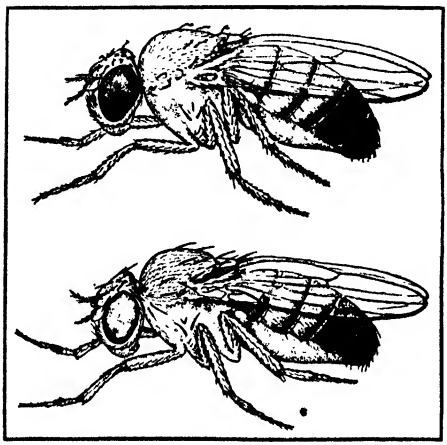


FIG. 94. Progressive and Reverse Mutations in *Drosophila melanogaster*

Above, fly with forked bristle (a mutational change) and normal eye. Below, fly with normal bristle and spectacle eye, both of these characters arising as mutations, after irradiation, from the fly shown above. The trait of normal bristle represents a *reverse* mutation of the mutant gene for forked to nonforked bristle. This is a case of double mutation. (After Patterson and Muller, courtesy of *Genetics*)

Although, in general, mutations originate germinally, still occasionally they may make their appearance also in somatic tissues. When such somatic mutations arise in organisms which can be propagated asexually, they may afford the means of establishing new varieties. This is especially true in many domesticated plants, especially vegetables and fruits. For example, the navel orange so universally grown in various regions of the globe first presented itself as a somatic *bud mutation*, and this has since been propagated through asexual means. Because the higher animals cannot be reproduced in any other manner

than the sexual one, somatic mutations, when once they originate, pass out of existence with the death of the individual. Here the germinal mutations are the only ones which may be transmitted to future generations and thereby lead to the establishment of modified types.

Because mutations rather than fluctuating variations are now considered responsible for species formation, one must not infer that the other general factors of evolution as enunciated by Charles Darwin must therefore be discarded. The truth is that these factors are just as potent today as they have ever been, and most modern biologists accept them. The trouble with Darwin's conception was that he did not distinguish carefully between changes that were permanent, or germinal, and those that were transitory, or somatic. Had he done this, he would have realized what every present-day geneticist knows, that no matter what the agency is that is doing the selecting, whether it be nature or man, it must single out only those new acquirements for perpetuation that are germinal in origin and of the nature of mutations.

Causes of Variation

While variations are the means of bringing about improvements in animals and plants, yet the causes which account for variations are little understood. When one studies the history of biology, one realizes that a number of conceptions have been propounded to account for the origin and development of modifications. One of the oldest of these is to the effect that in some manner the various factors of the environment operate to induce changes in organisms. This is the belief which was common among most of the naturalists of the nineteenth century. That the environment is important in shaping the life course of the individual no one can deny; but how really significant it is, is still a debated question. When one studies the animals and plants which have existed in bygone ages, one soon realizes that changes in the environment oftentimes have led to such tremendous modifications

in certain portions of organisms as to unfit them for existence in any other surroundings. When other transformations in the environment took place, or when the organisms found themselves in a modified locality, no adjustment in the over-specialized variations was possible, and the result was that the prevalent types were soon exterminated and supplanted by newer ones. In recent years the work on *geographical isolation*, especially that which concerns itself with the effects of various *barriers*, has shown that changes in the environment may account for modifications in organisms, leading to the establishment of entirely new varieties and species. Of course those who are advocates of the Weismannian point of view believe that environmental influences are of little importance in inducing transformations. However, if we disregard the environment as a factor in bringing about change, especially if stimulating agents act over long periods of time, then it is difficult to explain many of the modifications which have been engendered in organisms during past and present eras of geological history.

A second belief is that the functions of the various parts of organisms determine the changes engendered within them. This conception was developed toward the end of the eighteenth century, and during the early part of the nineteenth century it culminated in Lamarck's theory of evolution, based chiefly on the principles of the *use or disuse* of structures of organisms. According to this view, when an organ is used, it becomes specialized in certain directions to the extent where specific changes are engendered within it; and at the same time the effects of these modifications are, in some mysterious fashion, transferred to the germinal material of the individual and thereby transmitted to the offspring of the next generation. Likewise, the disuse of an organ causes it to atrophy; and, as in the previous case of the effects of used structures, these transformations in the minus direction also become reflected in the germ plasm for the purpose of transmission to the offspring. Those who advocated this view believed implicitly in the inheritance of acquired modifications. In recent

years there has been a revival of this theory, as was pointed out in a previous chapter, due largely to the work of such investigators as Guyer and Griffith; this has led to the school known as *parallel induction*, which attempts to explain the manner in which various stimuli of the environment, either external or internal, may be instrumental in inducing permanent germinal modifications in organisms.

A third explanation of the cause of variation is embodied in the principle of *amphimixis* enunciated by Weismann, which states that through reproduction two different streams of germ plasm are united and in the resultant mixture new variations are apt to crop out. The Mendelian principles have shown how, during the crossing of species, there occur not only a combination of their germ plasms but also a reshuffling and realignment of the determiners for traits brought into the combination by the germ cells of the respective parents; this often leads to the emergence of new expressions of traits.

Finally it is a well-established fact that living matter tends to vary spontaneously in one direction or another. What accounts for this is as yet a debated question; but it is well known that every now and then modifications crop out in species, and these lead to permanent changes resulting in the establishment of new varieties, types, or species. These are now considered to be the discontinuous, germinal variations known as mutations. In some forms the spontaneous variations continue to appear generation after generation, irrespective of influences of the environment, proceeding in a definite direction, with the result that the modifications engendered may lead to the extinction of the species in question. Such variation is spoken of as *orthogenetic*, and it may be recognized in a host of organisms. In regard to the question of what accounts for these spontaneous variations, no adequate answer is yet possible.

In the final analysis we must admit that as yet it is impossible to explain fully the factors which cause variations. We do know that transformations originate and that on

occasion they lead to the origin of new types of organisms. Only those variations which are germinal in origin are salient for the creation of new forms, and the breeder who desires to modify or improve his stock must take advantage of them. As already mentioned, such variations are the discontinuous kinds, the so-called mutations, which appear suddenly and are either large or small, and either beneficial or detrimental; they are the ones which lead to permanent modifications in species. In those instances where the change is a detrimental one, the resulting individuals are removed quickly in the struggle for existence. On the other hand, where the modification is a beneficial one, it leads to the establishment of an improved variety or species, and this soon supplants the one from which it arose.

CHAPTER XV

Improvement of Organisms

NOW that we have discussed the basic principles involved in the operations of heredity and variation, it may be well to consider the various means utilized by geneticists and breeders in improving organisms, particularly those types that are of importance to man. Before this is done, however, we must focus our attention once more on the importance of the Mendelian principles of breeding and the more recent developments in cytology, particularly in regard to the chromosomal basis of heredity. Disclosures in these fields have revealed clearly that the characters of organisms in very large measure depend for their ultimate expression on the constitution of the germ cells which combined to produce the individuals. It has also been conclusively shown that often types which look alike externally differ considerably in their germinal make-up, and when they are utilized for breeding purposes they may give origin to distinctly different kinds of organisms. Therefore the knowledge gained from these fields has been of immeasurable value, since it has enabled the breeder to test out organisms carefully before putting his stamp of approval on them as being the possessors of certain traits that will not only breed true but will be transmitted to following generations. Needless to state, by this means a great deal of time, energy, and money have been saved when compared with the hit-or-miss methods in vogue prior to the advent of modern genetics.

Throughout this discussion of the improvement of organisms, we must bear in mind that even though the art of breeding organisms is an old one and has been practiced by man for countless generations, nevertheless it is only within comparatively recent years that the breeder has been able to

understand some of the basic facts underlying many of his practices. Although there exist some slight modifications in breeding methods in the animal kingdom and in the plant kingdom, yet the practices are so strikingly similar that they may be discussed under the same general headings.

Selection of Organisms

Before organisms are mated together for the purpose of producing offspring, the breeder must have well in mind the characters which he wishes to incorporate in his stock. Throughout the ages man has emphasized certain qualities in his animals and plants which he regards as absolutely essential, and these are the ones which the breeder must keep constantly in mind in his effort to establish new varieties, types, or breeds. It is true that often the characters which man has chosen for perpetuation would not stand the slightest possible chance of survival in the wild state; but in actual practice this has nothing to do with the question, for the practical breeder must take into consideration not what can survive effectively under the competitive conditions of nature but rather what the public desires in those plants and animals which it utilizes for consumption or pleasure.

In selecting organisms for breeding purposes most breeders rely on the eye for appraisal and choose largely those organisms which seem to meet the standardized demands. At the same time all the others are rejected. The guiding assumption behind this practice is that "like begets like"; in general this is a good assumption, for it has proved to be correct in most instances, and has led to the establishment of varieties and breeds embodying the desirable traits. The two chief kinds of selection resorted to by breeders are *mass selection* and *line selection.*

Mass Selection

Mass selection consists in choosing from a large number of individuals in each generation the most desirable types for

propagation. Some breeders, such as Hallett, believe in picking out the best types of organisms from individuals raised under the most suitable conditions. Other breeders, following the practice of Rimpau, are of the firm conviction that the finest results can be obtained only when the most superior forms selected from a group reared under poor conditions are chosen for perpetuation. Those who advocate the former method are of the opinion that the favorable environment gives the germinal entities for the desirable traits the fullest opportunity for development, thereby insuring the most complete heredity of the traits. On the other hand, Rimpau's adherents assume that where characters show up under the severest of environmental conditions they must have a permanent germinal basis that will cause them to breed true in following generations. Although mass selection, whether practiced by one or by the other group of breeders, has yielded highly beneficial results, it is not considered a trustworthy method. This is due largely to the fact that in mass selection the external appearance of the organism is relied upon almost exclusively; this may be grossly misleading, for, as has been pointed out under the study of Mendelism, the types selected for perpetuation may have covered-over recessive traits, which may crop out and interfere with the results hoped for.

Line Selection

Line selection emphasizes the individual rather than the group. The breeder studies the progeny of a single organism and very carefully selects for breeding purposes only those that meet the specific standards of quality. If the organism lends itself to propagation by means of self-fertilization, it then becomes possible to establish pure lines embodying the characters desired. As will be recalled, pure lines merely represent the separate traits that are common to the entire population to which the individuals belong. In those instances where the organism can be propagated through such asexual means as cuttings, buddings, runners, bulbs, tubers, and the like, separate lines of individuals known as *clones*

may be established, embodying the desirable characters. A similar condition is encountered where reproduction is through parthenogenesis. Where the individual cannot be propagated by self-fertilization, but only by cross-fertilization, then the same result may be accomplished through the establishment of a strain that is homozygous for the traits in question, and it will breed true in following generations. Many plants, irrespective of whether they are reproduced by self-fertilization or by cross-fertilization, lend themselves to further propagation through asexual means. Not so with the higher animals, where reproduction is exclusively through the sexual method of cross-fertilization, thereby making the problem a little more difficult than in the plant kingdom. Line selection emphasizes the inner, germinal nature of the individual rather than its outer, somatic appearance, which, of necessity, is the chief criterion relied upon in mass selection. From the genetic standpoint, line selection is really a more reliable experimental method than mass selection and leads to a greater degree of permanence in the quality of the particular breed or variety of organism.

Breeding for Type

After selecting the individuals, the breeder crosses them with a view to establishing a type or variety which will combine the desirable qualities for which the organisms were chosen. When the methods of breeders are examined, they are found to differ considerably in their approach to this problem. In order to appraise them, it becomes necessary to consider the principal practices of modern breeders in establishing and improving the different varieties of animals or plants.

Inbreeding

In order to fix types of organisms, inbreeding of related individuals has been practiced from time immemorial. At the present time it is a common method among all professional

breeders. The basis for this practice is the assumption that animals or plants coming from the same parental stocks will, as a rule, possess similar germinal traits; and by means of inbreeding these characters will become definitely established

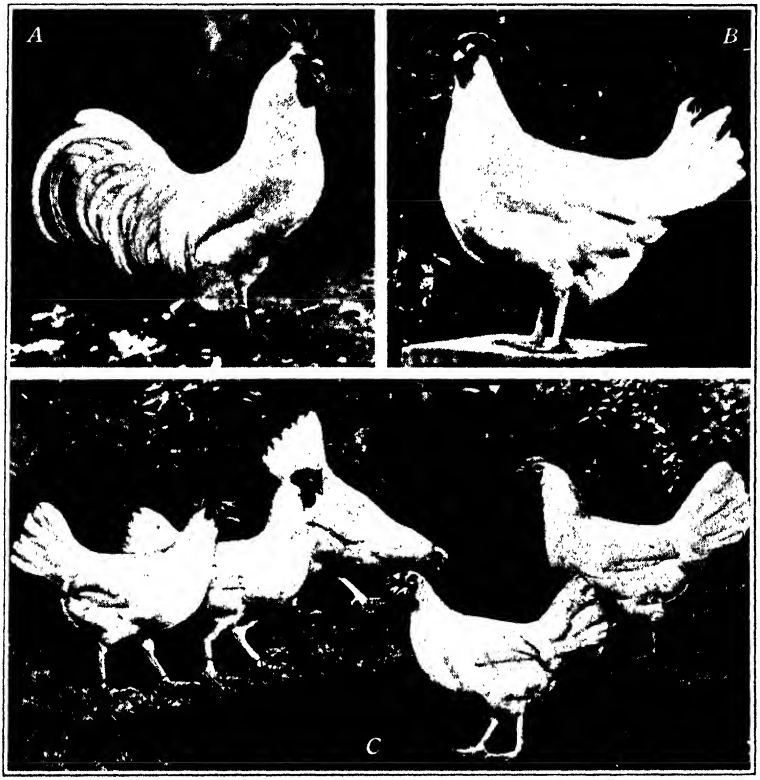


Fig. 95. Hanson's Pedigreed Leghorns

A, best rooster in America, selected by the *Breeders' Gazette*; *B*, foundation hen for a long line of hens, each averaging 300 eggs a year; *C*, 1930–1931 world's record egg-laying pen, laying 1542 eggs in 52 weeks. (Courtesy of J. A. Hanson)

and perpetuated in following generations. Sometimes breeders use the term *inbreeding* to designate only such crosses as those between sire and daughter, or dam and son, or brother and sister. In the human family, matings of this sort would be designated as *incest*. Where other relatives, such as cousins,

for example, are crossed, it is called *line breeding* in the lower forms and *consanguineous breeding* among human beings. All the cases cited are really different degrees of inbreeding; they must be practiced with a great deal of care in order to prevent undesirable covered-over traits from getting the upper hand and thereby leading to the gradual deterioration of the type, for occasionally, even under the best of conditions, inbreeding does cause deterioration and running out of a strain. Nevertheless, instances are on record where inbreeding and line breeding have been practiced on certain organisms for a great many generations without any harmful effects on the offspring; on the contrary, they have afforded the means of materially improving the strains. By prolonged and continuous inbreeding, all our *pure-bred* stocks of animals and plants have been established. Fig. 95 shows representatives of J. A. Hanson's pedigreed strain of Leghorn chickens, which have won world renown. The photograph labeled *C* is of the pen of five pullets awarded the world's record at the all-American egg-laying contest for 1930–1931. Mr. Hanson's prize Leghorns, developed on his famous poultry-breeding farm at Corvallis, Oregon, are the products of careful selection and inbreeding of blood lines.

Outbreeding

In outbreeding, often alluded to as *outcrossing*, two inbred individuals possessing similar characters but belonging to different strains of the same blood line are crossed, with beneficial results to the progeny. Breeders consider this absolutely essential for renewing vigor of strains which have run down or deteriorated through close inbreeding. It is a process often resorted to by practical breeders, and, as pointed out, it has helped to maintain as well as to reëstablish the vigor and quality in numerous inbred varieties of organisms.

In connection with the above discussions on inbreeding and outbreeding it must be admitted that there is considerable difference of opinion among geneticists in regard to the

effects of these practices on offspring. Castle (*Bi. 22*) recounts that such workers as Ritzema-Bos and Weismann, who inbred rats for a number of generations, came to the conclusion that close inbreeding was responsible for the deterioration in the size, vigor, and fertility of many of the offspring. This is also the opinion of Eaton (*Bi.* 62), who published the results of twenty-five years of inbreeding in guinea pigs. On the other hand, such investigators as Sewall Wright (*Bi. 211, 212*), with guinea pigs, Helen Dean King (*Bi. 127*), with rats, and William E. Castle (*Bi. 22*), with vinegar flies, found that very close inbreeding had absolutely no effect on the progeny. On the contrary, it led to improvement and uniformity in size and constitutional vigor. Moreover, these investigators also succeeded in showing that if unrelated individuals from different inbred families of the same type are crossed, the resulting offspring are even better specimens than those of either inbred strain. In practice, therefore, it has proved to be profitable to outbreed occasionally in order to increase quality and vigor.

Before dismissing the topics of inbreeding and outbreeding, mention must be made of their relationship to human welfare. In general, there has been grave objection to inbreeding of related individuals in the human family, because in many instances such matings have yielded deficient or defective offspring. This is not surprising when it is recalled that most human beings lack any adequate knowledge of their ancestry, and quite often related individuals may have covered-over traits in the form of recessives which may become intensified and expressed when such individuals marry and have children. Where the heredity is good and there are no undesirable covered-over traits, there is no objection to the intermarriage of such relatives. Frederick Adams Woods (*Bi. 210*) and Paul Popenoe (*Bi. 168*) have proved this to be true in royal family lines, where genealogies have been kept and consequently the heredity can be traced. But how many in the human family really know very much about their past heredity? So often there exist these recessive genes which do not

gain expression so long as they are united with genes for corresponding traits which either dominate or interfere with them. Only when the recessive genes have an opportunity to combine with similar ones so as to be present in homozygous fashion will they make their appearance. Such an opportunity is offered them when persons of near kin are allowed to marry. It is largely because of this fact that the ban on the marriage of immediate relatives has become an accepted custom in practically all civilized communities.

Pedigree Breeding

Pedigree breeding is the mating of pedigreed stock — that is, individuals whose heredity has become fairly well established through experimental methods — for purposes of insuring the production of desirable offspring. In recent years various agencies have been organized for the registration and certification of

FIG. 96. Effects of Pedigree Breeding[1]

A, Carmon, stallion of United States Government shed at Buffalo, Wyoming; *B*, Albion, one of Carmon's first sons; *C*, Defender, son of Albion

[1] From *Farmers' Bulletin 1167*. Courtesy of United States Department of Agriculture.

pedigreed animals and plants. Through such channels it is now possible to trace the heredity of pedigreed stock, so that when one buys such types he is assured of a certain quality which invariably manifests itself in the offspring. Because pedigreed stock has been produced experimentally and has proved its genetic value, it generally brings a much higher price on the market than nonpedigreed stock. Pedigree breeding emphasizes not only the external appearance of an organism but more particularly its internal germinal makeup, which makes possible the expression of the desired visible traits. Figs. 96 and 97 show the differences in the results obtained in horses where pedigree breeding was practiced and where no attention was paid to it. The results are overwhelmingly in favor of pedigree breeding.

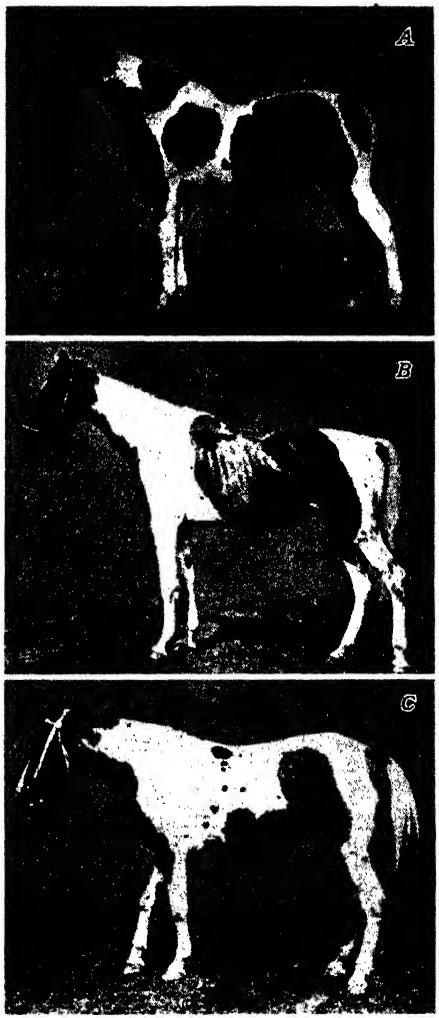


FIG. 97. Scrubs Breed Scrubs[1]

A, a spotted stallion extensively used as a sire and his daughters, *B* and *C*. Note that the characteristic spotting, shape of body, and poor posture present in the sire are inherited by the offspring

[1] From *Farmers' Bulletin 1167*. Courtesy of United States Department of Agriculture.

Hybridization, or Cross-breeding

Cross-breeding has been utilized by geneticists as a means of improving varieties and species; and in many instances it has led to the production of new types of value to man. Hybridization may be of two kinds: (1) *intraspecific*, consisting in the crossing of either different varieties or different lines within a species, or (2) *interspecific*, where independent species are crossed.

In the former case, where different lines or varieties within a species are crossed, it has been possible, through careful selection and mating among parents and offspring, to establish desirable strains for purposes of perpetuation. Such intraspecific crosses have, as a rule, led to the production of fertile offspring, and where care has been exercised in the future matings it has often resulted in considerable improvement in the particular strain or variety of organism. It must be remembered that, in reality, when all the modifications that are exhibited by the different lines within the species are examined carefully, they are found not to differ from those which are common to the entire species. Crossing and selection merely tend to segregate, recombine, and fix the different characters in distinct individuals, leading to definitely recognizable varieties, which are virtually of the nature of species. Inasmuch as practically all these varieties are fertile, the traits which they possess are likely to be perpetuated.

In the case of interspecific hybridization, where distinct species are crossed, improvements are often brought about in the immediate offspring; but in those instances where the species propagate through sexual reproduction, it is generally impossible to perpetuate the hybrids, because invariably they are sterile. Some plants, aside from reproducing sexually, may also be perpetuated through such asexual means as cuttings, graftings, bulbs, and runners, and where this is the case the improvements engendered through hybridization may be transmitted to following generations without diminu-

tion. In the higher animals asexual reproduction is impossible, so that the improvements manifest themselves only in the first generation. Occasionally some interspecific hybrids are

FIG. 98. Cross between Inbred Nana and Dwarf Strains of Corn

A, nana plants; *B*, plants of F_1 hybrids; *C*, dwarf plants. (Courtesy of Connecticut Agricultural Experiment Station)

fertile, and when this occurs the breeder may, by careful selection and inbreeding, produce strains which show certain characters in homozygous fashion, and these may become the foundations for new and improved forms of organisms. But

here the reader must be cautioned not to expect too much, for the characters entering such crosses behave in Mendelian fashion and tend to segregate out again in the offspring. Only when traits are combined in pure, or homozygous, fashion in the individual will they breed true. Where this is not the case, no lasting effects will ensue, and the resulting progeny will show resemblances to the parents in more or less Mendelian fashion.

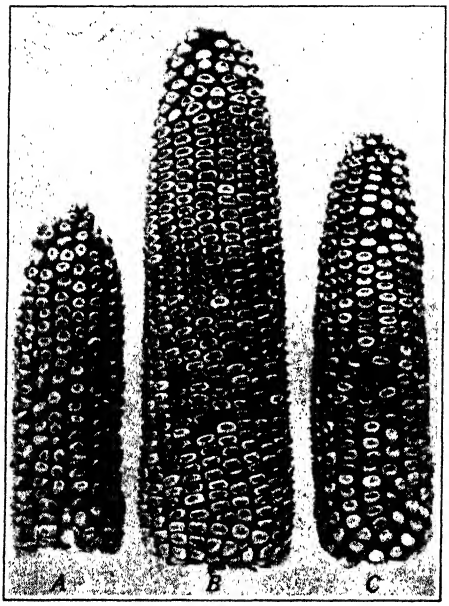


FIG. 99. Cross between Two Inbred Leaming Strains of Corn

A and *C*, ears of the two inbred Leaming strains; *B*, ears produced by the F_1 hybrids. (Courtesy of Connecticut Agricultural Experiment Station)

There exist many instances of hybridization where the hybrids show a greater size, yield, or vigor than the original parental stocks. This phenomenon is known technically as *heterosis*, and because it results in improving the hybrids, it has proved to be a valuable practice for the breeder to maintain separate stocks of the parental types for the express purpose of crossing them to produce marketable hybrids. Figs. 98 and 99 illustrate heterosis in corn. Note the larger and more prolific plants and ears in the F_1 generation.

Grading Up

Grading up means the mating of inferior-type organisms, known as *scrubs*, to *pure-breds* for the specific purpose of improvement. By repeatedly picking out for grading up those offspring that show the most desirable expression of char-

acters and utilizing the remainder for commercial or other purposes, an improved breed of animals will gradually be built up. This method has been utilized by many breeders to improve nearly all our domestic breeds of poultry, sheep, hogs, cattle, horses, and the like. Continued selection here has the effect of grading up the progeny and making it conform more and more to the desired type, embodying the characters for which the matings were planned. Fig. 100 shows the results obtained by the trained breeders of the United States Department of Agriculture in grading up poultry.

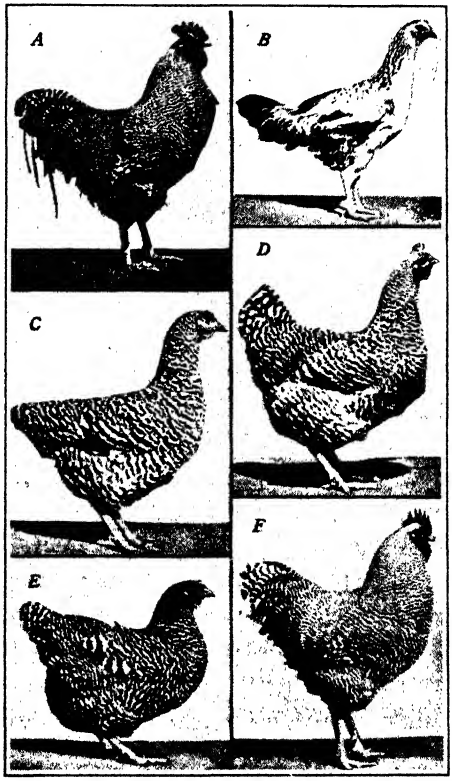


FIG. 100. Grading Up in Poultry[1]

A, standard-bred barred Plymouth Rock male; *B*, mongrel hen; *C*, grade hen, ½ blood; *D*, grade hen, ¾ blood; *E*, grade hen, ⅞ blood; *F*, grade cock, ⅞ blood

Mutations

In all organisms new modifications are constantly arising spontaneously. Some of these are merely the results of responses of bodily structures to environmental stimuli and are not inherited; others are germinal changes of the nature of mutations, and when these occur they may be handed on to future generations. Although this cannot be classified as any systematic method of breeding, nevertheless the breeder must

[1] From *Bulletin 905*. Courtesy of United States Department of Agriculture.

be everlastingly on the lookout for favorable mutations, because through the wise selection of them he may succeed in establishing new types, varieties, or species of organisms. All our domesticated breeds of plants and animals afford numerous examples of such mutational changes. It is apparent that a good many of these mutations undoubtedly would have had no possible chance of survival in a competitive state of nature, but under the artificial protection of man they have been nurtured along and helped to become established. There are some mutations which, irrespective of the environment, survive from their very inception and make for a distinctly different type of species. In the wild state these are the ones which would completely supplant many of the other types to which man has taken a fancy and which he has helped to survive. Often breeders find it of value to perpetuate the old and new types side by side. Sometimes, for some obvious reasons, it is of distinct advantage to perpetuate only the newly arising mutations; where this is the case, it is not long before the new completely supplants the old and affords the basis for all the mutations that follow.

The breeder has absolutely no control over mutations; they occur in a plus or in a minus direction, some improving the species and others handicapping it. Even though improvements may result, the breeder can never be certain when *reverse mutations* may arise, giving origin to preëxisting ancestral forms which were the forerunners of the improved types. What the causal factors are which account for mutations is a question which no geneticist can answer adequately. All that we know definitely is that mutations arise spontaneously in all organisms and that on occasion they lead to the emergence of new types possessing more desirable qualities than the old ones.

Breeding Methods in General

Because of their various modes of reproduction, plants afford more striking illustrations than animals of the practical applications of the laws of inheritance. Plants may be

divided into two large units, asexual and sexual. The sexual forms, in turn, may be divided according to pollination into four minor subdivisions: naturally selfed, naturally crossed, often crossed, and dicœcious.

In the *naturally selfed* group there are wheat, barley, oats, beans, peas, and tomatoes, and so on. Among the *naturally crossed* types may be included corn, rye, clover, and many grasses. In the *often-crossed* forms are found alfalfa, sorghum, and certain grasses. In the *dicœcious* group the sexes are separate, certain plants bearing male flowers, and others female flowers. The condition is similar to that found among the higher animals. Representatives of this group are hops, hemp, spinach, and asparagus.

As a rule, selection has been found to be of little value in asexually reproduced plants unless mutations occur. In certain of them, like citrus fruits and apples, mutations have appeared fairly frequently, and these have led to the establishment of some excellent new varieties. In others, like potatoes, for example, where mutations have been of rare occurrence, selection for the purpose of developing new varieties has proved of little value. In forms like potatoes, where propagation usually is through cuttings, the means utilized to improve the plants is by the sexual method of seed production. Since such seeds vary in their gene constitution, the seedlings which result from them are apt to show considerable differences. Potatoes are representative of an asexually propagated group illustrating the pure-line theory and the futility of selecting within a pure line.

The pure-line theory also has been demonstrated in naturally selfed plants. Here selection within a variety has proved to be of value only when the variety consisted of a population, that is, an aggregation of pure lines. If the variety happened to be a pure line, selection was of no avail. Hybridization could then be resorted to with a view of combining desirable factors in Mendelian fashion.

Selection has been found to be of real value in the crossed groups, for these consist of plants that are heterozygous and

differ in inheritance. In corn, for example, almost any type, except higher-yielding ones, may be obtained by continued selection. Yield, as a rule, is not affected favorably by selection, because corn carries so many unfavorable recessives that they may be readily concentrated into one plant so as to reduce its vigor. Heterosis, on the other hand, is of distinct value in corn-breeding, particularly when inbreds are crossed for first-generation hybrids and these express the favorable dominants of both parents. In fact, this genetically sound method of breeding is actually giving results where practically all others have failed.

In general, it may be stated that plants, because of their cheapness and the possibility of reproducing them in large numbers in the manner outlined above, lend themselves to much more economical handling by the breeder than do animals. While in the animal kingdom methods of reproduction are found which are in all ways comparable to those existing in the plant kingdom, nevertheless in all higher animals, especially those that are economically important, the dicœcious condition prevails, so that reproduction by the sexual method of cross-fertilization is the only one available. Moreover, the animals utilized by man are so expensive that it is out of the question to carry on any extensive experiments to test out animals for breeding purposes. Such a procedure becomes possible only in the lower forms, those that are of little or no economic importance and therefore are inexpensive. In the domesticated forms the breeder must obtain his results through a long period of grading up and inbreeding for type. In doing this he must be sure to pick animals that outwardly as well as inwardly appear to possess the characters which he desires to establish in his types, and to breed from them exclusively, in the hope of "fixing" the traits. By such a procedure he will build up slowly but surely more and more animals possessing the desirable characters. Even then he cannot be certain when unexpressed recessive genes may combine and assert themselves, leading to the production of inferior rather than improved types. These are the chances

which he must take where so much expense is involved. Of course improvement can also come through mutations, and when these present themselves the breeder, by carefully selecting his animals, may better his types considerably.

It is thus seen that animal-breeding has many more disadvantages than plant-breeding, and perhaps the greatest disadvantage of all is the great cost involved in keeping a considerable number of stock animals for breeding purposes. Because of this it becomes almost impossible to carry on extensive experimental breeding tests before utilizing animals for purposes of improving breeds or varieties. The best that the animal-breeder can hope for under the circumstances is to build up, over a process of many years, types which more and more conform to the standards for which he is breeding. He will thereby succeed in fixing a more uniform type or breed than otherwise; but he can never be sure that, when once obtained, his organisms will stay fixed, because of the difficulties which have already been pointed out. As in the plants, heterosis sometimes yields more vigorous and more desirable kinds of market animals, but it must be remembered that beyond the first generation these animals do not stay fixed, because Mendelian segregation asserts itself and the characters of the parents which happened to be combined in the hybrids separate out again in the formation of the proggeny. Because of this, many farmers and practical breeders find it of value to maintain separate strains of the parental types in order to cross them for purposes of yielding improved market animals.

CHAPTER XVI

Eugenics

IN RECENT years the human race has been the subject of study by many biologists, including geneticists. Although considerable progress has been made along the lines of human genetics, it must be realized that the human individual is not a favorable subject for genetic study, because he cannot be handled in the same way as the lower organisms. An animal of the highest degree of intelligence, man has likes and dislikes that interfere with the experimenter's desire to cross certain human individuals for purposes of observing the behavior and transmission of some of their traits. Man cannot be used in this manner for laboratory experimentation. Consequently, while much has been learned regarding the genetics of the lower forms, human genetics is still in its infancy, with tremendous progress to be made in future generations. It is true that we have accumulated a considerable amount of information regarding man's heredity, but this has come chiefly from studies of scattered genealogies, a few continuous records kept by various public institutions, and material collected by a very limited number of privately endowed agencies for the study of such problems. Therefore it is not at all surprising to find that geneticists are extremely cautious in speaking of the genetic factors which influence man during his development.

Since the latter part of the nineteenth century the biological and sociological problems growing out of considerations of human genetics have led to the establishment of the science of *eugenics*. Leonard Darwin (*Bi. 40, 41*), in speaking of eugenics, compares it to a signpost with three directions. One of these indicates the influence of heredity on the fate of nations. Another points to the rules that an individual

should strive to carry out in regard to parenthood, based on the laws of human heredity in so far as they are known. The third arm indicates the regulations to be adopted by society to encourage racial progress.

In recent times the subject of eugenics has been attracting the attention of large numbers of people. So important has eugenics become, especially during the last few years, that it has influenced state legislatures in enacting various laws directly affecting the welfare of the human family.

History of Eugenics

In ancient times there were many allusions to human heredity. Not only that, but in some of the recorded works which have been preserved from these periods there may be found certain laws and regulations affecting the welfare of the human family. While the ancients had little accurate knowledge concerning the laws of heredity and variation as these are now understood, still they deduced enough from observation to realize that "like invariably begets like," and therefore the regulations which they prescribed may be considered as systems of human betterment. The primary aim of many of the ancient systems of eugenics was to produce a race of physically perfect human beings. Whenever a child was born that was crippled or defective physically, the law prescribed the manner in which it was to be eliminated from the group. At the present time most of these regulations are regarded as revolting and inhuman, but it must not be forgotten that the chief purpose for which the laws were devised was to prevent the physically imperfect from coming to maturity and perhaps reproducing their kind. When this is remembered, it becomes apparent that these seemingly cruel practices really were effective eugenic measures for producing the desired types of human individuals best suited to the needs of the time.

The Greeks, who rose to eminent heights a few centuries before the Christian Era, had definite ideas regarding eugenics

and incorporated them into their regulations, to be followed by all citizens. Sparta and Athens constituted the two most important divisions of ancient Greece, and although the citizens of these localities had somewhat different ideals in regard to the types of individuals best suited to the needs of the respective states, nevertheless in both instances the methods employed for bringing about the hoped-for results were somewhat similar, and were incorporated in eugenic measures applicable to all members of the groups.

In Sparta a physically perfect manhood was the chief aim, so that everything was done to promote and foster the reproduction of those individuals best fitted from this standpoint. At the same time precautions were taken to hinder those individuals who were physically defective from having any offspring. The results speak for themselves; soon there was developed in Sparta a splendid population of individuals, with fine physiques, capable of enduring tremendous hardships, and fitted for the warlike purposes for which Sparta stood.

The Athenians, on the other hand, nurtured the intellectual achievements of man. Here philosophy, art, politics, and science were emphasized, and it was prescribed that only those individuals who were normal and gifted in these directions should perpetuate their kind. As a result of such a national policy, marriages were encouraged only between individuals of splendid family attainments, with the result that the offspring inherited those sterling qualities for which the citizens of Athens became famous. Furthermore, the Athenians decreed that the descendants of good families should use the utmost care in mating and refrain from polluting their blood with individuals of inferior stocks. History tells us that Athens rose to its greatest heights of achievement during the years between the sixth and the fourth centuries B.C. Galton (*Bi. 78, 79*) has pointed out that during this short period of time there were produced within the borders of the small territory of Athens, with an area no larger than the present state of Rhode Island, something like

twenty-five of the most illustrious men that the world has ever known.

As E. G. Conklin (*Bi. 27*), of Princeton University, points out, many students of genetics agree with Galton that the emergence of such a large group of eminent individuals was due, in large measure, to a rigid selection of mates, in whom were incorporated the attributes that cropped out in the offspring. It must be remembered that from both the social and the intellectual standpoint Athens was famous, and it attracted to its shores the most gifted individuals from the neighboring cities along the Mediterranean. These individuals, mated with the good native stock, made possible the emergence of a splendid group of citizens keenly interested in social, political, and intellectual advancement.

What accounted for the decline of Greece is hard to say. Opinion seems to be divided on this question, but there are many who assert that the decline was due, in large measure, to the fact that shortly before the Christian Era laws were enacted in Greece countenancing marriages between citizens and slaves. Inasmuch as most of the slaves were brought into Greece from the outside, following conquests, little was known of their ancestors. Even though many of the slaves appeared normal, yet they may have had defective parents, with the result that their germ plasms contained entities for traits that yielded similar defects in the offspring. Gradually a more and more deficient population came into existence. Since such individuals pay little attention to higher social and intellectual standards, it was not long before such standards were lowered and the race declined.

Following the decline of Greece and until the nineteenth century, there was little interest in eugenics. In fact, there are those who believe that the ideas promulgated interfered with rather than helped the eugenic ideal. People were imbued with the notion that it was their duty to lend a helping hand to helpless, defective individuals who could not care for themselves in the struggle for existence. Accordingly all sorts of agencies were established to aid human sufferers,

with the result that defective members of society were protected and helped to survive rather than eliminated from the race. No discrimination was made between those unfortunates who were the products of undesirable heredity (the result of defective germ plasm) and those who owed their malformations to accidental injuries or other harmful agencies of the environment. The ideal was to help everybody and for no one to question whether such charity was bringing about real improvement and permanent betterment within the human family.

In the nineteenth century modern eugenics had its inception, largely through the efforts of numerous scientists, notably Charles Darwin, Francis Galton, and Gregor Mendel. While Charles Darwin did not deal directly with eugenics, nevertheless the evolutionary principles which he discovered stimulated work along eugenic lines. As will be recalled, Darwin's contributions were chiefly along three main lines. In the first place, he accumulated a large number of facts in substantiation of evolution and showed how, through the agency of selection, especially natural selection, the various groups of plants and animals have developed to their present stages of complexity. In the second place, he showed that man, even though he has reached much higher levels of organization than the rest of the living kingdom, is also the product of evolutionary forces. In 1871 Darwin wrote *The Descent of Man* (*Bi. 37*), in which he indicated the various reasons for regarding man as a product of evolution from lower forms. Finally Darwin pointed out how man, through intelligence, has been able to direct evolution among many of our domesticated plants and animals, thereby being the real guiding force responsible for the emergence of new varieties, types, or species.

Since Darwin showed how man was able to do this with the lower forms, thinking people soon began to wonder whether man, by applying similar laws to himself, could not consciously direct his own evolution. This question was soon answered in the affirmative by Francis Galton (Fig. 101), a

cousin of Charles Darwin, who is credited with being the real founder of the modern movement of eugenics. Galton conducted numerous investigations along many different lines of human heredity, variation, and evolution. He pointed out that while man has been studying and directing the evolution of the lower organisms, he at the same time has completely ignored himself,— so much so that human defectives are increasing at such an alarming rate that, unless some efficient methods are devised for keeping them in check, they will endanger the welfare of the entire race. Galton, through his researches and publications on human heredity, attracted the attention of a considerable group of biologists, many of whom became so much interested in the various problems that they followed Galton's lead and undertook studies along different lines of human genetics. In the year 1883 the science of eugenics was definitely established by Francis Galton, who defined it as the "study of all of the agencies under social control which may improve or impair the inborn qualities of future generations of man either physically or mentally."

FIG. 101. Francis Galton[1]

At first little progress was made along the lines of eugenics, but with the rediscovery of the Mendelian principles of heredity at the beginning of the twentieth century, new impetus was given to the study of plant and animal genetics, including the genetics of man. Inasmuch as the Mendelian principles have been fully elaborated, it is necessary to point out only the salient facts applicable to the present discussion.

[1] Courtesy of *Popular Science Monthly.*

As will be recalled, the Mendelian principles of breeding disclosed an experimental method of studying the manner in which the hereditary traits of individuals behaved in crosses and also how such traits segregated out of crosses in later generations. Although studies along these lines have been confined chiefly to the lower organisms, nevertheless geneticists have also been able to apply them to human genealogies, indicating clearly that the same principles hold good for man. Because of this it has become possible for various investigators to study human heredity scientifically.

FIG. 102. Charles Benedict Davenport

In recent years the eugenics movement has become firmly established in various countries, especially in the United States and Great Britain. This has been accomplished largely through the establishment in these countries of numerous agencies for the purpose of studying the various factors affecting the welfare of man. In 1904 the American biologist Charles Benedict Davenport (Fig. 102) was called upon by the Carnegie Institution of Washington to organize a research station for the study of experimental evolution at Cold Spring Harbor, Long Island, New York. Although this station, known under the name of the Station for Experimental Evolution, was established chiefly for the purpose of studying problems of plant and animal evolution, nevertheless it soon included in its program various projects dealing with the evolution of man. In the year 1910 a distinct subdivision of the Station for Experimental Evolution was organized as the Eugenics Record Office, and this agency has been investigating human problems, chiefly along lines of heredity and evolution. Since its inception this organization has

diligently gathered the records of thousands of human families, and many of these have been the subjects of successful studies by numerous students. These studies have indicated that while human heredity may be somewhat more complicated than that of the lower forms, still it follows the same general laws applicable to the rest of the animal kingdom. As a direct result of the interest engendered by these eugenic researches during the present century, numerous civic organizations have been established throughout the world to foster and promote eugenic knowledge among the laity. In England the Eugenics Education Society (now Eugenics Society) was organized shortly after the beginning of the present century under the capable leadership of Leonard Darwin (Fig. 103), the son of Charles Darwin; this organization now occupies one of the leading positions among the scientific societies of Great Britain. In the United States the American Eugenics Society was organized in the year 1922, and, like its sister organization in Great Britain, it is the great national agency for the dissemination of such eugenic knowledge among the public as will lead to social betterment. Moreover, since the beginning of the present century three International Congresses of Eugenics have been held for the express purpose of discussing the numerous advances in the field of eugenics throughout the civilized world. The first of these was held in London in 1912 and was presided over by its first president, Leonard Darwin. The second was held in 1921 in New York

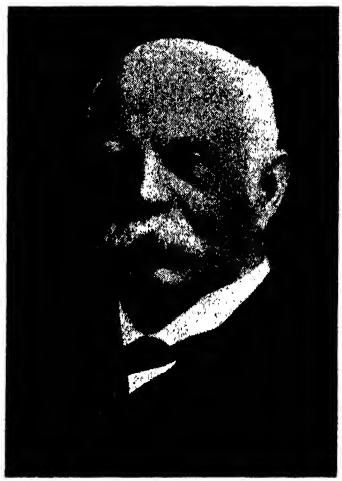


FIG. 103. Leonard Darwin[1]

[1] From *Eugenics, Genetics and the Family*, Vol. I. Courtesy of Williams and Wilkins Company, Baltimore.

City under the able leadership of its distinguished president, Henry Fairfield Osborn (Fig. 104), former head of the American Museum of Natural History. As one of the direct outgrowths of this second congress may be mentioned the establishment of the American Eugenics Society. In the summer of 1932 the Third International Congress was held, also in New York City, and this was presided over by its president, Charles Benedict Davenport. The various exhibits and scientific contributions of the delegates participating in these sessions have been incorporated into volumes and published as separate proceedings of the various congresses. These afford a permanent record of the progress which has been made in the study of the factors that operate toward improving or impairing the welfare of the human family.

The Basis of Eugenics

The science of eugenics rests largely on the fact that the human being is an animal, subject to the same laws and principles that govern the rest of the animal kingdom. Although most people of the present generation take this fact for granted, yet it must not be forgotten that until comparatively recent times the human species considered itself distinctive, really in a class by itself, and not subject to the same laws that apply to the lower animals. Therefore, while man was willing to apply the principles of heredity and variation to the breeding of better types of other organisms, at the same time he completely ignored himself and failed to recognize that, in common with the rest of the organic world, he is affected by the factors and forces which influence all living species. This attitude has been responsible for the fact that the human family has grown in a rather hit-or-miss manner; where the mating has been good, desirable offspring have followed, but where the mating has been bad, undesirable offspring have resulted. In many instances, even though the immediate parents did not seem to have any visible undesirable traits, it has been shown that they were the possessors

of covered-over recessive genes for defective traits which, on combining during the process of reproduction, led to the establishment of the homozygous condition and thereby gave origin to progeny with undesirable characters.

Since the middle of the nineteenth century biologists have succeeded in showing that from a biological point of view man is an animal. Not only that; it has been established that modern man in his development has undergone an evolution from the lower forms. Students of the problem consider man as belonging to the order of mammals known as Primates and as related particularly to such higher apes as the gorilla and the chimpanzee. Fig. 105 shows the evolution of man and his relationship to the apes. While there is considerable controversy as to whether man emerged from some primitive ape-like ancestor or whether man and the modern apes are both independent offshoots from a common generalized ancestral stock, nevertheless all biologists are in agreement that man is an animal possessing the same attributes as the rest of the animal kingdom; therefore he is subject to the same fundamental laws of genetics that apply to them. It is true that man has progressed in his evolution considerably beyond the other animals, particularly in the direction of his mental capabilities; but, in spite of all this, man reveals his animal ancestry and animal characteristics.

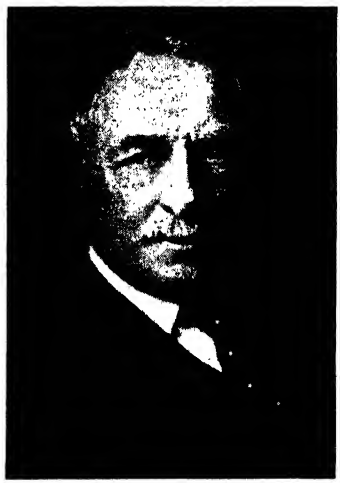


FIG. 104. Henry Fairfield Osborn

Man's mental evolution has been such that he has become the most intelligent animal in existence, and because of this it has become possible for him to apply the laws of genetics toward the breeding of better and more distinctive types of organisms. Since man has been able to do this with the lower

forms, it is only natural to ask whether, by applying the same laws to himself, he could not bring about similar improvements in the human species, so that the race of tomorrow will be better suited to the needs of civilization than the race of today. In other words, man, being the possessor of a greater

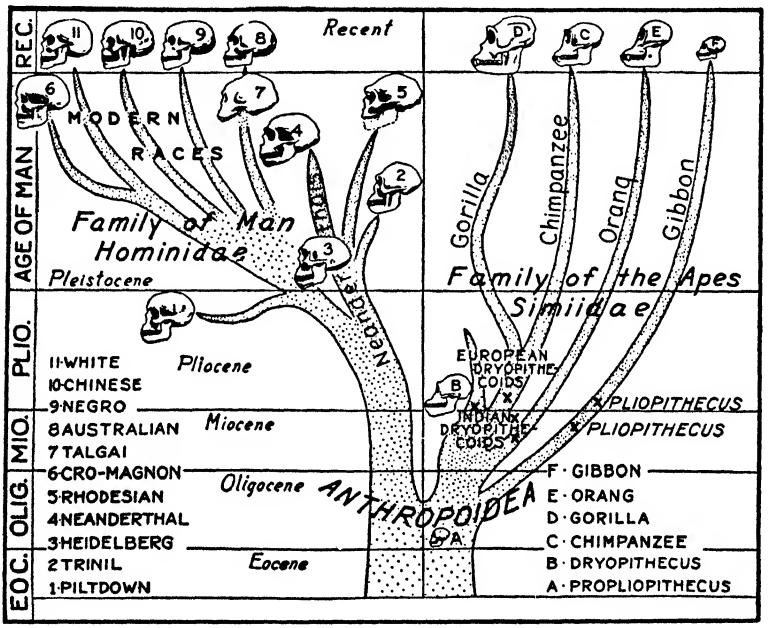


FIG. 105. The Evolution of Man and of Apes[1]

degree of intelligence, is in a position to become master of his own destiny and to consciously direct his own evolution, making possible not only the emergence of fitter types but also the elimination of those that he considers defective. This is exactly what man has been called upon to do with the lower forms, particularly those that are of economic importance. The modern student of human genetics is of the firm conviction that there is no logical reason to assume that this same thing cannot also be done for the human species.

[1] Courtesy of *Science*.

Family Studies

In this connection it is significant that since 1900, when Mendelism was rediscovered, certain family studies have been made which have shown that in the human individual many traits are transmitted, as in the lower plants or animals, in accordance with the laws of Mendelian inheritance. In reality, such studies on human families have afforded a scientific basis for the field of eugenics, inasmuch as they have indicated definitely that, as in the rest of the living kingdom, desirable or undesirable traits depend for their expression on the factors, or genes, carried by the chromosomes of the germ cells of parents which combine to form the new generation. In other words, in man, as in the lower organisms, there must be a hereditary basis for the emergence of the various traits of the offspring. Generally speaking, when there is a union of individuals with desirable traits the foundation is laid for the development of splendid citizens; but where the uniting individuals possess undesirable traits, the chances are that the union will lead to deficient or defective offspring. Thus the race is affected in one direction or another, and this is exactly what these family studies have indicated.

The Jukes

One of the earliest family histories to be worked out showing the effects of heredity is that of the Jukes. This is a family consisting largely of professional paupers and criminals who dwell in the state of New York. The history of the Jukes was first described by Dugdale (*Bi. 57*) in 1875; he studied nearly 1200 individuals and showed that among them there were 310 professional paupers; 440 physical wrecks from debauchery; 50 prostitutes; over 200 criminals, 7 of whom were murderers. There were also 300 deaths in infancy among them. Moreover Dugdale estimated, conservatively, that it cost the state of New York approximately $1,250,000 to care for the criminal, defective, and immoral progeny of this family.

In later years Estabrook (*Bi. 65*), special investigator of the Eugenics Record Office of the Carnegie Institution, Washington, reinvestigated this family, studying a total of 2094 individuals, the results of which he published in a monograph entitled *The Jukes in 1915*. This reveals the latest history of this family, and in all essential details it checks and

FIG. 106. A Jukes Dwelling[1]

agrees with the findings of Dugdale. The Jukes are a worthless, shiftless, and intemperate family that have given origin to a large number of defective progeny. Fig. 106 shows a typical Jukes dwelling, representative of the hovels in which many of the other Jukes reside.

The Zero Family

The representatives of the Zero family embrace a large number of professional beggars and criminals who lived chiefly in Switzerland. This family was described by Jörger (*Bi. 124*) as starting with a female who was a confirmed drunkard and who gave origin to over 800 descendants in six gen-

[1] Courtesy of *Eugenics*.

erations. Among them there were 102 professional beggars, 181 prostitutes, 107 illegitimates, and 54 inmates of almshouses. Over 80 of them were convicted of serious crimes, among them being 7 murderers. A conservative estimate places the cost to society for taking care of these defectives at well over a million dollars.

The Tribe of Ishmael

This is a family of paupers, beggars, feeble-minded, and immoral individuals dwelling chiefly in the state of Indiana. Undoubtedly most of them are the descendants of paupers, criminals, or prostitutes who were deported from England to the colonies during the seventeenth and eighteenth centuries. During the westward migration some of this stock settled in central Indiana, where they soon constituted some four hundred interrelated families. Estabrook (*Bi. 66*), who studied and described this tribe, estimated that at present their descendants must number close to ten thousand individuals, distributed mainly over the states of Indiana, Illinois, Ohio, Kentucky, Iowa, Michigan, and Kansas. All through this strain the traits common to the family reveal themselves, there being among them any number of paupers, beggars, thieves, prostitutes, and shiftless individuals who are constantly roaming from one place to another. They have filled almshouses, penitentiaries, reform schools, and houses of refuge, and have cost the various states in which they have settled tremendous sums of money to take care of the degenerate offspring produced by them.

The Kallikaks

One of the most interesting family histories ever traced is that of the Kallikaks, worked out by Goddard (*Bi. 90*). It so happened that Goddard, when he was superintendent of the Vineland School for the Feeble-minded at Vineland, New Jersey, became interested in a little girl, Deborah Kallikak, who was an inmate. In an effort to evaluate the rôles played by the factors of heredity and environment in development,

Goddard took Deborah Kallikak into his own home and subjected her to the same treatment and influences as his own child. While his own offspring progressed normally, Deborah remained defective and could not go beyond a certain age level in her mental development. Inasmuch as the institutional records revealed that a number of the Kallikaks had been inmates of the Vineland school, Goddard became interested in the family and undertook the task of tracing its history. The study involved not only a great deal of time but much expense and had to be made by many workers in numerous states. The history of the Kallikaks was traced back for four generations beyond Martin, the young man with whom our story starts. Goddard found that the ancestors of Martin were honored and respected individuals of good English blood, who had settled in the colonies. Martin therefore came of good family. At the beginning of the Revolutionary War this young man had an illegitimate son born of a feeble-minded girl. After the Revolutionary War Martin Kallikak married a girl of good stock, and from this union a legitimate son was born. Goddard and his associates traced the offspring from these two lines for approximately five generations. From the illegitimate mating of Martin and the feeble-minded girl, there were something like 480 individuals investigated. Of them, 143 were definitely feeble-minded, and only 46 apparently normal, while the rest were unknown or doubtful; 33 were sexually immoral, mostly prostitutes; 24 individuals were confirmed alcoholics; 3 were known to be epileptic; 3 were desperate criminals; 8 were keepers of disreputable houses. Also 33 of the children of this line were illegitimate, Deborah Kallikak being one of them; and 82 offspring died in infancy.

From the legitimate mating of Martin, 496 individuals were traced. Here only 15 children died in infancy; there were no epileptics or criminals; only two were known to be alcoholics; and only one known to be sexually immoral. The rest of the legitimate children attained prominence in all walks of life, becoming successful doctors, lawyers, judges, educators,

traders, and landholders. Nearly all the legitimate offspring of Martin Kallikak were normal men and women prominent in every walk of life.

The Edwards Family

The history of this family shows how good traits may be transmitted generation after generation, accounting for normal, wholesome, and gifted individuals of great benefit to civilization. This family was traced to the Puritan Jonathan Edwards, from whom, up to 1900, have come 1394 descendants, all of whom have proved to be worthy citizens, many have attained eminence in various walks of life. Among them were successful teachers, lawyers, physicians, statesmen, clergymen, business men, and so on. Moreover, the evidence indicates that not a single member of this family was ever convicted of a crime.

The Darwin Family

This is the famous English family which has been responsible for many eminent scientists for a number of generations, the greatest of whom was the distinguished evolutionist Charles Darwin. Those familiar with the history of science know that the father of Charles Darwin, Robert Waring Darwin, was himself an eminent physician, while his grandfather, Erasmus Darwin, was one of the great physicians and evolutionists of the eighteenth century. Charles Darwin's sons have been among the leaders in science of the present century, and one of them, Leonard Darwin, is an eminent authority in the field of eugenics. As will be recalled, in recognition of his work in this field Leonard Darwin was chosen president of the First International Congress of Eugenics. It must also be remembered that Charles Darwin's cousin, Francis Galton, who became eminent in many branches of biology, was the real founder of the modern science of eugenics. Fig. 107 is a chart indicating the matings between the Wedgwood, Darwin, and Galton families, responsible for numerous distinguished individuals prominent in science, among them being Charles

Darwin and Francis Galton. The black symbols represent individuals of marked scientific ability. Those indicated by R attained such distinction in their chosen fields as to merit their election as Fellows of the Royal Society of Great Britain (*Bi. 82*).

The Bach Family

Just as the Darwin family of England distinguished itself in science, so the Bach family of Germany attained eminence

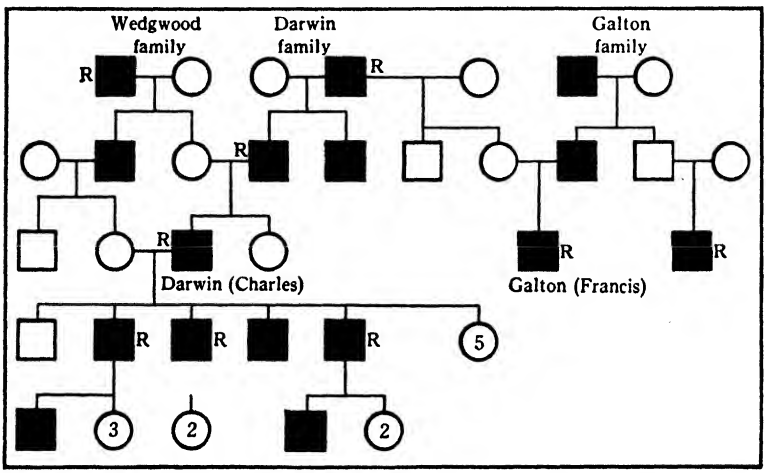


FIG. 107. The Ancestry and Kinship of the Darwin Family[1]

The black symbols indicate marked scientific ability. The letter R denotes a Fellow of the Royal Society. Figures in circles indicate numbers of daughters, if more than one. (After Gartley, courtesy of *Journal of Heredity*)

in music. The history of this family has been traced back to the sixteenth century, and it reveals that, generation after generation, good musicians made their appearance among them. In eight generations of the Bach family, 136 individuals were produced, 99 males and 37 females. Little is known of the musical attainments of the females, but over 50 of the males were splendid musicians and composers. The greatest of them all was Johann Sebastian Bach (Fig. 108), who lived from 1685 to 1750 and whose compositions for the organ have never been equaled.

The Need for Eugenics

From studies such as those indicated in the above family histories, as well as those related in Chapters XVII and XVIII, where specific studies in the heredity of human traits are given, it becomes apparent that there is need for eugenics. As was indicated in previous chapters of the volume, the development of all organisms, including the human individual, depends on both hereditary and environmental factors. Moreover, it must be remembered that for the best development both good heredity and good environment are essential. Genetic studies reveal that where there are bad factors no amount of good environment will make for any appreciable change in them. However, in such an environment some of the bad factors may not have an opportunity of gaining expression. Likewise, good factors in a bad environment may be suppressed or limited in their development. But even in the best environment there is little possibility for change of bad hereditary factors. For the emergence of favorable traits there must be present within the zygote the right combination of genes for such expressions. Therefore biologists believe that the factors of both heredity and environment are extremely important in development.

FIG. 108. Johann Sebastian Bach[1]

One often hears persons assert that it does not really matter from what source a human being is derived,— so long as the environment which surrounds him is favorable, the end result

[1] Taken from *A History of Music in Pictures*, edited by Georg Kinsky, published by E. P. Dutton & Company, New York, and Griffel Verlag, G.m.b.H., Germany.

will be desirable. While no eugenist ignores the environment, yet he is convinced that it alone is ineffective in producing the hoped-for results in those instances where the heredity is deficient. Usually a bad social environment is the product of individuals possessing bad heredity, and a good social environment is the creation of those with good heredity. In a good environment those with bad heredity have been found to benefit but little, being incapable of taking advantage, to any extent, of the opportunities afforded. This has proved to be true in so many cases that it may be asserted most emphatically. Children from defective strains have been taken into the homes of splendid people and raised under the best of circumstances, but in spite of it, in many instances, the hereditary tendencies of these children soon asserted themselves so as to reveal clearly their ancestral deficiencies. The case of Deborah Kallikak may be cited as a good illustration of the point in hand.

Not only does a study of these families indicate the need for eugenics but, as will be recalled from the discussion in our first chapter, the need of eugenics is apparent from the standpoints which were there outlined for genetics: education, sociology, and civilization. People must be awakened to the gravity of the situation and then must apply the necessary remedies if conditions are to be bettered. Students of eugenics have been pointing out that two developments have been in progress side by side which are most alarming from the point of view of the future welfare of the human species: one is the declining birth rate among the normal and superior stocks, and the other is the relatively rapid increase of the abnormal and defective stocks. These assertions are not mere guesses; they are based on the actual facts as revealed by the studies of competent students. In an interesting article R. Homer Gleason (*Bi. 85*) ably summarizes the facts in this connection as follows:

But even now we have figures which are shocking to one's optimism when they are understood. Every 7.5 minutes 22.5 babies are born in the United States. On the basis of carefully gathered

statistics we know that only one will attain a high grade of intelligence, 1.5 will be potentially criminal, 7.5 will be morons, and 12.5 will be average.

Here is another way of looking at the situation. Our white population numbers approximately 100,000,000. Classified according to the United States Army standards and records of intelligence, 7,100,000 will rate as very inferior; 17,000,000 as inferior; 23,800,000 as low average; and 27,100,000 as above average. Twelve million will rate as above high average; of this number only 4,000,000 will rate as superior. Keep in mind that the number of very inferior is almost double the number of the superior, and that those who rate as inferior are more than twice as many as those who rated above high average but not superior. Now in connection with these figures compare the size of families in the various groups. It is safe to say that college graduates represent the best of life—mentally, physically, and temperamentally. Not all our best people are college graduates, nor are all college graduates among our best. But statistics concerning college graduates may be fairly accurately applied to those groups which rate as above high average. College graduates who marry have an average of one child per family; but 25 per cent do not marry, 40 per cent of college women do not marry, and 46 per cent of women in Who's Who do not marry. On the other hand, the group which rates the lowest in intellect has an average of eight children per family. Or, if you wish to put it on the basis of pairs of adults rather than families,—for many of the worst are not allowed to marry or able to reproduce, —we discover that the birth rate drops from more than four per pair of adults in the worst class to less than one per pair of adults in the best class. Now put the figures together: The worst class, already nearly twice as large as the best, is producing four times as many children for each pair of adults.[1]

The increase in the abnormal and defective population has thrown a tremendous burden on modern society, and concretely this has manifested itself during the last few years in the ever-increasing sums collected from the public in taxes to pay for the maintenance of the defective population. In the final analysis, these burdens are shouldered largely by our normal and superior stocks; and since these are not even

[1] R. Homer Gleason, "Wanted: a Better Humanity," *Eugenics*, Vol. 2, No. 8 (1929), pp. 9–10.

repopulating themselves, it means that every normal child of the future will have to face even greater burdens and responsibilities than the child of the present. Every thoughtful person must face these facts squarely and realize the need of eugenics for bringing about a changed attitude which will lead civilization in the reverse direction,— increasing the normal and gifted population and at the same time decreasing the abnormal and deficient population.

The Aim of Eugenics

The aim of eugenics is just what has been emphasized in the closing sentence of the last paragraph. Through various means — educational, civic, or otherwise — every eugénist is attempting to develop a social consciousness which will result in the humane treatment and eventual elimination of the hopelessly crippled, diseased, and mentally incompetent and at the same time increase the number of children produced by the normal individuals constituting our present civilization. The eugenist, contrary to the opinion so often proclaimed by many popular writers and orators, does not aim to establish a new race of supermen but desires, rather, a race of sturdy, intelligent, and healthy individuals similar to the large proportion of the human family now in existence.

Most eugenists believe that the factors of heredity and environment are both essential to the development of the physical and mental traits of human beings. Scientific studies have indicated, however, that fundamentally the environment acts largely on those hereditary capacities brought in by the germ cells which unite to form the new individuals. Eugenists therefore stress the importance of heredity, believing that this is the primary factor, although not the exclusive one, in the evolution of the race. Eugenists are of the opinion that, by a sensible application of the laws of biology and health, man may chart those lanes along which he desires to travel, perpetuating the stable and wholesome traits inherent in him and, at the same time, eliminating those traits which produce misery, suffering, and waste.

CHAPTER XVII

Problems of Eugenics — Physical and Physiological Traits

FROM the standpoint of eugenics all factors connected with the human individual are of importance. The human being of today is what he is because of certain national, social, or personal factors which have been of direct influence in molding him. Needless to state, it is impossible to deal with all these factors in the confines of one or two chapters. The best that we can hope to do is to consider the more obvious ones and not only to point out the manner in which they are transmitted but, wherever possible, also to indicate how they have operated toward the evolution of modern man. It has seemed wise to segregate the various items into two units, "Physical and Physiological Traits" and "Mental Traits and Social Factors." These will be dealt with separately in distinct chapters, the former traits being discussed in the present chapter, and the mental traits and social factors in the following chapter. Even so, these discussions will of necessity have to be limited. For fuller treatments of the various aspects of human heredity the reader is referred to items *Bi. 14, 83,* and *167* of the Bibliography.

Although the social factors may be segregated from the others, yet it must be kept in mind that the physical, physiological, and mental characteristics of the human individual are all interrelated to such a degree that it is difficult at times to separate them distinctly. Certain physical structures readily obvious to everyone may depend for their expression on some physiological reactions, and likewise certain mental traits may be the result of both physical and physiological transformations. This must be kept in mind at all times, even though, for purposes of presentation, the physical and physio-

logical traits are segregated from the mental ones. In the present chapter the transmission of certain of the more obvious physical and physiological traits of the individual will be considered, such as those of the body, limbs, skin, eyes, hair, ears, mouth, and blood. Also the interesting topic of the heredity of certain diseases will be elaborated.

Bodily Characteristics

Under this heading may be grouped such obvious traits as stature, body build, and abnormalities of the anterior and posterior limbs.

Stature

At the present time stature is believed to be a composite character dependent for its expression on the action of numerous genes. Stature was one of the earliest of human characters to be studied by Francis Galton (*Bi. 81*). Although at first it was regarded as a simple trait, later studies have shown that it is a rather complicated character and that not all the details of its inheritance are known. Davenport (*Bi. 45*), who studied the trait, is of the opinion that the height of the individual is determined by the length of the component parts of the body, —head and neck, torso, and legs. He believes that there are independent factors which control the length of these particular regions. Other investigators are not in agreement with this opinion; instead, they are inclined to the belief that there are certain general genes which affect growth uniformly in the various portions of the body. As a rule the offspring of tall parents are tall, invariably being above the average in height. When one parent is tall and the other short or when both of them are short, some tall individuals may develop. It seems evident that in crosses between short and tall individuals tallness acts as a recessive and shortness as a dominant. Inasmuch as stature is a composite character dependent for its expression on a number of genes, the height of the individual will depend on the number of factors for tallness and dwarfness present in the growing individual.

Body Build

By body build is meant the size, shape, and weight of the individual. In accordance with these characteristics, human beings are classified as chunky, stout, or slender. The development of fat may further affect the size, build, and weight of the individual. Most students of human genetics are of the

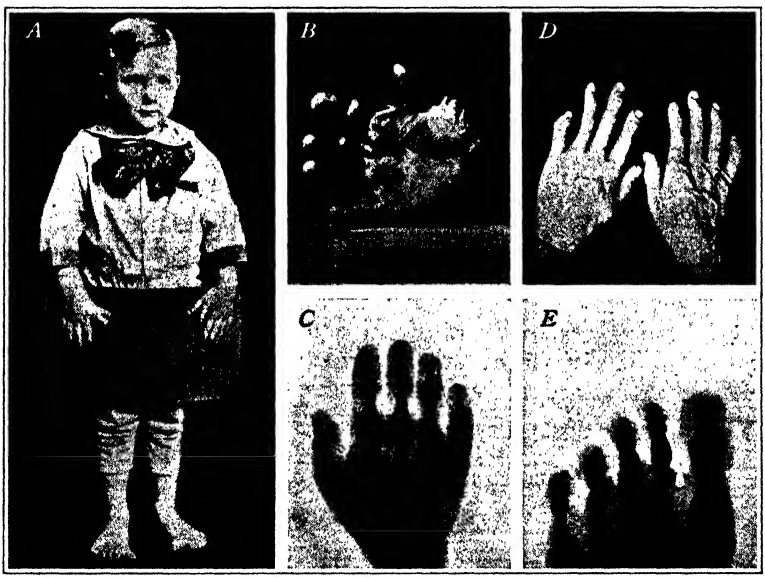


FIG. 109. Limb Abnormalities in Man

A, polydactyly; *B*, brachydactylous hand; *C*, X ray of brachydactylous hand; *D*, symphalangy; *E*, zygodactyly. (*A*, *D*, and *E*, courtesy of *Journal of Heredity*; *B* and *C*, courtesy of *Journal of Genetics*)

opinion that body build, like stature, is not a simple character, but rather a composite one, depending for its expression on at least two or more pairs of factors. In general, studies reveal that the factors for stoutness tend to dominate those for slender build.

Limb Abnormalities

In connection with the anterior and posterior limbs, a number of mutational modifications have appeared which

are classified as abnormalities or defects. Most of them appear to behave as simple dominants. Among these may be mentioned the following: (1) *polydactyly*, a condition in which more than five fingers or toes are produced; (2) *brachydactyly*, a condition where the fingers or toes are considerably shortened owing to the fact that two joints are developed instead of three, as in normal digits; (3) *symphalangy*, a condition in which some of the fingers become stiffened owing to a fusion of the bones at one of the joints; (4) *zygodactyly*, a fusion of the skin between neighboring fingers or toes, producing a webbed condition; (5) *lobster-claw*, a condition in which the thumb and little finger on the hand, or the great and little toes on the foot, are developed excessively and at the same time the intermediate digits are reduced considerably. Persons portraying such abnormalities as *zygodactyly* are referred to as web-fingered or web-footed individuals. Zygodactyly is now distinguished from *syndactyly*, in which there is a fusion of the bony elements of the neighboring fingers or toes that portray the webbed condition. Fig. 109 shows some of these abnormalities of the fingers and toes.

The Eyes

The heritable characters of the human eye have been studied for a considerable period of time. In particular, the inheritance of eye color and of various eye abnormalities or defects has been traced by geneticists.

Eye Color

The color of the eye is undoubtedly due to the interaction and coöperation of a number of genes. Eye color depends for its expression on the presence or absence of different degrees of the brown and dark pigments, giving origin to shades varying from pure brown through a number of intermediate gradations ranging from dilute brown to pure blue. The dark pigments are always found in the inner layers of the iris, whereas the brownish pigments occur in the outer layers.

The thickness and texture of the outer coats of the eye as well as the amount of brown pigment present determine the degree of blue coloration which may be noticed. Where no granules of pigment are present in the layers of the iris, the eye appears red because of the fact that the red blood coursing through the blood vessels of the inner walls of the eye becomes observable. This condition of affairs is discovered in *albinos*. Where both parents possess pure-blue eyes, all the offspring will be blue-eyed; where both parents have pure-brown eyes, all their children will have similar brown eyes. On the other hand, when the eyes of the parents are not pure with respect to brown or blue, but instead are admixtures of the two colors, then there are various possibilities for the expression of eye coloration, depending on the number of genes for brown and blue eyes brought in by the gametes that combined to give origin to the progeny. Gray eyes, as well as different shades of blue, are the resultant products of the masking of the dark inner-coat pigments by the degree of thickness of the outer layers of the iris. Green eyes result from a covering over of the inner dark pigments by yellowish ones occasionally found in the outer regions of the iris. When eye color was first investigated, it was thought that it was a simple Mendelian character in which a single pair of allelomorphic factors were involved, — those for brown and blue eyes, in which the former dominated the latter. Later studies, however, have shown this character to be more complicated and dependent for its expression on a number of genes.

Eye Defects

In connection with the eye numerous abnormalities and defects have arisen as mutations which have proved to be inherited. Some of these are distinctly sex linked in transmission, appearing in males and covered over in females. Some good examples of these are the following: (1) *night-blindness*, a condition where the individual is unable to see in faint light; (2) *color-blindness*, or the inability to distinguish certain colors; (3) *Leber's disease*, a malady caused by the

degeneration of the optic nerve, leading eventually to blindness. Although there may be many different types of color-blindness, one of the most common forms is that in which the individual is unable to distinguish red color from green. The inheritance of this or similar types of color-blindness has already been indicated in Figs. 75 and 76 of Chapter XII.

Aside from the sex-linked eye defects mentioned, other abnormalities of the eye have been shown to have a hereditary

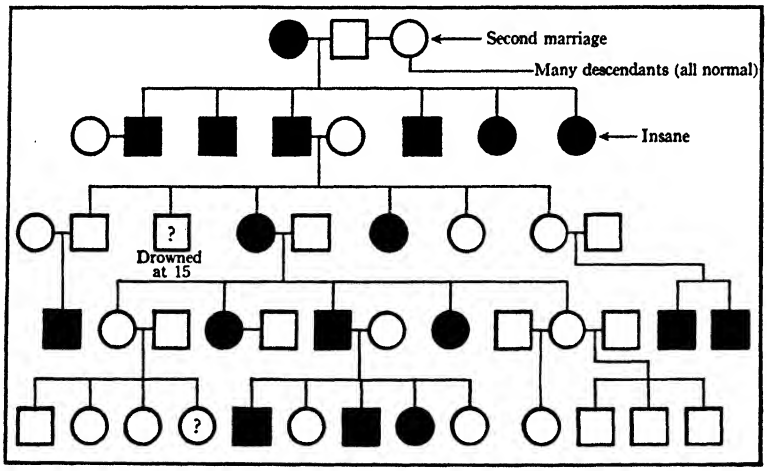


FIG. 110. Dominant Inheritance of Glaucoma

This chart traces the defect through five generations. Squares represent males and circles females. The dark symbols indicate affected individuals. (After Carris, courtesy of *Journal of Heredity*)

basis, being transmitted after the manner of either ordinary dominants or ordinary recessives. Among these may be enumerated the following: (1) *Retinitis pigmentosa* is a condition where pigment is deposited in the blood vessels of the retina. The disease invariably comes on in youth, interfering greatly with sight, and it continues to progress until about the age of forty, when it produces blindness. In some families the condition seems to be dominant; in others it has proved to be recessive. (2) *Ophthalmoplegia* is an abnormality characterized by paralysis of some of the eye muscles. It behaves as a simple recessive in heredity, coming out especially in cousin mar-

riages. (3) *Glaucoma* is a condition of increased pressure within the eyeball caused by an obstruction of the lymph drainage canal, which interferes with the normal circulation of lymph through the visual organ. Occasionally glaucoma may be caused through infection, but in a good many instances the defect is a hereditary one, transmitted in certain families. Indications are that sometimes the trait behaves as a dominant (Fig. 110) and at other times as a sex-linked recessive.

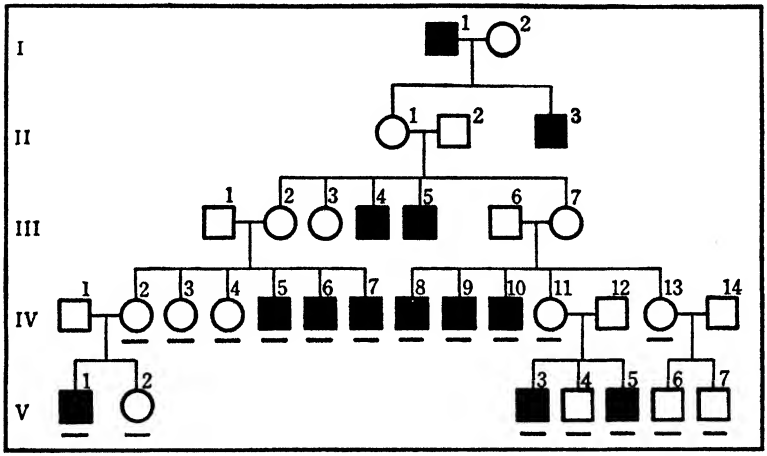


FIG. 111. Sex-Linked Inheritance of Myopia

Squares represent males and circles females. The darkened symbols indicate myopic individuals, and those that are underlined are the individuals who were examined. The information regarding the others was obtained from relatives. (After Worth, courtesy of *Genetics*)

(4) *Aniridia* is a partial or complete absence of the iris of the eye. In most instances the trait behaves as a simple dominant. (5) *Cataract* is a condition where the lens of the eye or its surrounding regions become opaque, a gradual and progressive condition leading to blindness. There are a number of types of cataract, and most of them seem to be inherited as dominants. (6) *Myopia*, or nearsightedness, seems to be inherited as a simple recessive in some families, while in others it appears to behave as a sex-linked trait (Fig. 111). (7) *Hyperopia*, or farsightedness, is a more complicated phenomenon, which also appears to have a hereditary basis. However, not

all the factors in regard to its transmission are as yet completely understood. In some families this trait seems to behave as a recessive, while in others it behaves as a dominant. (8) *Retinal detachment* is a condition in which the retina seems to become separated from its underlying membranes. The inheritance of this defect does not seem to be uniform; in certain families it behaves as a dominant, in others as a recessive, and in still others as a sex-linked character.

The Skin

Numerous traits of the skin, such as texture and coloration, have been studied from a hereditary standpoint.

Texture of Skin

Certain types of skin abnormalities have been shown to have a hereditary basis. Among them may be mentioned the following: (1) *Ichthyosis* is a condition where the skin becomes thickened, dry, and scaly in appearance. The characteristic seems to be dominant over normal skin. Moreover, indications are that in the homozygous condition the abnormality is lethal, causing the death of the individual. Sometimes ichthyosis behaves as a sex-linked character, showing up in the male and not in the female. (2) *Keratosis* is a thickening of the skin on the palms of the hands as well as on the soles of the feet, invariably behaving as a sex-linked recessive. (3) *Cutis laxa,* or "rubber skin," is a condition in which the skin has become loosened, so that it may be pulled out from the body to a distance of a number of inches. The indications are that this characteristic of the skin behaves as a simple Mendelian dominant.

Skin Color

Although skin color was at first considered to be a rather simple hereditary trait, subsequent studies have revealed that it is considerably more complex in its make-up. Color differences of the skin of the white race have been shown to be due usually to single pairs of factors, those producing dark

skin dominating over those for lighter skins. On the other hand, the crosses between the black and the white races have indicated definitely that at least two pairs of cumulative factors are involved. Undoubtedly there may be other minor modifying genes, but the two cumulative pairs which have

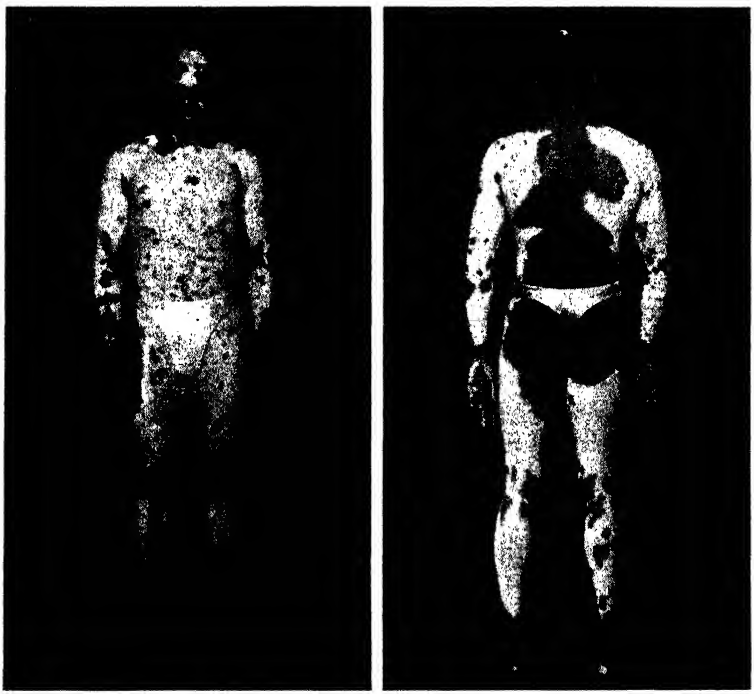


Fig. 112. Piebald Individual, Front and Back Views

The piebald trait is inherited as a simple dominant unit character. (Courtesy of Clyde E. Keeler and *Journal of the American Medical Association*)

been mentioned previously in Chapter XI, where such crosses between Negroes and whites were considered, appear to be the ones of primary importance. As will be recalled from the discussion in this previous chapter, the presence or absence of these cumulative factors determines the color of the skin of the individual, which may range from coal black through intermediate shades of brown to pure white.

Piebald Skin

In crosses between Negroes and whites an unusual condition of skin coloration often originates, in which there is spotting, owing to the fact that the dark pigmentation becomes concentrated in certain patches, leaving the other areas of the skin entirely devoid of any coloration. This is spoken of as the *piebald* condition (Fig. 112), and wherever the heredity of the trait has been traced it has been found to be dominant over uniform coloration. This was the conclusion reached by Simpson and Castle (*Bi. 189*), who studied the character in 1913. Recently Clyde E. Keeler, of Harvard University, reinvestigated the inheritance of this trait in the family and relatives of the individual shown in Fig. 112. In the July 21, 1934, issue of the *Journal of the American Medical Association* Keeler asserts that this individual belongs to a family who in four generations have given origin to twenty-five piebald Negroes out of a total of eighty-five individuals. Moreover, in ten matings of piebalds with normals there have been produced twenty-four piebald and eleven normal offspring, revealing that the piebald trait is inherited as a simple dominant unit character.

The Hair

The human hair also has been the object of considerable study by geneticists. Only a few of the more obvious characteristics of the hair can be considered here.

Type of Hair

The kind of hair possessed by an individual — curly, wavy, kinky, or straight — is determined by the degree of flatness or roundness exhibited by the cross sections of the independent hairs. Straight hair is found to be circular in cross section, while curly, wavy, or kinky hair is flattened. As a general rule, the flatter the cross section, the curlier the hair, and vice versa the rounder the cross section, the straighter the hair. Although many geneticists consider the curly trait dominant over the straight one, yet not all the details in

regard to the heredity of the character are known. The probability is that type of hair is dependent for its expression on the interaction of a number of factors.

Baldness

There are a number of distinct degrees of baldness, varying from a rather small spot to a total absence of hair. This latter condition is rather uncommon. Although many theories have been put forth to account for baldness, such as disease, lack of circulation of the scalp, pressure on the scalp due to tight hatbands, yet Dorothy Osborn's studies (*Bi. 157*) have indicated that most cases of baldness are inherited. Furthermore, these studies have revealed that baldness is a *sex-limited trait*, being dominant in males and recessive in females. It takes a single dose of the factor to produce baldness in the male and a double dose to produce it in the female. A sex-limited trait must not be confused with a sex-linked one. As pointed out in Chapter XII, when a trait is sex limited its genes are carried within the autosomes and the character usually expresses itself in either one or the other of the sexes. Most of the sex-limited traits are mainly the secondary sexual characters which have been described in Chapters V, VI, and VIII. Sex-linked characters, on the other hand, are produced by genes within the sex chromosomes. Ordinarily a single dose of the sex-linked gene is responsible for the trait in the male, and a double dose for its appearance in the female.

Hair Color

The color of the hair may vary considerably, being either blond or black or possessing shades in between these two and manifesting itself as different gradations of brown, chestnut, and red hair. While workers have been studying the inheritance of human hair coloration for a considerable time, yet not all the facts in regard to the development and transmission of this trait are known. Most investigators consider it to be a composite character in which at least two pairs of genes are involved.

The color of the hair is due chiefly to the two basic pigments, brown and red. In most hair some of the brown pigment is invariably present, whereas the red pigment occurs only occasionally. The presence or absence of these pigments and the respective amounts of them existing within the hair determine, in large measure, the shades which become visible to the naked eye. When brown-pigment granules are present in considerable quantities, the hair is dark; when smaller amounts of these pigment granules are found, the color of the hair ranges from light brown to blond, the exact shade depending on the specific quantity of brown pigment present. Many investigators believe that in light or blond hair, aside from the small amounts of brown pigment present there also exists a basic yellow pigment, which, when present alone, produces the out-and-out blond coloration.

Brown pigment, which accounts for dark hair, is usually dominant over light or yellow pigment, which is responsible for blond hair. Therefore from a hereditary standpoint, blond hair is considered to be recessive to dark hair. When hair is entirely blond, it is due to the fact that mainly recessive genes for pigmentation exist. When the color of the hair is entirely black, the probability is that only the dominant brown pigments are present. Various shades of brown or chestnut hair between the pure blond and pure black colors are due, largely, to the presence of different numbers of dominant and recessive genes. Some investigators are of the opinion that in addition to these major factors there may be on hand also certain minor modifying genes. Such a view would tend to indicate that the inheritance of hair color is not an example of complete dominance but rather one of partial dominance in which intermediate shades may crop out. Red hair is due to a factor which causes the production of reddish pigment. Where the factors for red hair are present with the ones that ordinarily produce blond hair, the red coloration becomes evident. On the other hand, the red color becomes more or less concealed when the genes which produce it find themselves associated with those for chestnut or black hair.

In connection with similar considerations of the expression and inheritance of hair coloration, mention must be made of the interesting relationship which has been found to exist in most individuals between the coloration of the hair, that of the eyes, and that of the skin. Blue eyes, blond or light brown hair, and fair skin generally go together; likewise, brown or dark eyes usually are associated with brown or black hair and a dark skin. Since such an association seems to be the general rule, some geneticists are of the opinion that

FIG. 113. Inheritance of Albinism

A, Robert Roy; *B*, Mrs. Robert Roy; *C*, their son, K. C. Roy. (After Davenport, courtesy of *Journal of Heredity*)

the genes for these characters must be linked within the same chromosome and that the only way of separating them is through the process of crossing over between homologous pairs — a process which has been alluded to previously. Other biologists are inclined to explain the matter differently, largely on the basis of physiology.

Albinism

Albinism is a condition in which no pigmentation is found in the hair, skin, and eyes (Fig. 113). Here again there is shown the intimate relationship existing between the coloration of the three structures — hair, eyes, and skin. The absence of pigmentation in any one of them usually means a similar absence of coloration in the other two. When an

albino individual is examined, the skin and hair are found to possess a ghastly, straw-colored appearance, whereas the irises of the eyes show a deep pinkish hue. This pink coloration is due to the fact that the red blood which courses through the blood vessels of the inner walls of the eyes becomes visible through the colorless, transparent outer membranes. In crosses between albino and pigmented individuals, it has been shown that the latter condition dominates over the former one.

Some investigators are of the opinion that albinism may be the result of glandular disturbances, especially those of the

FIG. 114. Inheritance of White Lock

A, *B*, *C*, related individuals showing the trait; *B* and *C* are sisters. (After Miller, courtesy of *Journal of Heredity*)

adrenal glands. As will be recalled from the discussion of the glands of internal secretion, in Chapter VIII, disturbances in the adrenal glands may often lead to distinct modifications in the normal pigmentation of the individual.

White Lock

Aside from the albino condition of the hair, mention must be made of another rather unusual modification sometimes encountered, namely, a distinct patch or blaze of white hair in the fore part of the head (Fig. 114) that stands out from the remainder of the hair, which is invariably blond or brown in appearance. Geneticists believe this to be a special type of

piebaldism, similar to the piebald condition in skin coloration, and, like the latter, it also seems to be dominant over uniform hair pigmentation.

Premature Grayness

Albinism and white lock must not be confused with premature graying or whitening of the hair. In some instances this may be due to sudden fright, shock, or illness, in which cases it is not inherited. There are some families, however, in which the trait is an inherited one, coming on either slightly before or shortly after the age of twenty-one. In these instances the trait seems to be inherited equally by both males and females, after the manner of a simple Mendelian dominant.

Ear and Mouth Characteristics

Certain traits involving structures within the ear and mouth have been studied, indicating clearly that they are inherited. The size of the external ear appears to be decreasing in the human family. As a general rule Negroes have the smallest ears, while the yellow and brown races have the largest ears. The white race has an ear intermediate between that of the Negro and that of the yellow races. The complete absence of the external ear has shown itself in certain families, and this has proved to be inherited as a simple dominant trait. Various degrees of deafness and hardness of hearing have also been recorded in numerous families. While these traits seem to have a hereditary basis, yet their exact mode of inheritance is not understood completely. True *deaf-mutism*, where the individual is born deaf and as a result of it does not learn to speak, has been shown to be inherited. Some investigators claim that this trait is transmitted as a recessive in inheritance, while others regard it as a dominant. The probability is that the heredity of deaf-mutism is rather complicated, so much so that not all the factors involved in its transmission have yet been established. True deaf-mutism, which is due either to heredity or to a germinal variation or

mutation, must not be confused with accidental deaf-mutism, which oftentimes occurs in children as the direct result of the detrimental effects of certain diseases such as measles, meningitis, and syphilis. Accidental deaf-mutism due to any of these latter causes is not inherited.

In connection with the mouth, variations in the quality of the teeth have been shown to be inherited. The hardness and thickness of the enamel of the teeth afford an index to their quality, accounting for good or bad teeth. Basically the development of hard and thick enamel or soft and thin enamel depends on genes, and therefore these traits are inherited. It has been shown also that certain teeth may be absent in some individuals. In one family in India a number of the males lacked teeth entirely. Although the females did not show this toothless condition, yet they were carriers of the trait and transmitted it to half their sons. This behavior indicates that the character is sex linked, behaving in a manner similar to color-blindness, namely, appearing in males and being hidden in females.

The Blood

Certain conditions in the blood have proved to be transmitted through heredity. Those which have been studied mainly are *hemophilia* and *blood groups*.

Hemophilia

This is a grave condition, in which the blood of an individual who is suffering from it, refuses to clot. Studies on the inheritance of hemophilia have revealed that it is a sex-linked character behaving like the trait for color-blindness. Moreover the evidence at hand indicates that in the homozygous condition hemophilia is lethal, leading to the early death of the individual. Geneticists have pointed out that unquestionably this is the reason for the fact that there are no females in existence which show the trait. But the males suffering from hemophilia develop and live. Investigators have explained this on the basis that in the males, while the bleeding effect

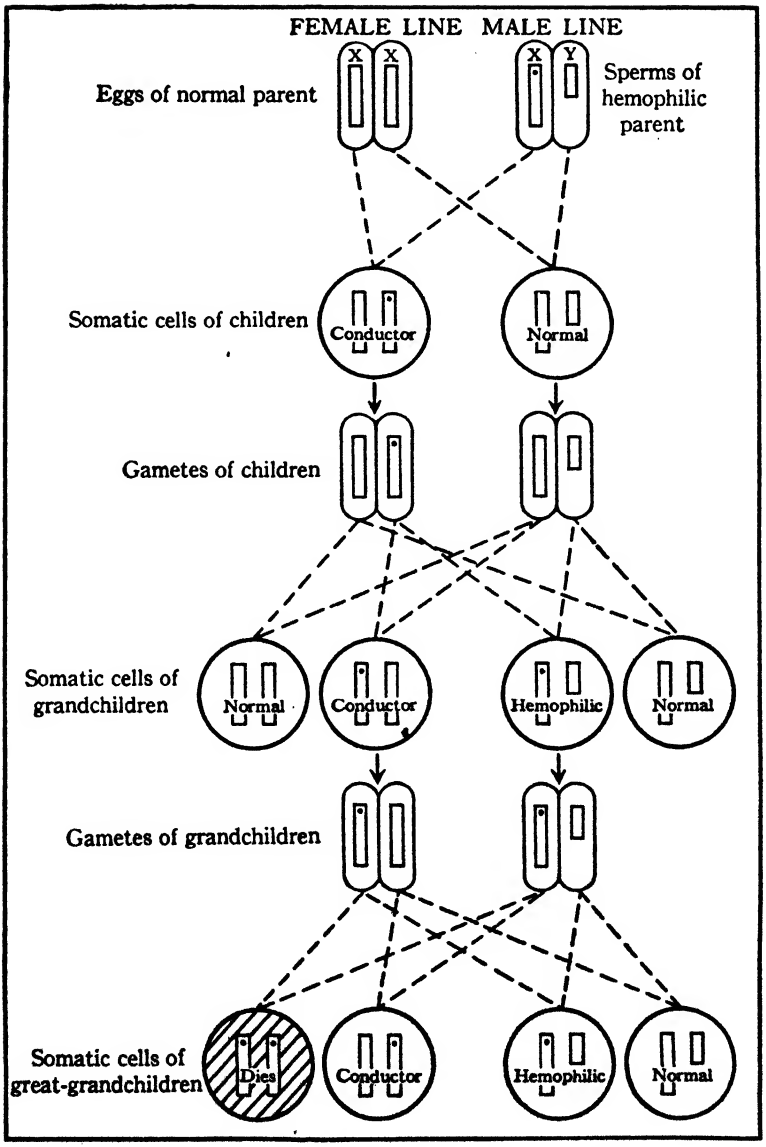


Fig. 115. Sex-Linked Inheritance of Hemophilia

The dot in the upper end of the X-chromosome represents the gene for hemophilia. (After Davenport, courtesy of *Genetics*)

of this gene carried by the X-chromosome is dominant, yet its lethal effect must be recessive to and overshadowed by a dominant nonlethal carried by the Y-chromosome. Fig. 115, taken from a paper by Davenport (*Bi. 46*), is a schematic diagram illustrating the sex-linked mode of inheritance of hemophilia along male and female lines.

Blood Groups

Biologists recognize four classes of blood among human beings, designated respectively as Groups I, II, III, and IV. Snyder (*Bi. 192*), who has recently reviewed the achievements in this field of research, has indicated the importance of the blood groups, especially from the standpoint of carrying out successful blood transfusions. The significance of this will become apparent from the discussion that follows. The various blood groups which have been mentioned are distinguished from each other by possessing or lacking certain entities which cause a clumping, or agglutination, of the red blood corpuscles. Two distinct entities have been discovered which may induce agglutination, one known as *agglutinin*, located in the serum or clear liquid of the blood, and the other known as an *agglutinogen*, found within the red corpuscles. In recent years two kinds of agglutinins, a and b, have been recognized within the serum and also two kinds of agglutinogens, A and B, within the corpuscles. In any one blood there can exist only a or A and not both; and likewise only b or B. Agglutination is brought about only in cases where either A and a or B and b become united. Analyses of different bloods have indicated that Group I lacks A and B and contains a and b; Group II lacks a and B and contains A and b; Group III lacks A and b and contains a and B; Group IV lacks a and b and contains A and B. Tests of the blood of these groups have revealed the following salient facts. The serum of Group I agglutinates the corpuscles of Groups II, III, and IV; and at the same time the corpuscles of Group I remain unaffected by the sera of any of the other bloods. The serum of Group II agglutinates the corpuscles of Groups III

and IV, but the corpuscles of Group II are agglutinated by the sera of Groups I and III. The serum of Group III causes a clumping of the corpuscles of Groups II and IV, whereas the corpuscles of Group III are agglutinated by the sera of Groups I and II. The serum of Group IV has no effect on the corpuscles of any of the other groups, since it lacks both a and b and its corpuscles contain A and B. However, the corpuscles of this fourth group are clumped by serum from any one of the other groups. The following table indicates the agglutinins, agglutinogens, and the reactions within the four groups of human blood.

The Human Blood Groups

CLASS OF BLOOD	SERUM — AGGLUTININS			CORPUSCLE — AGGLUTINOGENS		
	Contains	Lacks	Agglutinates corpuscles	Contains	Lacks	Agglutinated by serum
Group I	a, b		Groups II, III, IV		A, B	None of groups
Group II	b	a	Groups III, IV	A	B	Groups I, III
Group III	a	b	Groups II, IV	B	A	Groups I, II
Group IV		a, b	None of groups	A, B		Groups I, II, III

Because each person has only one of the blood groups, the blood must be carefully tested before any transfusion between individuals is undertaken, and only those individuals should be chosen who possess blood groups with entities that will mix freely without any agglutination. Furthermore, this specific group character of the blood of the individual has been shown to be inherited in typical Mendelian fashion.

Many students of the problem believe that the two sets of factors which have been mentioned, A, a and B, b, are the only ones involved, so that, from the standpoint of heredity, the genotypes for the four different types of individuals representing the four blood groups may be indicated as follows: Group I, aabb; Group II, Aabb or AAbb; Group III, aaBb or aaBB; and Group IV, AaBb or AABb or AaBB or AABB.

On such a basis of two pairs of factors being involved, crosses between different individuals belonging to the different groups may be traced readily by the checkerboard method, and also the results may be tabulated so as to indicate to which one of the groups the progeny belongs. In some instances, although not in all, such knowledge has been extremely useful in determining the legitimate parentage of certain children. For example, when the blood of a child is of Group IV (AaBb or AABb or AaBB or AABB) and that of the mother is of Group I (aabb), then the father's blood cannot be of Groups I (aabb), II (Aabb or AAbb), or III (aaBb or aaBB). Then again, when the child's blood belongs to Group II (Aabb or AAbb) and the mother's to Group I (aabb), the father cannot have blood belonging to Group I (aabb) or Group III (aaBb or aaBB).

More recent investigation seems to point to the conclusion that instead of there being two independent factors to account for the blood groups, three *multiple allelomorphs* are involved. As already explained in Chapter X, in a multiple allelomorph more than two genes for a trait are in existence. Undoubtedly these multiple allelomorphs arose through mutations, and it is believed that they are located at the same loci within the chromosomes. In the fruit fly (*Drosophila melanogaster*) a large number of multiple allelomorphs are known, and the same is true for other organisms, including man. In a multiple allelomorph each gene is allelomorphic to any one of the remaining genes. Within each individual only two such genes can exist, corresponding to the two homologous chromosomes in which they are located. In the case of blood groups, the investigators who hold to the multiple allelomorph hypothesis assert that the three factors involved are **A**, **B**, and **O**. **A** and **B** stand for the two agglutinogens, as in the two-factor hypothesis first considered, and **O** for the absence of both of them. Probably **O** is the primitive condition from which **A** and **B** have originated by mutation. In accordance with this interpretation, Group I is represented as **OO**; Group II as **AO** or **AA**; Group III as **BO** or **BB**; and Group IV as **AB**.

Diseases

Although diseases by themselves are not inherited, yet tendencies leading to the expression of structural and physiological defects are, and these may afford the means by which specific maladies gain a foothold. There has been considerable controversy in regard to the inheritance of certain diseases, especially tuberculosis and cancer, and it may be well for us to consider some of these at greater length.

Tuberculosis

This is a bacterial disease affecting various structures, such as lungs, glands, bones, and joints. Most competent authorities believe that individuals are not born tubercular; rather they inherit genes for the development of either weak structures or nonresistant protoplasmic constitutions or both, which make them more susceptible to the ravages of the bacilli of tuberculosis than would otherwise be the case.

Cancer

Much has also been written in regard to the inheritance of cancer, but here, as with tuberculosis, all that can be said is that some individuals and some families seem to show a greater susceptibility to cancer than others. In a number of studies on the inheritance of certain tumors and cancers in mice, numerous investigators, notably Maude Slye (*Bi. 191*), have revealed the existence of certain strains of these animals in which the disposition to cancer appears to be inherited after the manner of a simple Mendelian recessive. Since cancerous conditions in mice appear to be similar to those in man, the conclusion which seems to be warranted under the circumstances is that heredity also is of importance in the development of cancer in human beings. From all the facts available in regard to human cancer, the conclusion seems justifiable that some human strains possess a greater disposition to cancer than others.

Allergic Diseases

In this group are included a number of disorders which manifest themselves as reactions of various parts of the body to protein substances, giving origin to such common maladies as hay fever, asthma, migraine (headache), protein food poisoning, eczema, and the like. The general term of *allergy* is used in medicine to cover these conditions. Students of

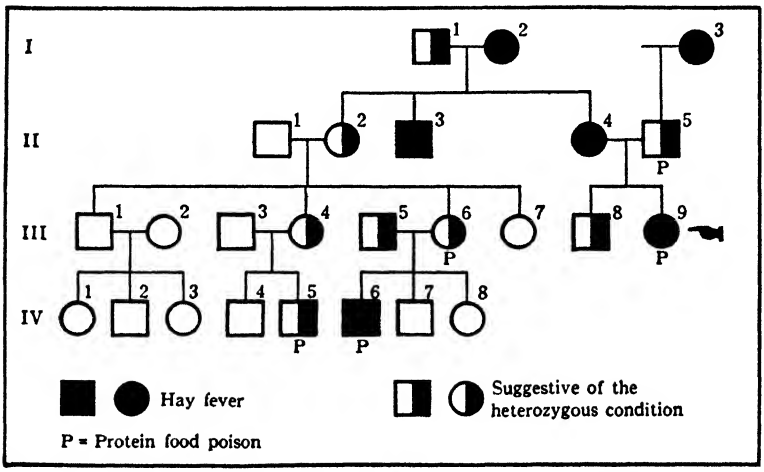


FIG. 116. **Inheritance of Hay Fever and Protein Food Poisoning**

Squares represent males and circles females. The hand points to the individual from whom the pedigree chart was traced. (Courtesy of *Eugenical News*)

allergy are of the opinion that heredity plays a very large part in most of these disorders. Moreover, they believe that what is actually inherited is not the disease itself but rather a factor for sensitiveness toward such disturbances. Where there are no stimulating agencies in the environment, this sensitiveness does not manifest itself. On the other hand, where there are stimulating agencies in the environment, such as certain types of pollen or other irritating protein particles, then the sensitive disposition of the individual may manifest itself in one or another of these diseases depending on which stimulating agent is present to provoke it. Workers

who have studied the inheritance of allergy have arrived at the conclusion that such conditions invariably act as simple dominants. What is really inherited is the gene for sensitivity to an allergic disturbance, but the specific allergy which makes its appearance is determined by the factors present in the environment.

In a recent paper by Richards and Balyeat (*Bi. 178*) on this subject, such a view in regard to the inheritance of allergy is maintained. These authors also point out that individuals suffering from allergic disturbances, as a rule, tend to marry persons with similar symptoms more often than normal ones. This conclusion has been based on a considerable number of studies which these investigators themselves have made, and it agrees also with the observations made by other specialists in the field. The real explanation for this situation is problematical, but it has been discovered that those families which are sensitive to substances producing allergy usually possess a higher degree of intelligence than the average. It is only natural, therefore, that persons of such intelligence should be attracted to each other and marry. Although the evidence is not conclusive, yet it points strongly in this direction, since in the group of individuals suffering from allergic disturbances, a group which constitutes a rather small part of the population, a large number of marriages have been recorded. The inheritance of allergic conditions is revealed in the chart shown in Fig. 116, which is based on the study of the inheritance of hay fever and protein food poisoning through four generations of individuals in the family of one of the collaborators of the Eugenics Record Office (*Bi. 67*). It is evident that here the inheritance of the hay-fever complex depends for its expression largely upon dominant rather than recessive factors.

CHAPTER XVIII

Problems of Eugenics — Mental Traits and Social Factors

AT THE beginning of the preceding chapter it was pointed out that the mental factors also are a part of the individual's make-up and that it is rather difficult to segregate them from the physical and physiological factors. Just as in the case of the latter traits, the mental traits also have been shown to have a hereditary basis. One must clearly understand what is meant by a mental trait. Ordinarily what is referred to as the mental side of the individual is his general behavior, having to do in large measure with the reactions of his nervous system. The concrete manifestations of a mental trait may involve not only the physical structure and physiological reactions of the nervous system but also those of other coördinated organ systems, leading to the distinctive behavior and responses which may be observed. While there are many mental traits, only those of general mental ability, insanity, feeble-mindedness, epilepsy, and criminality will be considered here.

Concerning the social factors one cannot speak with the same degree of assurance as in the case of individual ones, for the reason that the social factors are of the nature of general influences which have operated toward the molding of the great mass of the population. Although heredity may not be involved, yet the social factors may lead to the production of individuals and families with biological tendencies and traits that may influence indelibly the future fate of civilization. Not only that, but these factors may also afford a means of establishing an environment which is inimical to the highest development of the most desirable qualities of the human race. Under social factors may be included such items as war, venereal disease, and immigration.

General Mental Ability

It has been found that specific levels of mental ability run in families, so that it is safe to conclude that this general trait

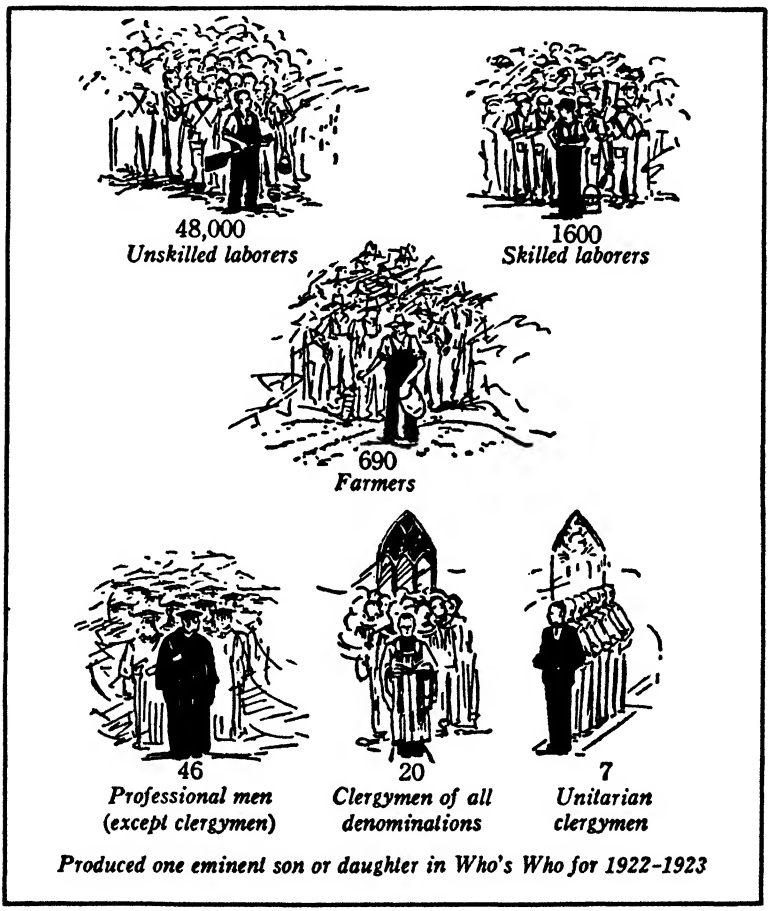


FIG. 117. Occupational Division of Parents of Eminent Persons in Who's Who[1]

is unquestionably inherited. Where parents have good mental attainments, as revealed by their positions in society, their

[1] From Huntington and Whitney's *The Builders of America*. By permission of William Morrow and Company, publishers.

children, as a rule, inherit similar mental capabilities. This has been established by numerous statistical studies in Great Britain and the United States. Huntington and Whitney (*Bi. 116*), in their interesting volume *The Builders of America*, point out that when the occupations of the parents of those listed in Who's Who in America are tabulated, it is found that most of these prominent individuals are the sons or daughters of parents with the highest cultural and moral attainments. According to the statistics gathered by Huntington and Whitney for the year 1922–1923, among the laboring class one individual out of 48,000 unskilled laborers attained prominence as compared with a ratio of one to 1600 for skilled laborers. Of the farming class one individual in 690 attained eminence. Among professional classes of all kinds, excluding the clergy, one in 46 attained distinction, and among clergymen one in 20 received such honors. Especially significant are the statistics for Unitarian clergymen, where one in 7 attained distinction. Fig. 117 clearly illustrates the occupational division of parents of eminent individuals. Such statistics indicate the importance not only of heredity but also of environment. There is no doubt that both of these account for the results obtained. This same conclusion becomes inevitable when such family histories as those reviewed in Chapter XVI are examined carefully.

Insanity

The term *insanity* is a general one applied to conditions which have to do with degenerative changes in the nervous system leading to abnormal behavior on the part of the individual. Studies indicate that many types of insanity have a hereditary basis, behaving, as a rule, after the manner of a simple Mendelian recessive. There are, of course, instances where insanity is brought on through accident, alcohol, disease, or other similar circumstances, but where this is the case it is questionable whether inheritance plays any part whatsoever or whether the trait, when once engendered in this man-

ner, is ever inherited. On the other hand, many facts are at hand to show that insanity runs in families and is inherited. Castle (*Bi. 22*), in discussing insanity, states:

> I am convinced that the inheritance of insanity in general is, indeed, unifactorial and recessive, but also that there are different gene mutations which cause insanity and that some at least of these are complementary, borne in different chromosomes and non-homologous genes. All insanity is consequently not the same genetically.[1]

A large number of cases of insanity come on during adolescence or during middle age. Up to these times the individuals are apparently normal in all respects and cannot be distinguished from the remainder of the normal population. Two of the most obvious types of such insanity are dementia præcox and Huntington's chorea.

Dementia Præcox

This is a condition of general melancholia which comes on during adolescence. Geneticists are of the opinion that this form of insanity is transmitted after the manner of a simple Mendelian recessive. Degenerative changes are set up within the nerve cells, or neurones, and also within the reproductive glands, often leading to a disintegration of the spermatozoa in the male and the ova in the female. Such transformations within the sex glands interfere with the output of the usual amount of sex hormones, which play such a tremendous rôle in the development of the secondary sexual characters of the individual.

Huntington's Chorea

This is a condition which comes on during middle life, and is characterized by impediments in speech and general tremors of the body, especially of the head and limbs. Also degenerative changes take place in the nervous system, leading to a state of dementia, and often this may be accompanied by

[1] W. E. Castle, *Genetics and Eugenics* (Fourth Edition), p. 378. Harvard University Press, Cambridge, 1930.

suicidal tendencies on the part of the individuals affected. Persons suffering from Huntington's chorea (*Bi. 172*) hand on the condition to their offspring, the trait behaving invariably as a simple Mendelian dominant (Fig. 118). Inasmuch as the symptoms of this mental state do not manifest themselves until middle life, an afflicted parent may transmit the condition to approximately half his offspring before he

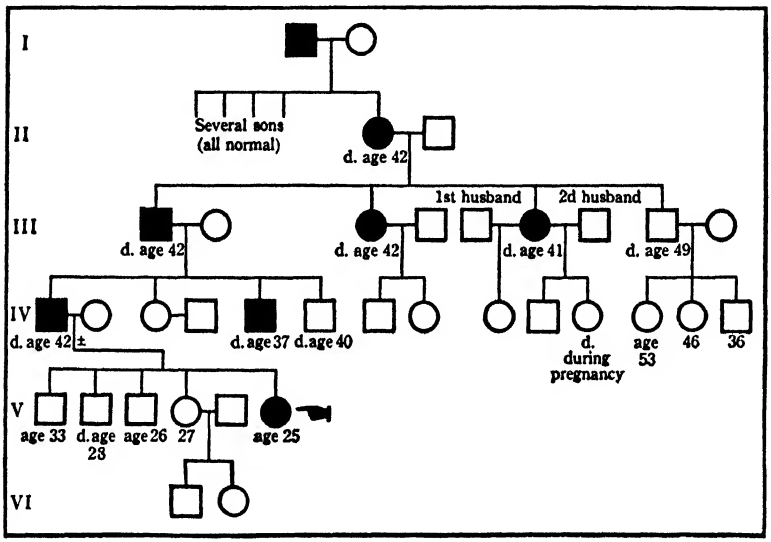


FIG. 118. Five Generations of Huntington's Chorea

Squares represent males and circles females. Dark symbols indicate individuals who revealed the malady. The hand points to the individual from whom the pedigree chart was traced. (After Popenoe and Brousseau, courtesy of *Journal of Heredity*)

realizes that he is the possessor of it. This, of course, is a tragedy that can be prevented only by every person's having full knowledge of his ancestry for a number of generations.

Statistics reveal that in the United States there have been recorded about a thousand cases of Huntington's chorea, and these have all been traced as coming from six persons who emigrated from England to America in the seventeeth century and settled in New England.

Feeble-Mindedness

In discussions of heredity insanity and feeble-mindedness are often grouped together, giving the impression that they are exactly the same thing. However, one must distinguish clearly between them. If, as has already been indicated, insanity is considered a disease or degeneration of the nervous system, *feeble-mindedness* may be said to be a condition in which the mental development is deficient and limited to such an extent that it does not progress beyond a certain childlike stage of development. An insane person may be normal in every way up to a certain age, and then degenerative changes may set in, leading to the establishment of the peculiar abnormalities accompanying the specific condition. On the other hand, the feeble-minded person may be normal from the standpoint of physical development, but nevertheless be deficient from the mental standpoint, never progressing beyond a certain maximum stage of childlike development.

Students of feeble-mindedness recognize three classes of such individuals, namely, *idiots*, *imbeciles*, and *morons*. An idiot never develops a mentality beyond that of a normal child of two and is incapable of caring for himself. An imbecile may progress to the mental age of a normal child of six, and while he may be able to care for some of his physical functions, at the same time he is incapable of supporting himself. Both the idiot and the imbecile are distinctly institutional cases, generally taken care of for life at either public or private expense. A moron is a feeble-minded person who has reached the maximum mental development of a normal child of about twelve years of age, and while he may attain physical and sexual maturity, yet his mental development never reaches beyond the stage indicated. Morons often appear to be normal and cannot be distinguished except by special tests. As adults, morons may be found engaged in various manual occupations and may even become self-supporting, but usually they are incapable of any mental achievement beyond the range of an ordinary child of twelve.

They are the individuals who constitute many of the lower-grade families,— low from the physical, mental, moral, and spiritual standpoints; and studies seem to indicate that from this moron class of the feeble-minded originate a large proportion of those who constitute the ranks of prostitutes, criminals, the shiftless, and paupers.

Although feeble-mindedness may be caused by accident or disease, yet in the vast majority of instances the condition is

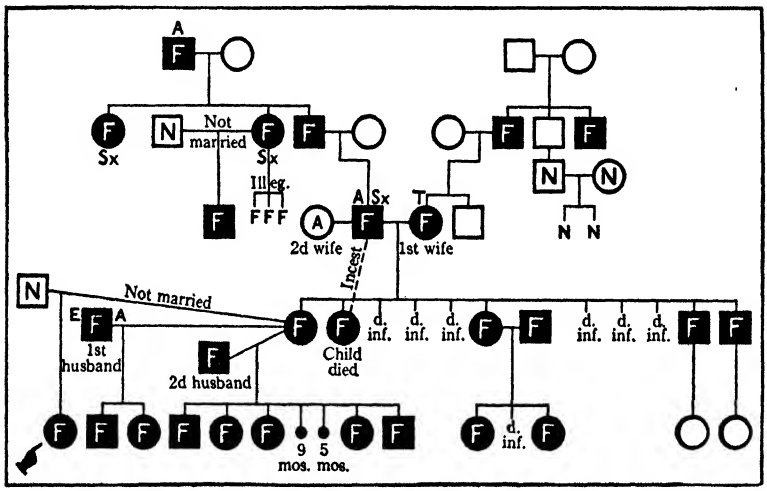


FIG. 119. Inheritance of Feeble-mindedness

The squares stand for males; the circles for females. A, alcoholic; E, epileptic; F, feeble-minded; N, normal; Sx, grave sexual offender; T, tubercular; d. inf., died in infancy. Small black circles indicate miscarriages. The hand points out the individual from whom the record was traced back. (After Goddard, courtesy of American Genetic Association)

largely hereditary, being transmitted as a simple Mendelian recessive. Henry H. Goddard, who has accumulated the greatest amount of material on the subject and has studied feeble-mindedness in a good many families, is convinced that in about 65 per cent of all cases the condition is hereditary, being transmitted after the manner of a simple Mendelian recessive (*Bi. 86–90*). Fig. 119 is a copy of one of Goddard's charts, showing the inheritance of feeble-mindedness.

Epilepsy

Epilepsy is the name applied to a number of nervous disorders manifesting themselves in loss of consciousness, and quite often accompanied by spasms, convulsions, and frothing at the mouth. While epilepsy is frequently caused by syphilis, yet it is also found to be a trait inherent in certain families, where it is inherited as a simple Mendelian recessive. Although the traits of feeble-mindedness and epilepsy are not the same, still in a good many instances they are found to be linked, coming out together in individuals.

Criminality

The term *criminality* is used to apply to a condition where individuals do not abide by the laws and customs of the social group of which they are an integral part. Included in the criminal class are those persons who rob, defraud, commit murder, forgery, arson, and so on. However, what is a crime in one country is not necessarily so in a different country. In the United States the criminal class is that group which attempts to live by disregarding the prescribed laws and in so doing may rob, murder, or in other ways interfere vitally with the welfare of the law-abiding social group.

When the topic of criminality first absorbed the minds of students, two schools attempting to explain it sprang up. One school regarded criminality as due entirely to environmental factors, while the other school believed it to be due exclusively to heredity. Moreover, many students believed that there were certain distinctive characters which distinguished the criminal type from other individuals, such as a massive jaw, protruding forehead, peculiarly shaped skull, flat nose, unsteady eyes, and so on. The Italian criminologist Lombroso, in particular, was active in this field, and for a long time most students followed him in their characterizations and interpretations of criminals. Although the Lombroso school believed that from a physical standpoint one can

readily distinguish the criminal type, yet careful studies have shown that no such distinctions exist, and, by and large, the criminal class exhibit no more physical differences than the normal population.

While this may be true in regard to physical traits, nevertheless criminals in a good many instances have been found to possess mental characteristics which clearly set them apart from the rest of society. A careful examination of the criminal population in institutions has revealed that approximately 30 per cent of them are subnormal mentally, being either feeble-minded, insane, alcoholic, syphilitic, or epileptic, or having a combination of a number of these abnormalities.

That criminal tendencies run in families is revealed by numerous investigations which have been made in recent years, and some of these, such as the histories of the Jukes and Zeros, have already been recounted in an earlier chapter. Undoubtedly criminality is a condition which depends for its expression on a combination of certain hereditary factors leading to various degenerative nervous disorders, such as feeble-mindedness and epilepsy, coupled with an antisocial environment in which the defective mental traits, instead of being repressed, have a fuller opportunity to develop. It is out of the question to speak of the inheritance of criminality, since the phenomenon is, rather, a complicated one dependent for its emergence on the interaction and coöperation of certain mental and environmental tendencies. This much is certain: the more the criminal is studied, the more does it become apparent that he is an individual who possesses either defective intelligence or defective emotions or perhaps a combination of both these deficiencies.

War

Among the social and biological factors which influence the welfare of man there is no other so devastating as the factor of war. The reasons for this become obvious when one realizes the manner in which modern wars are conducted. In the first place, every such conflict is fought and carried on largely

by young individuals, those just emerging from youth to enter the prime of life. Nations, in choosing their fighting units, pick over their youthful citizens, selecting only those who are best fitted from a physical and mental standpoint to carry on the problems engendered by the conflict. The old, the decrepit, the maimed, and the defective are left at home, while those of our picked youth adjudged the best by draft boards are sent to the trenches for fighting purposes.

As everyone knows, modern warfare is conducted largely by gun fire, poison gas, submarines, airplanes, and the like. Huge numbers are concentrated for action, and in any one engagement hundreds of the best individuals may be wiped out entirely by a few bombs. Here survival has come to mean the survival not of the most cultured nation or of the most gifted individuals, but rather of those governments which have at their command the mightiest weapons of offense and defense. It thus becomes evident that, in a relatively short time, war exterminates many of the ablest and best fitted individuals in a nation. During the World War millions of the finest youth in all the participating countries were killed. These were removed totally from life, and most of them did not even leave offspring for the future — in a word, their germ plasms, with all inherent traits, were lost permanently to civilization. From this standpoint alone, if from no other, the world is much poorer today than before the war.

Another reason why war is a terrible thing, interfering with the best evolution of man, is because it consumes so much of public taxes. Few people realize how much war and its aftermath are costing nations individually and civilization generally. Inasmuch as the figures have already been cited in the opening chapter, it will be necessary only to summarize the salient facts as far as our own country is concerned. Competent authorities have pointed out that in the United States nearly 80 per cent of the national taxes go for the maintenance of the various organizations of war such as the army, navy, pensions, hospitals, and so on, leaving approximately 20 per cent for all the other agencies necessary to the welfare of the nation.

Finally, war invariably brings with it an increase in certain diseases, decimating not only the fighting units but also large numbers of the civilian population. Witness, for example, the severe outbreaks of typhus in Serbia, cholera in Russia, and edema in Belgium and Germany during and immediately after the World War. Perhaps more important than these epidemics is the fact that war always brings with it an increase in the incidence of sexual diseases among the men composing the armies. Numbers of our fighting units become infected with serious sexual diseases, which not only may undermine their own vigor but also may be the means of disseminating similar maladies among the civilian population with whom they may later come in contact. The "sins of the fathers" may thus be visited on a host of innocent mothers and children. Many authorities, in commenting on the eugenic aspects of war, have pointed out that perhaps this is the worst one of them all.

The tragic history of all wars during the last few centuries has been that the best manhood of the nations has either become crippled or diseased or has been permanently removed from the race. In general, it may be said that war tends to remove the normal and the gifted, and at the same time leaves the perpetuation of the race to those with less desirable qualities. Students of the question believe that in large measure this has accounted for the decline of modern nations.

Venereal Disease

Venereal disease is associated in the main with the institution of *prostitution*, and it manifests itself chiefly in the diseases known as *gonorrhea* and *syphilis*. While these maladies are not hereditary, yet they may be the means of producing so much injury to the reproductive glands and other structures, as well as to developing embryos, that they may be looked upon as just as potent agencies as any hereditary factors which induce deterioration in offspring. These diseases produce so much misery and harm that all persons should

know something about them and particularly of their effects on the individuals who constitute society.

It has been asserted that these diseases are disseminated largely through the medium of prostitution, which has existed and still exists in many civilized communities. That such a vicious system has been allowed to flourish in our midst is one of the sad indictments of our modern educational and social orders. Not that the prostitute is to be condemned; rather she should be pitied, for studies reveal that most prostitutes are either subnormal or deficient mentally and ought to be protected by society from exploitation. Prostitution itself is revolting to the finer sensibilities of all thinking individuals, and because it has been the means of disseminating virulent sexual diseases affecting man, the system must be considered one of the gravest menaces to the welfare of the human family.

Although reliable statistics on venereal diseases are difficult to obtain, those which are available reveal the seriousness of the situation. The data presented here have been gathered largely from numerous bulletins of the United States Public Health Service and also from the volume *Essentials of Healthful Living* by William S. Sadler (*Bi. 183*), eminent physician, and director of the Chicago Institute of Research and Diagnosis. Of special value is the United States Public Health pamphlet entitled "Today's World Problem in Disease Prevention," a nontechnical discussion of syphilis and gonorrhea, by John H. Stokes (*Bi. 198*), chief physician in charge of the Section of Dermatology and Syphilology of the Mayo Clinic at Rochester, Minnesota. Stokes (*Bi. 199*) has also given a very interesting account of the history and characteristics of syphilis in his book *The Third Great Plague.*

Estimates reveal that in the United States approximately 98 per cent of all prostitutes suffer from at least one or the other of the sexual diseases which have been mentioned. In about 90 per cent of the cases of infection with these diseases among the public, prostitutes have been found to be the causative agents. When these infections have once obtained a foothold, they may undermine the physical and mental

vigor to such an extent as to cause great misery and harm. Not only that, but few people realize that in the United States these diseases are the means of ultimately causing about two and a half times as many deaths per annum as tuberculosis, the figures revealing a death rate of around 100,000 per year from tuberculosis and about 250,000 during the same period from the effects of venereal disease. This does not mean that venereal disease is necessarily the immediate cause of death but rather that, in many cases, it institutes those degenerative changes which account for the maladies that finally bring about the death of the individual.

In order to convey some idea of the grave effects of venereal diseases, Daisy M. O. Robinson (*Bi. 181*), of the United States Public Health Service, quotes the following statement, made by Assistant Surgeon General Pierce, before the House Appropriations Committee in 1920:

The inefficiency that is due to venereal diseases was very marked in the army. More than four men in every thousand were always out of action because of these diseases. If we applied that same rate to the coal miners in the country — and it is fair to assume that coal miners would be subject to syphilis and gonorrhea equal to that of the men in the army — it would mean that there were two million tons of coal not produced last year on account of the miners being sick with venereal diseases. Probably one half of all the abdominal operations on women are due to gonorrhea. The yearly cost to the United States of venereal diseases is a subject, of course, which can only be estimated; we will never know accurately just what these diseases cost the people of the United States, but we have some data of which we can be sure, and we can include that proven data in a table and present it without any fear of contradiction. For instance, it costs about $10,000,000 each year for the care of insane due to venereal diseases. We can estimate that the annual economic loss on the insane would be $250,000,000; that is, if these people who are in the insane asylums were not there but out at work, they would be worth $250,000,000 to the country. There is a cost of $3,600,000 for blindness due to venereal diseases and $10,000,000 is expended on the treatment or other cases of venereal diseases. Then the economic loss caused by venereal infection in the general population, on a basis of 4,000,000 incapaci-

tated during the year, amounts to $300,000,000. It is certainly conservative to say that $2,000,000 is expended every year by people who are infected with venereal diseases on quack treatments. So that would make a total cost, including those items, of $575,000,000 a year.[1]

Gonorrhea

This venereal disease is produced by a bacterial organism which usually finds entrance into the individual through the tissues of the reproductive system. When once the disease has established itself, it may lead to numerous degenerative changes. Quite often gonorrhea is driven inward and is covered over for a long time, giving one false assurance that he has been cured of the disease, but later on in life it may break out anew and attack vital organs, producing profound changes which not only cripple the system but also may lead to death. Therefore it is very important that one who is suffering from this disease receive proper treatment, which in many instances must be quite prolonged, from a qualified medical authority in this field. It has been asserted by many competent students that in many of the larger cities between 60 and 80 per cent of the men have had gonorrhea. Conditions in smaller cities and even in rural communities are not considered to be radically different.

The effects of this disease are quite marked. It has been estimated that about 50 per cent of the childless marriages are due to gonorrheal infection. So potent are the effects of gonorrhea in this direction that medical men often refer to it as "the sterilizer of the race." Between 10 and 25 per cent of all adult blindness has been attributed to this infection and also about 75 per cent of the blindness of newborn children. In recent years much of this infant blindness has been overcome, largely through insistence on the part of state and city health departments that attendant midwives or physicians wash out the eyes of all newborn babies with a silver nitrate

[1] D. M. O. Robinson, "Heredity and Venereal Diseases," *Eugenics in Race and State*, Vol. II, p. 321. The Williams & Wilkins Company, Baltimore, 1923.

solution. Gonorrhea is transmitted by those infected with the disease. It is as a direct result of such infection that over 70 per cent of the severe internal operations on women have to be performed. Not only that, but to this disease has been attributed nearly 80 per cent of the deaths caused by infection and inflammation of the female reproductive organs.

Syphilis

Syphilis, like gonorrhea, is produced by a microscopic organism which invades the reproductive tissues, and from there it may be distributed to other structures of the body, especially the nervous system. The effects of the syphilitic disease are most devastating, leading to various kinds of physical and mental degeneration. So severe are these effects that syphilis is alluded to as "the killer of the race." If treatment for the malady is undertaken during the early stages of its progress, a permanent cure may be accomplished. On the other hand, if the disease has progressed for a considerable period of time, a cure becomes impossible and degeneration invariably sets in in numerous bodily structures, leading to physical and mental deterioration. Since the organism which produces the disease seems to have a special disposition to attack nervous tissue, it may be the means of bringing about such profound modifications in the nervous system as to render the individual unable to care for himself. Many forms of insanity are the direct result of the degenerative changes produced in the nervous system by syphilis. *Paresis*, or softening of the brain, accompanied by muscular paralysis, in almost all instances is produced by syphilitic infection.

In recent years the effects of syphilis on offspring have been studied to a great extent, so that the results are fairly definitely known. In a great many instances the embryos developing within a parent having syphilis become so heavily infected with the disease as to interfere vitally with their normal development to maturity. On the other hand, some of them complete their development, and these are the ones which later show vital defects of a physical or mental sort.

The tragedy of it all is that the disease from at least one of the parents has here been visited on the children, and these in turn may not be the only sufferers, for they also may transmit the same taint to other healthy persons as well as to generations yet to be born.

While most venereal disease is spread mainly through the medium of sexual intercourse in which one of the individuals is infected, yet cases are on record where such infection has been accidental. In children's wards a towel polluted with gonorrheal organisms, when used on other children, may be the means of spreading the disease. On rare occasions, healthy persons have been known to become infected through using toilets that had been used previously by infected individuals. Syphilis, in addition to being spread through the means mentioned for gonorrhea, also may be spread occasionally by kissing and by drinking cups, eating utensils, combs, brushes, razors, and dentists' and surgeons' instruments that have been contaminated with the syphilitic microörganisms because they were used by or on individuals suffering from the disease.

Immigration

Immigration must be considered a factor of the greatest significance to every nation that encourages it. This is particularly true of the United States, where, until a few years ago, there existed a policy of more or less unrestricted immigration, with the result that our population has increased tremendously during the last half century. While we have received many individuals with sterling qualities, yet at the same time we have received also a large number of others with delinquent or defective tendencies, and these have been the ones who have partly accounted for the rapid increase in the undesirable classes within our country. Only within recent times have we given any thought or attention to the immigrant types that have come to our shores. Since 1920 we have been restricting our immigration to certain percentage quotas of the foreign nationalities already in our midst.

While this has bettered conditions considerably, yet at the same time it has not solved them entirely. Competent students have indicated that what is necessary for the United States is not restriction on the basis of a percentage quota but rather restriction on the basis of quality of traits.

Such restrictive measures would necessitate careful investigations into the family traits of all individuals who seek entrance into the United States. Of necessity, this would have to be accomplished in the foreign countries from which the persons desire to emigrate. While at first thought this would seem to be a tremendously expensive undertaking, yet reflection should convince one that the expense could be kept comparatively low for the reason that these investigations could be conducted through the offices of the legations already existing in the various foreign countries which the individuals are seeking to leave. As everyone knows, all nations, including our own, maintain legations in the other countries, and competent investigators could be attached to them for the purpose of making the necessary inquiries into the past records of prospective immigrants. Such investigations would soon reveal who are desirable prospects and who are not. With this information at hand, it would be a relatively easy matter for our immigration officers to restrict entrance into this country to those persons possessing desirable qualities. At the same time, the feeble-minded, the insane, the criminals, and the various other undesirables would not be approved in their native lands, and thereby such individuals would be discouraged from undertaking the useless expense of the passage to this country.

In this connection it is of interest to note that during the last few years our immigration authorities have actually been making investigations of this sort through our legations in Belgium, Czechoslovakia, Denmark, Germany, Great Britain, Holland, Ireland, Italy, Norway, Sweden, and Poland. However, this does not include all the countries from which our immigrants have been coming. At present only about half of all prospective immigrants are examined at their source,

but if the maximum good is to be obtained such a procedure must be followed in all cases. In the final analysis, it must be pointed out that, even though such a system of investigation would be costly at first, eventually it would pay for itself many times over by saving the country the mounting costs of maintaining the ever-increasing number of defective offspring which would be bound to originate from those undesirables allowed to enter because no adequate knowledge of their poor family histories was obtained.

In dealing with the factor of immigration — and this is true also for the human family generally — it must be remembered that there exists proof that many individuals who appear normal may, at the same time, be the possessors of dormant, covered-over recessive factors for defective traits which may crop out in later generations. Of course, where hereditary deficiencies reveal themselves in the prospective immigrants, these persons ought to be excluded without question. Where they do not reveal themselves, a careful search into the ancestry may bring them to light. Even so, it must be admitted that there will be many normal-appearing individuals, coming from seemingly normal ancestors, who may be carriers of recessive genes for defects, although they will escape detection. In such cases our government will have to take a chance and hope that these persons and their children will become good, law-abiding citizens.

CHAPTER XIX

Eugenics and Human Betterment

SINCE the beginning of the present century biologists have been devoting much time and effort to the study of the various problems of genetics and evolution. In particular, they have been paying considerable attention to the genetics of the domesticated plants and animals and also of man. These studies have attracted the attention of the press and the pulpit to such an extent that these agencies have at times become effective allies in spreading genetical knowledge among a great many of the intelligent laity. Almost daily one may find some item of eugenic interest discussed in our current newspapers. Not only that, but the science of eugenics, which rests on knowledge gained from inquiries into the genetics and evolution of modern man, is supported by such a vast amount of factual material from allied fields of knowledge (Fig. 120) that it commands the attention of a large number of the thinking public. During the last few years especially, people have become eugenically minded and have interested themselves in questions of human heredity, human variation, and human evolution. The result of this widespread interest in eugenics has been that many people have not only become conscious of the existing conditions, but they have also been raising many questions in regard to the future of the human individual, in the hope of discovering some remedies which will lead definitely to human betterment. The eugenist is of the firm conviction that there are numerous ways of bringing about improvement in the human family which will lead gradually to the production of a finer and fitter race of people, thereby insuring a nobler civilization for the future. Therefore it may be well to outline briefly the program which the eugenist has in mind for human betterment.

Educational Program

In the first place, an extensive campaign of education should be undertaken to instruct people along lines of human

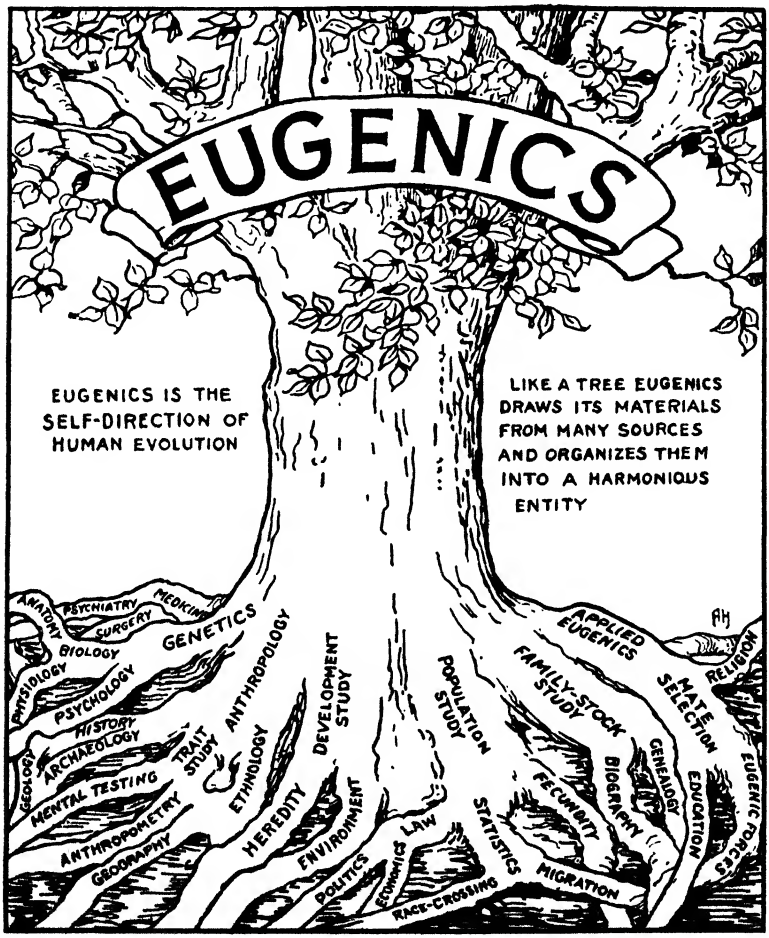


FIG. 120. Scientific Relations of Eugenics[1]

biology, with special emphasis on health and a correct understanding of the principles of heredity, environment, eugenics,

[1] *Courtesy of Eugenical News.*

and sex. It should be clearly pointed out why this knowledge is of value in molding the human individual as well as human society. Although in recent years some of these topics have been emphasized in the educational curriculum, yet very few people, especially our young folks, have adequate knowledge concerning them. Every child should be taught human biology, particularly the basic laws of health and the factors which make for a strong, clean body both physically and mentally. Throughout such a course he should be taught the real value of being the possessor of a clean, healthy, and vigorous body (*Bi. 128*).

A similar attitude should be maintained in dealing with problems of heredity, environment, and sex. All the discussions, while for the primary purpose of bringing out the scientific facts in regard to these factors, should stress the necessity of individuals' being the possessors of good normal traits, to be handed on to following generations through the medium of the reproductive powers implanted in their bodies. Moreover, it should be pointed out that the environmental facilities ought to be the very best possible in order to afford the greatest opportunities for the development of the innate potentialities.

An individual's development has often been compared to a triangle whose sides consist of the three factors heritage, environment, and response. Although all three of these are exceedingly important in development, still geneticists have placed the primary emphasis on heritage, because this embodies the genes, or endowments, out of which will emerge the final structure of the individual. Heritage, therefore, is supposed to form the base of such a triangle, with environment and response the other two sides. Environment affords the medium for development, embodying such elements as food, temperature, shelter, enemies, friends, and surrounding aids and obstacles. Unless hereditary factors have the proper environment for development, they may remain either wholly submerged or limited in their expression. Response is the side of the triangle representing what the organism does with

heritage and environment. In the human being this would mean training or education, which would enable him to take fullest advantage of environmental opportunities. The heritage factor of the individual is often referred to as *nature*, whereas the environment and response factors are referred to as *nurture*. It should be emphasized that, for the most desirable result, one should strive to obtain the best combination of both nature and nurture.

Not only should our educational system foster courses for children, such as those outlined, but parents should be the most enthusiastic supporters of them. This should be true especially in regard to sex education. In the past most parents have paid little attention to the education of children in matters pertaining to sex, particularly sex hygiene. As a direct result of such a situation, most children have grown up either in utter ignorance of the facts concerning sex or with such distorted or unwholesome notions in regard to it that great harm has resulted therefrom. If any decided change is to be accomplished, sensible parents must come to the realization that nothing good can come from the belief, so commonly held by a large number of adults, that ignorance in matters of sex means innocence. Such an attitude has often made it impossible for parents to become helpful guides to their children. By their very reactions these parents have shut the door completely to any frank discussion of the problems of sex. The result has been that their children, instead of coming to them for enlightenment, often have gone to others, who may have been just as ignorant concerning these matters as they themselves are or else may have had sordid and unwholesome conceptions of them.

Attitude toward Marriage

A second corollary to the general educational program is the belief on the part of eugenists that much good can come through a changed social attitude toward marriage. Instead of regarding marriage in the light in which some people ap-

parently consider it today, — as a convenience, to be entered into and broken off at will,— people must be educated to consider marriage seriously. Certainly such is not always the case at the present time. The majority of young people contemplating marriage hardly give any thought to its significance as an institution to perpetuate the race and civilization. This is attested to by the fact that within recent years there has been a considerable increase of divorce in the United States. Statistics show that out of every five marriages undoubtedly one will end in the divorce court. The situation would be bad enough were the divorced ones the only sufferers, but studies reveal that in many of the broken homes there are children whose lives and general outlook become marred by the separation of the parents. According to the figures given in the 1934 World Almanac, over 100,000 children are affected directly by the divorces granted annually in the United States.

The above statements and statistics in regard to marriage do not mean that there may not be occasions when divorce becomes necessary and even desirable, but at the same time they reveal that there is probably something wrong or something lacking in the fundamental preparation of our youth for marriage. A changed attitude is essential to bring about any real improvement. After all, the family must be considered the primary basis of our social order, and anything which tends to undermine it is bound to leave its mark on the entire fabric of civilization.

Fitness for Marriage

The above considerations lead us to another proposal often advocated by eugenists, namely, the passage of suitable state laws and regulations making it imperative for persons contemplating marriage to undergo rigid physical and mental examinations with a view to discovering whether they possess any salient defects which may be transmitted to children. Persons found to be deficient from either the mental or the

physical standpoint should either be prevented from marrying or they should be allowed to marry only after they have undergone operations which would make it impossible for them to reproduce offspring. At the present time many individuals shrink from the thought of having to undergo such examinations before marriage; but if they were educated properly, the vast majority of them would undoubtedly insist on such procedures, for they would soon come to realize the importance of parents being the possessors of normal traits, insuring desirable offspring. The more people became educated about heredity, the simpler would it become for every state to insist on physical and mental health certificates accompanying marriage licenses. Where such certificates could not be obtained, no minister or state official would be permitted to perform the marriage except in those instances where the individuals concerned were made incapable, through operations, of reproducing offspring.

Attitude toward Charity

The eugenist believes that we must change our attitude toward charity, especially regarding the expenditures of money for our socially undesirable groups. Heretofore persons belonging to these classes have either been aided by direct grants of money or have been placed in institutions, in which they have been maintained for shorter or longer periods at public expense. At the same time little or no thought has been paid to the types of individuals who were being helped or to the families from which they originated. We now know that in a large number of instances these individuals arise from family stocks in which the defective traits have been present for a number of generations, and so long as the individuals possessing them are helped to survive, there exists the possibility of their reproducing their kind and allowing these taints to crop out in later generations. What good do charity and public aid accomplish, when, instead of decreasing the number of undesirables, such agencies merely aid in per-

petuating the stock and even increasing its numbers? All students of human biology are beginning to realize that while nations are taxing themselves to take care of their socially undesirable groups in a humane way, at the same time they must devise means of preventing individuals belonging to these groups from perpetuating their kind.

Sterilization or Segregation of Defectives

Eugenists are of the opinion that the only sensible way of reducing our socially undesirable individuals is to prevent them from having offspring. This can be done in one of two ways: either through segregation of the sexes among such individuals, keeping them separate for life under supervision in institutions maintained at public expense, or through *sterilization*, by means of which they are deprived of the powers of reproduction. The first of these remedies, while it accomplishes the same purpose as sterilization, is exceedingly costly, for the reason that the individuals must be housed throughout life in institutions maintained at public expense. Moreover, a large number of competent supervisors must be employed to watch over them closely; otherwise many of the defectives may wander off and, finding individuals of the opposite sex, reproduce their kind. Sterilization, on the other hand, makes it possible to deprive the individual of the powers of reproduction without in any way interfering with any of his other functions.

The operation for sterilization, called *vasectomy* in the male and *salpingectomy* in the female, is a simple one, easily accomplished by any skillful surgeon. In 1899 the first sterilization operation for eugenic purposes was performed by Dr. Harry Sharp, of the Indiana State Reformatory. It consists of cutting out portions of the tubes, *oviducts* in the female and *vasa deferentia* in the male, leading from the reproductive glands and then tying the cut ends so as to seal them over completely. This method of sterilization, although accomplishing the same purpose as *castration* (removal of testes) and

ovariotomy (removal of ovaries), nevertheless differs from both of the latter in that it does not in any way interfere with the sex life of the individual. Furthermore, after sterilization operations many persons suffering from certain hereditary taints could be liberated from institutions so as to become self-sustaining, thereby saving considerable public tax money (*Bi. 93, 109, 114, 129, 170, 173*).

Some people object strenuously to sterilization, asserting that it is not only inhumane but that it interferes with the rights and privileges of the individual. Such objections are not warranted, because medical authorities consider the operation to be a rather simple one that does not leave any permanent injury other than depriving the individual of the power of procreation. For the female the operation is a little more complicated than for the male, but even for the female it is no worse than an ordinary operation for the removal of an appendix.

Others oppose sterilization on different grounds. One objection which has been put forth is that sterilization, by preventing procreation, would tend to increase promiscuity on the part of those who have undergone the operation. The facts, however, do not warrant such a conclusion. The Human Betterment Foundation of California has studied carefully various phases of the sterilization problem, including this one (*Bi. 93, 114*). The investigation included a large number of feeble-minded individuals of both sexes. Among the males who were sterilized, not a single instance of promiscuity resulted from the operation after the individuals were released from an institution. Paul Popenoe, the director of the Human Betterment Foundation, points out that most feeble-minded males who are sent to state institutions are not sex-offender types. The fact is that they are undersexed rather than oversexed. On the other hand, most of the feeble-minded females committed to state institutions are sex delinquents; nine out of twelve of them actually show such tendencies. After sterilization and parole, it was found that sex delinquency among these females was reduced to the extent

where only one in twelve could be classed as a sex offender. Therefore, instead of increasing such delinquency, sterilization actually has had the opposite effect of reducing it by eight ninths. Needless to state, Popenoe points out that there may be other factors, in addition to sterilization, to account for this reduction in sex delinquency, such as the constant supervision and help given to sterilized individuals by officials administering the sterilization law.

Another group objects to sterilization on the ground that it would be a means of spreading venereal disease. As was pointed out in connection with the argument for the increase of promiscuity and sex offenses, so with this argument, the facts do not substantiate the contention. The investigation in California has proved this beyond any question. The Human Betterment Foundation had the active coöperation of a large number of social workers and state officials dealing with the care and treatment of defective individuals, and they were practically unanimous in their conclusions that sterilization increases neither promiscuity nor venereal disease. On the contrary, all the facts seem to indicate the reverse.

Some objectors to sterilization hold that inasmuch as not all the facts in regard to human heredity are known there is danger, first, that sterilization may prevent the birth of some geniuses and, second, that sterilization may be used on individuals whose defects are due to accidental circumstances rather than hereditary ones. In answer to the first of these arguments, geneticists who have studied the question find that practically no superior individuals or geniuses have arisen from such defective parents as those for whom sterilization is advocated. One cannot name a single genius that has arisen from such stocks as the Jukes, the Zeros, or the Tribe of Ishmael. Not only do such defective stocks lack the necessary genes for genius, but the environment in which they live is inimical to the emergence of great or talented individuals. In regard to the second objection, that sterilization may be used by unscrupulous individuals on normal persons, the

experience in those states where sterilization laws are in practice is sufficient argument to refute the contention. Most of the individuals sterilized are institutional cases, chiefly feebleminded and insane, particularly those where the facts indicate that the defects are due to germ plasms which carry genes for the defective traits,— in other words, the defects of the individuals are due to heredity. Sterilization of such defectives is left to the judgment not of one official but of a board of officials, usually comprising heads of various state institutions, who review the facts of each case impartially. Not only that, but, even though sterilization laws usually do not require it, in most instances the consent of the individual's near relatives is obtained before the operation is performed.

About thirty states have already passed eugenic sterilization laws, and up to the present time over 27,000 persons, including representatives of both sexes, have been operated on in the various institutions within these states. When these laws were first adopted they met with a good deal of criticism on the part of the public. In recent years, however, many people have come to regard such measures in a more serious light, so that gradually a number of states have been adopting them as a practical means of reducing the undesirable population, in the hope that in due time they will tend to lower considerably the ever-mounting tax burdens. The following table, on page 350, based mainly on statistics supplied by Paul Popenoe, of the Human Betterment Foundation of Pasadena, California, reveals the situation in the various states of our country where sterilization laws have been in effect.

In the state of California, where a sterilization law has been in continuous existence since 1909, over 12,000 persons of both sexes have been sterilized up to the present time. Gosney and Popenoe, in an interesting book (*Bi. 93*), have reviewed the results obtained in California through this method of reducing the undesirable population, and they have also indicated the many benefits that have been derived from this practice. As these authors point out, if sterilization were adopted and

Eugenical Sterilization in the United States to 1938

States	Date of First Law	Operations Performed (chiefly in state institutions)		
		Males	*Females*	*Totals*
1. Alabama	1919	129	95	224
2. Arizona	1929	10	10	20
3. California	1909	6,270	5,910	12,180
4. Connecticut	1909	23	377	400
5. Delaware	1923	273	241	514
6. Georgia	1937	0	0	0
7. Idaho	1925	4	10	14
8. Indiana	1907	383	277	660†
9. Iowa	1911	70	83	153
10. Kansas	1913	1,151	764	1,915
11. Maine	1925	14	125	139
12. Michigan	1913	420	1,395	1,815
13. Minnesota	1925	270	1,189	1,459
14. Mississippi	1928	105	225	330
15. Montana	1923	35	74	109
16. Nebraska	1915	132	201	333
17. Nevada	1911*	0	0	0
18. New Hampshire	1917	51	302	353
19. New Jersey	1911*	0	0	0
20. New York	1912*	1	41	42
21. North Carolina	1919	86	432	518
22. North Dakota	1913	90	263	353
23. Oklahoma	1931	49	236	285
24. Oregon	1917	435	783	1,218
25. South Carolina	1935	0	1	1
26. South Dakota	1917	139	244	383
27. Utah	1925	63	82	145
28. Vermont	1931	50	111	161
29. Virginia	1924	1,197	1,719	2,916
30. Washington	1909	48	245	293
31. West Virginia	1929	1	30	31
32. Wisconsin	1913	129	776	905
National Total		11,628	16,241	27,869†

practiced universally as a eugenic measure, it would be the most effective means of cutting off (1) a considerable part of the stream of bad heredity, (2) a large number of the carriers of recessive genes for defective traits, and (3) a host of underprivileged children. In regard to the objection that steriliza-

* No law now in effect. In New York, law passed in 1912; declared unconstitutional in 1918; repealed in 1920.

† This does not include 230 radium sterilizations of the female, primarily for therapeutic reasons.

tion interferes with the rights of the human individual, one must call attention to the fact that all laws regulating individual conduct are really of this nature; but it is well to remember that modern democratic society is built on the principle of having laws and regulations which will make for the greatest good of not one particular individual or one particular class but rather of the vast majority of normal human beings constituting the social order. As has been emphasized many times in this book, society can progress only if in some way our normal, gifted population not only maintains itself but is induced to increase its numbers and at the same time our defective, deficient population not only does not maintain itself but is forced, through various means, to decrease in numbers.

Limitations and Possibilities of Eugenics

The program of eugenics really may be said to consist of two phases: *negative eugenics*, dealing with the detection and eradication of the undesirable classes of society, and *positive eugenics*, dealing with various positive means for the encouragement and perpetuation of those classes with good, normal, or superior qualities.

It must be admitted that up to the present time most eugenics programs for human betterment have been confined to the various phases of negative eugenics. The critics of such programs point out, however, that little good will result from an application of remedies suggested to eliminate defectives because many defective characters depend for their expression on recessive genes, and that even though we eliminate the individuals in whom such genes express themselves, the actual reduction of defectives will be, figuratively speaking, "a mere drop in the bucket." Inasmuch as many defective traits depend for their expression on recessive factors, large numbers of apparently normal individuals undoubtedly harbor them. When such individuals mate, there exists the probability of many chance combinations of these covered-

over recessives, making for the emergence of a large number of similar defectives in the next generation.

It has been pointed out in previous portions of this volume that each parent contributes to the newly formed individual one factor for every trait. Where the factor is dominant it expresses itself; where it is recessive it remains dormant and does not gain expression. Only where both recessive factors for a trait happen to be combined in the zygote will the trait gain expression in the new individual. There must be in existence, in a considerable number of the population, many covered-over recessive factors for desirable as well as for defective characters, which are held in reserve in each generation. Be that as it may, eugenists point out that the effort to eliminate such defectives, even though it may be a slow and prolonged process, is well worth while.

A. Franklin Shull (*Bi. 188*), of the University of Michigan, asserts that R. A. Fisher (*Bi. 74*), dealing with the problem of hereditary feeble-mindedness, has estimated that absolutely preventing such defectives from reproducing, generation after generation, would reduce their number considerably. On the assumption that these defectives constitute 1 per cent of the population, such rigid elimination would reduce them 17 per cent in one generation, 30 per cent in two generations, and 40 per cent in three generations. In reality, the rate of decrease of the defectives would be proportional to their number,—the greater the number, the higher the percentage of decrease; the smaller the number, the lower the percentage. In any event, such reduction of defectives would be permanent and would remove just so much deficient germ plasm from the population.

Where deficiencies are due to dominant factors, preventing such individuals from having offspring would at once remove the possibilities for perpetuating such deficiencies. Then, again, it must be remembered that even where some deficiencies appear to depend on recessive factors, not all the facts in regard to them are known. Samuel J. Holmes (*Bi. 109*), in his volume *The Eugenic Predicament*, questions the assump-

tion that mental defect, for example, is dependent on genes which are completely recessive, and he asserts that by eliminating individuals showing mental defects we may be destroying a larger percentage of either total or partially dominant factors for such expressions than many believe to be the case.

While all this is true, still it must be admitted that at the present time there is no method of absolutely eradicating all possibilities for the emergence of defective individuals, and so long as there are covered-over recessives there will be developed in each generation a group of defectives. Some students of genetics (*Bi. 122*) have pointed out that absolute relief in this direction can come only when some biochemical means is discovered for detecting the existence within the organism of the recessive genes responsible for the emergence of defective characters. It would then be a simple matter to apply tests to all individuals and discover those who possess the recessive factors for defective traits. Needless to state, it will take considerable time and research for the discovery of such unique tests, and until that time no absolute relief can be assured. But, in the meantime, does the failure to possess such tests mean that all efforts in the direction of eliminating defectives, slow though they may be, should be abandoned?

The problem of eliminating defective individuals would be simplified were we dealing with lower animals rather than man. As was pointed out in Chapters X and XV, where fixing and grading up of types were considered, the breeder of lower animals concentrates on those individuals showing the qualities which he desires to inculcate in his strain and eliminates all others that reveal undesirable qualities. Gradually he builds up more and more of the type conforming to his standard qualities. In the human species the problem is not so simple. One cannot reduce human mating to the method of the breeding pen, but, by and large, the essential principles are the same. Preventing undesirables from reproducing, and continuing this generation after generation, leads to the elimination of a considerable number of such defectives from the population, with the result that the per-

petuation of the race is left to those individuals that seem to possess normal traits. The race in general gradually approaches a more normal pattern. Preventing the unfit from being numbered among the parents of the next generation would provide that generation with better parents than it would have had otherwise. To a corresponding degree, also, the potentialities of this generation for producing normal and desirable types would be increased, and at the same time its capacity for producing abnormal and undesirable types would be decreased.

Here one must pause to comment that it is difficult to define clearly the standards of desirability or the standards of perfection in the human family. Even so, most normal persons would agree that the hopeless cases of physical and mental defectives, those that are incapable of caring for themselves, particularly where it is certain that such defects are the results of hereditary factors, are no asset to society and should be eliminated as quickly as possible.

Clarence G. Campbell (*Bi. 20*), president of the Eugenics Research Association, has divided the human family into three groups — the best stock, the good stock, and the bad stock. According to Campbell, the best and the bad stock each constitute about one tenth of the population, leaving approximately eight tenths of the population in the good stock.

In the best stock are numbered those individuals with superior qualities, who are recognized as leaders in society. These are the individuals whose endowments are such that they not only control their own environment but also control and direct that of others.

The good stock consists of the element in the population who are law-abiding and normal citizens, performing their social and economic tasks not alone for their own well-being but also for the benefit of civilization. From this group superior individuals often originate, thus adding to the superior stock.

The poor stock comprises the so-called *dysgenic* group,— those with defective qualities that make for the degeneration of society. Here are included the feeble-minded, the insane,

the paupers, the confirmed criminals, and the grave sex offenders. This group, in general, is a tremendous burden on society. Genetic evidence has been accumulating to reveal that most of these defects are due to heredity. Social workers also have discovered that from this stock the largest percentage of the dependent individuals originate. Geneticists and social workers, therefore, believe that nothing but good can come from efforts in the direction of the rapid elimination of this branch of society.

Positive eugenics has for its program the encouragement of the first two stocks mentioned by Campbell, namely, the normal and superior branches of the human family, to increase their rates of reproduction to the point where they are not only repopulating themselves but are actually increasing. To accomplish this end, various measures have been proposed. Among them may be mentioned the following: (1) encouragement to marry at a younger age; (2) adequate incomes to support, in comfort, an average-sized family, consisting of a wife and at least three children — some students have advocated a minimum salary, plus an additional wage increase for every child; (3) reductions in taxes for heads of large families; (4) government bonuses for children born, to help with the cost of bringing them up, as well as the cost of educating them; (5) heavier taxes, as well as employment and housing discrimination, for bachelors, spinsters, or couples without children.

Not only should attention be paid to hereditary factors, but society should strive to make environmental factors the best possible for human development. The time is past for arguing whether hereditary factors or environmental factors are the more important. Both are essential for fullest development, and all programs for betterment must embody concrete proposals for the perpetuation of the most desirable elements in both of these directions. This has been emphasized recently in a volume by Gladys C. Schwesinger (*Bi. 186*). But as with human heredity, so with human environment, what exactly is the most desirable environment for human develop-

ment? No one can adequately answer such a question, even though many people may have splendid notions in regard to it. Here, also, study and research are necessary by competent students who can weigh critically the effects of the various factors existing in our present social order and appraise them scientifically. Meanwhile differences of opinion are bound to exist, some advocates expressing one set of convictions, and others, just as sincere, advocating an entirely different point of view.

In concluding this volume it must be asserted emphatically that human conditions can be modified only as human individuals come to understand the biological backgrounds of human society and apply the remedies necessary to bring about those transformations which would lead to human betterment. This chapter contains a number of concrete suggestions which, if put into practice, would lead, slowly but surely, to the improvement of the human family. In the final analysis, the key to the situation lies in society's safeguarding itself by inculcating within its youth the idea of taking the utmost precautions in mating. Just as the breeder of lower forms insists on choosing the most desirable types of organisms for perpetuating the qualities of his stock, so society must insist that only the normally endowed or superior individuals be permitted to perpetuate the race. At the same time, means should be devised that would lead to a definite check in the rapid increase of numbers of the undesirable population. In the last few years there has been an ever-growing sentiment among eugenists, doctors, and social workers that the method of sterilization affords the most scientific and humane means yet devised by man of accomplishing this purpose. The way to improvement thus seems clear. Instead of a decrease in the number of desirable families and an increase in the number of the undesirable ones, the relative rates of increase among these groups must somehow be reversed, so that the numbers in the normal or gifted population shall be on the increase and, at the same time, the numbers in the subnormal or deficient population shall be definitely on the decrease.

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GLOSSARY

accessory chromosomes. Special chromosomes (X, Y, or Z, W), known also as allosomes, odd chromosomes, and heterochromosomes, that appear to carry determiners for sex. In many instances these can be distinguished from the autosomes, or ordinary chromosomes.

accessory sexual characters. Those traits accompanying the primary ones, revealed by such structures as the vasa deferentia, penis, oviducts, and vagina, which aid in indicating an organism as male or female.

acquired character. A modification produced in a bodily structure as the result of some environmental or functional stimulus.

acromegaly. *See* gigantism.

Addison's disease. A malady caused by insufficient secretion from the outer, or cortex, region of the adrenal gland, leading to weakness of the body, low blood pressure, vomiting, aching of muscles, and bronzing of the skin.

adrenal glands (same as adrenals and suprarenals). Two small ductless glands, each of which is superimposed on the upper margin of one kidney.

adrenalin (same as adrenin and epinephrin). The hormone secreted by the inner, or medulla, region of the adrenal gland. It exerts an influence on the circulation and pressure of the blood, on the heart beat, and on the functioning of the salivary and sweat glands.

adrenals. *See* adrenal glands.

adrenin. *See* adrenalin.

agglutination. The clumping of the red blood corpuscles.

agglutinin. One of a pair of substances found in the serum, or clear liquid, of the blood of some people which determine whether the red cells from other blood are agglutinated in the serum.

agglutinogen. One of a pair of substances found in the red blood corpuscles of some people which determine whether these corpuscles are agglutinated by the serum of other blood.

agouti. Grayish or wild-type color. This is particularly well expressed in the South American rodent known under the name of agouti, which is a little larger than a rabbit.

albinism. The absence of pigment in the eyes, skin, and hair.

albino. An individual without pigment in the eyes, skin, and hair.

allelomorph. One of a pair of alternate or contrasted traits; one of a pair of genes responsible for the expression of such traits, and occupying the same positions in homologous chromosomes.

allergic diseases. Disorders manifesting themselves as reactions of various parts of the body to specific substances. The term "allergy" is often used to designate all conditions of this sort.

allergy. *See* allergic diseases.

allosomes. *See* accessory chromosomes.

alternation of generations. Alternation of sexual and nonsexual cycles during the life histories of certain organisms, particularly plants.

alternative inheritance. Galton's term to describe an inheritance where the characters which appear in the offspring seem to come from one of the parents. At the present time this is designated as Mendelian inheritance.

amitosis. The direct method of cell division.

amphimixis. The intermingling of maternal and paternal germ plasms during reproduction.

anabolism. Constructive metabolism. *See also* metabolism.

anaphase. That phase of mitosis in which chromosomes are pulled to opposite poles and the cytoplasm divides. *See also* mitosis.

aniridia. An eye deformity in which there is a partial or complete absence of the iris.

anther. The structure at the tip of the stamen which contains microsporangia.

antibodies. Chemical entities built up in the animal body to counteract injurious effects produced by toxic substances or injurious organisms.

antitoxins. *See* antibodies.

aphids. A group of insects. They have been used in experiments on sex determination.

artificial selection. Selection by man of those traits for perpetuation which happen to strike his fancy.

asexual reproduction. Any form of propagation which does not involve the union of two germ cells of opposite sex.

asters. The radiating lines (astral rays) surrounding the centrosome in a cell.

asthma. An allergy involving the respiratory tract.

atavism. The condition in which there is a reappearance of a character present in a more or less remote ancestor rather than in either of the immediate parents.

autonomic nervous system. *See* sympathethic nervous system.

autosite-parasite. A condition in conjoined twins where one twin is diminutive or abnormal and joined on somewhere to the normally growing one; the former, called the parasite, is maintained as an integral part of the latter, termed the autosite.

autosome. One of the ordinary chromosomes. All chromosomes, except the accessory ones, are termed autosomes.

back cross. Cross of a hybrid to one of the parental forms.

bacteria. Microscopic unicellular plants, some of which are responsible for diseases in higher organisms and others for the decay or decomposition of organic matter.

bar eye. A mutation in *Drosophila melanogaster* in which the eye is restricted to a narrow vertical bar with considerably fewer facets than the normal, which are 740 for the male and 780 for the female.

barrier. Something serving as a limitation or obstruction, interfering with the free migration and commingling of organisms.

bifid wing. A mutation in *Drosophila melanogaster* in which the longitudinal veins of the wing are fused at the base into a two-forked stalk.

biological immortality. The perpetuation of organisms, generation after generation, by means of reproduction.

biology. The science that deals with living matter, including both plants and animals.

biometry. The application of the statistical method to biological problems.

bisexual individual. *See* hermaphrodite.

blastocœle. The hollow, inner cavity of a blastula.

blastomere. One of the early cells formed by the division of the ovum.

blastopore. The entrance into the cavity (enteron) of a gastrula.

blastula. The hollow ball of cells resulting from the cleavage of an egg.

blending inheritance. Galton's term to describe an inheritance where the characters of both parents seem to blend in the offspring. At present this type of inheritance is believed to be due to multiple-factor effects.

brachydactyly. A condition in which the fingers or toes are shortened considerably owing to the fact that two joints are developed instead of three, as in normal digits.

bud mutation. A distinct change which makes its appearance in somatic tissues of plants. The modified portion may be distinguished clearly from the remainder of the organism.

callosities. Thickened, hardened portions of skin.

calyx. The first, or outer, layer of leaves of a flower, consisting of the sepals.

cancer. Growth of new tissue in the form of a tumor, composed chiefly of epithelial cells.

Cancer magister. The edible crab of the Pacific coast.

carnotite. A mineral containing traces of radium.

carpel. The portion of a flower bearing mature female gametes.

castration. The removal of the testes.

catabolism. Destructive metabolism. *See also* metabolism.

cataract. A condition of the eye in which the lens or its surrounding regions become opaque, gradually leading to blindness.

cell. The fundamental unit of organization of living things.

cell theory. The conception set forth by Schleiden and Schwann asserting that basically all organisms, both plants and animals, are similarly constructed, being composed of cells.

central body. The combined structure of centrosome and centrosphere.

centriole. *See* centrosome.

centrosome (same as centriole). A minute single or double body of protoplasm found near the nucleus in the cytoplasm of a cell. It plays an important part in indirect cell division (mitosis) and is considered the center of activity during that process.

centrosphere (same as idiozome). The condensed mass of material surrounding the centrosome.

character. A trait, or distinguishing feature, of an organism.

chromatin. The deeply staining matter found in the nucleus of the cell, out of which the chromosomes are organized during mitosis.

chromomeres. The serially arranged granules along the chromosome threads.

chromosome. One of the bodies into which the chromatin becomes organized during mitosis, the number of chromosomes being constant for the species. The chromosomes carry the hereditary determiners.

chromosome map. A map showing the position of genes within the chromosomes and their relative distances from each other.

cleavage. The mitotic division and segmentation of the developing egg.

clones. Lines of individuals obtained through asexual means from a single original type.

color-blindness. Inability to distinguish certain colors.

colt. A young horse, usually applied to the young male horse.

Columba livia. The wild rock pigeon.

complementary genes. Factors in different individuals which, when alone, are ineffective and unexpressed, but gain expression when they are combined within the same zygote.

conditioned reflex. A response which is acquired during the normal lifetime of an individual.

congenital disease. A disease which originated in the parent and has been transmitted to the offspring by infection while in its embryonic state.

conjoined twins. *See* Siamese twins.

conjugation. A temporary union of cells, as in certain Protozoa, for purposes of exchanging nuclear materials. It is comparable to fertilization in higher forms.

connective tissue. Tissue which serves to unite and support the various parts of the body.

consanguineous. Descended from the same ancestral strain, or being of the same blood relationship.

continuous variations. Small plus and minus modifications which continue to appear around a mean and which are due chiefly to environmental differences. *See also* fluctuating variations.

corolla. The second, or inner, layer of leaves of a flower, consisting of the petals.

corpus luteum. A yellowish body, composed of a mass of cells produced after an ovum has been discharged from the ovary.

cortex. The outer region of an organ, such as the cortex of the adrenal gland.

cortin. The hormone secreted by the outer, or cortex, region of the adrenal gland, a lack of which may lead to the production of the malady known as Addison's disease.

cretinism. A condition caused by deficiency of the thyroid gland, impeding normal physical and mental development.

criminality. The moral condition of individuals who do not abide by the laws and customs of the social group of which they are an integral part.

criminologist. One who studies crime and criminals.

cross-breeding. The breeding of animals or plants that possess different traits.

cross-fertilization. The method of reproduction in which male elements of one individual fertilize female elements of a different individual.

crossing over. The interchange of genes of homologous chromosomes, thought to take place during the process of synapsis.

cumulative factor. A factor which, if present with another similar factor, invariably affects the intensity or degree of expression of a character. Cumulative factors are often subdivided into intensifying, duplicate, diluting, and distribution factors.

cutis laxa. A condition of the skin in which it may be pulled out from the body to a distance of several inches.

cutting. The vegetative, asexual process of reproduction resorted to in the cultivation of many plants.

cytology. The study of cells.

cytolysins. Specific entities built up by the body to destroy invading cells.

cytoplasm (also known as cytosome). All living material of a cell between the outer cell wall and the nucleus.

cytosome. *See* cytoplasm.

dam. The female parent among mammals.

Darwinian. A believer in the conception of evolution as propounded by Darwin.

deaf-mutism. A condition in which the individual is either born deaf or, through some disease, becomes deaf in childhood and as a result does not learn to speak.

delayed dominance. The condition in which factors do not express themselves until the organism has continued to exist for some time independently.

dementia præcox. A mental condition of general melancholia which comes on during adolescence.

determiner. *See* gene.

diabetes. A condition characterized by an excessive amount of sugar in the blood and urine resulting from the insufficient manufacture of insulin.

dichæte. A mutation in the vinegar fly in which the wings are spread wide apart and uplifted and also a number of long spines on the body are missing.

dihybrid cross. A cross between two traits in which the parents differ.

diluting factor. *See* cumulative factor.

dicœcious. Having the male and the female reproductive organs in separate organisms.

diploid (same as duplex). Having the full number of chromosomes found in body cells and in immature germ cells.

discontinuous variation. A sudden change, germinal in origin, which may be very large or very small. *See also* mutation.

distribution factor. *See* cumulative factor.

dizygotic condition. The condition where two zygotes are formed leading to the production of unidentical twins.

dominant character. The factor or character which expresses itself in the offspring, covering over the allelomorphic factor or character received from the opposite parent.

double crossing over. A cross where genes in homologous chromosomes cross over in two places instead of one.

Drosophila melanogaster. The vinegar, or fruit, fly.

duplex. *See* diploid.

duplicate factor. *See* cumulative factor.

duplicate twins. *See* identical twins.

dwarfism. An abnormal stunting of the growth of an individual due to undersecretion of the anterior region of the pituitary gland.

dysgenic. Tending to impair the qualities of the race.

Echinus. A genus of sea urchins.

ectoderm. *See* epiblast.

eczema. An allergic disease of the skin in which there are inflammation, lesions, and the development of scales and crusts.

edema. A pathological condition characterized by puffiness or swelling of parts due to an accumulation of fluids in the tissues.

egg cell. The mature female reproductive cell.

emboîtement theory (also called incasement theory). Bonnet's belief that the germ cells contain miniature models of all individuals ever to be born in that particular strain.

embryo sac. The structure in the ovule of seed plants, consisting of the egg, plus five single nucleated cells and one double nucleated cell.

embryology. The branch of biology that deals with the development of the individual before birth, that is, before it reaches the adult stage.

endocrine glands. Glands of internal secretion that manufacture hormones. The hormones are poured directly into the circulatory stream and carried to other portions of the body, where they induce transformations in structure or function. The chief endocrine glands are the thyroid, parathyroids, adrenals, pituitary, pancreas, and reproductive glands.

endoderm. *See* hypoblast.

endosperm. Nutritive tissue around the zygote of the plant seed.

enteron. The cavity formed during the early gastrula stage; it is lined by the hypoblast. The enteron forms the digestive system.

environment. The sum of all the external influences upon the organism.

epiblast (same as ectoderm). The outermost layer of cells in an embryo of one of the many-celled animals.

epigenesis. Wolff's theory that the male and female gametes each contribute simple stuffs to the embryo, which, through growth and development, become more highly organized.

epilepsy. A nervous disorder manifesting itself as loss of consciousness and quite often accompanied by spasms, convulsions, and frothing at the mouth.

epinephrin. *See* adrenalin.

epistasis. The phenomenon where one distinct factor (epistatic factor) for a structure covers over and masks a different one (hypostatic factor) affecting the same structure.

epistatic factor. The factor which becomes expressed and at the same time covers over, masks, or inhibits the appearance of another (hypostatic) factor for the same structure. *See also* epistasis.

epithelial tissue. Tissue covering all free surfaces of the body.

equational division. Cell division in which the chromosomes divide equally.

eugenics. The science of improving the human race by the application of the laws of heredity and environment.

eugenist. One who has specialized in eugenics.

evolution. The subject dealing with those facts and principles which account for past as well as present expressions of matter throughout space.

exophthalmic goiter. A disorder brought on by oversecretion of the thyroid gland, characterized by increased irritability, loss of weight, puffiness of hands and face, increased heart rate, marked weakness, and bulging of the eyes.

F. Filial generation; F_1, the first filial generation; F_2, the second filial generation, and so on.

factor. *See* gene.

feeble-mindedness. A condition in which the mental development is deficient and limited so that it does not grow beyond a certain childlike stage. Feeble-minded persons are classified as idiots, imbeciles, or morons.

fertilization. The union of the male and female germ cells.

fetus. An embryo during the later stages of development. In man the term is applied to the embryo after three months of development.

filial regression. The resemblance between an individual and his ancestors. Galton incorporated this into the law of filial regression.

filly. A young female horse.

fluctuating variations. Small plus and minus variations due chiefly to environmental differences. *See also* continuous variations.

foal. A young horse. A colt or a filly.

fragmentation. The vegetative, asexual process of reproduction resorted to in the propagation of many plants.

fraternal twins. *See* unidentical twins.

freemartin. A sterile female individual of two-sexed twins in cattle, appearing externally like a female but internally like a male.

gamete. A mature reproductive, or germ, cell.

gametophyte. The sexual generation in the life cycle of plants, resulting in gamete formation.

gastrula. A two-layered larva in the development of the many-celled animals.

gemmule. *See* pangen.

gene (same as factor, determiner, or unit character). A single indivisible unit in heredity. The genes are believed to be chemical entities within the chromosomes responsible for the expression of inherited traits.

gene theory. The hypothesis that genes within the chromosomes of the germ cells account for the inheritance of characters.

genealogy. A record of individual or family descent from some ancestor.

generative nucleus. The structure formed when the nucleus of the pollen tube first divides. On division it produces the two sperm nuclei with the germinal sets of chromosomes that are capable of participating in fertilization.

genetics. The science of the resemblances (heredity) and differences (variation) exhibited by organisms related by descent.

genotype. A class of individuals having the same germinal makeup, that is, possessing the same genes, or hereditary factors. *Compare with* phenotype.

geographical isolation. The separation of organisms on account of land or water barriers.

germ cells (also known as gametes). Reproductive cells.

germ plasm. The material of the reproductive, or germ, cells which forms the material basis of inheritance.

germ-plasm theory. A theory propounded by Weismann that only those traits are expressed in offspring which were a part of the parental germ cells.

gigantism. An abnormal increase in the size of the bones of young individuals due to an oversecretion of the anterior lobe of the pituitary gland. When the condition occurs in adults, it is known as acromegaly.

glaucoma. Increased pressure within the eyeball caused by an obstruction of the lymph drainage canal, which interferes with the normal circulation of lymph through the visual organ.

goiter. A disease of the thyroid gland in which the gland becomes greatly enlarged. This abnormality is especially pronounced in regions where the drinking water and soil lack iodine.

Golgi bodies. Specific structures in the cytoplasm of many cells, the functions of which are not definitely known.

gonad. One of the glands that manufacture the reproductive, or germ, cells. *See also* ovary *and* testis.

gynandromorph. A sex intergrade, or organism in which one side or portion resembles the female and the remaining side or portion the male.

haploid (same as simplex). Having the single set of chromosomes found in the mature germ cells.

hemophilia. An inherited malady of the blood, characterized by its inability to clot.

heredity. The resemblance shown by individuals related by descent.

hermaphrodite. An organism possessing both male and female reproductive organs.

heterochromosomes. *See* accessory chromosomes.

heterosis. The process of stimulation through hybridization, whereby the hybrids show a greater size, yield, or vigor than the original parental stocks.

heterozygote. A zygote containing unlike factors.

Homo sapiens. Modern man.

homologous chromosomes. Pairs of chromosomes having approximately the same make-up and value as far as factorial constitution is concerned. Each of the chromosomes in such a pair is derived from one of the parents.

homozygote. A zygote containing like factors.

hormones. Substances manufactured by the endocrine glands and distributed by the circulating medium to other parts of the body, the structures or functions of which are thereby modified.

Huntington's chorea. A mental condition coming on in middle life characterized by impediments in speech, general tremors of the body, and degenerative changes in the nervous system leading to a state of dementia.

hybrid. The progeny of parents differing in one or more characters.

hyperopia. An abnormality of vision commonly known as farsightedness.

hypoblast (same as endoderm). The innermost layer of cells in an embryo of one of the many-celled animals.

hypostatic factor. The factor which is covered over or inhibited from gaining expression by another (epistatic) factor for the same structure. *See also* epistasis.

ichthyosis. A defect in which the skin becomes thickened, dry, and scaly in appearance.

identical twins. Duplicate individuals produced from the equal splitting of a single zygote.

idiot. A feeble-minded individual, possessing the mentality of a normal child of two.

idiozome. *See* centrosphere.

imbecile. A feeble-minded person who, though capable of exercising purely physical functions, does not develop beyond the mentality of a normal child of six or seven.

immunity. Exemption from contagion or infection.

inborn reflex. A reflex which is a part of the racial heredity of the organism. It is present at birth.

inbreeding. The crossing or mating of closely related individuals, such as dam and son, sire and daughter, or brother and sister.

incasement theory. *See* emboîtement theory.

incest. Crosses in the human family between such closely related individuals as father and daughter, mother and son, or brother and sister.

insanity. A condition where degenerative changes in the nervous system lead to abnormal behavior on the part of the individual.

insulin. A hormone manufactured in the cells of the islands of Langerhans, located in the pancreas, which controls the utilization of sugar by the tissues.

intensifying factor. *See* cumulative factor.

intersexes. Types of organisms that show resemblances to both male and female sexes.

interspecific hybridization. The crossing of independent species.

intraspecific hybridization. The crossing of different varieties or different lines within a species.

iodine. A nonmetallic element. It is the important chemical element in thyroxin.

irradiation. Exposure to rays given off from radioactive elements.

islands of Langerhans. Areas of special cells found in the pancreas that manufacture the hormone insulin, which controls the utilization of sugar by the tissues.

karyokinesis. *See* mitosis.

keratosis. A condition in which there is a thickening of the skin on the palms of the hands and the soles of the feet.

Lamarckian. A believer in Lamarck's view of evolution through the principle of use and disuse of organs and the inheritance of acquired modifications.

Lathyrus. A genus of plants including the peas and vetches. Bateson used one of these varieties of sweet peas in carrying on experiments on complementary factors.

Leber's disease. A malady of the eye caused by degeneration of the optic nerve, leading eventually to blindness.

lethal genes. Factors which may lead to the destruction or death of the organism in which they are present.

line breeding. Crossing or mating relatives other than those in the immediate family.

line selection. Selection from the progeny derived from a single organism for breeding purposes.

linin. The threadlike structures within the nucleus.

linkage. Inheritance of groups of traits, due to the fact that their genes are located in the same chromosome.

linkage phenomena. Inheritance in which genes are transmitted together because of their location in the same chromosomes.

linked genes. Genes that are located in the same chromosome.

linked heredity. *See* linkage phenomena.

liverworts. A class of lowly, mosslike plants. In this group sex chromosomes were first discovered in plants.

lobster-claw. An abnormality in which the thumb and little finger on the hand, or great and little toes on the foot, are developed excessively while at the same time the intermediate digits are reduced considerably.

locus. The position of a single gene within the chromosome.

Lymantria dispar. The gypsy moth.

macrospore. *See* megaspore.

mare. A female horse.

mass selection. Selection from a large number of individuals in each generation of the most desirable types for propagation purposes.

maturation. The various stages in the development of the mature sex cells characterized by a reduction in the number of chromosomes from the double to the single set.

mean. The average of two extremes or of several quantities.

measles. A contagious fever, affecting children mainly. It is characterized by discharges from the nose and an eruption of elevated dots or patches on the skin.

medulla. The inner portion of the adrenal gland.

megasporangium (*plural*, megasporangia). *See* ovule.

megaspore (same as macrospore). The large functional cell of a flower formed following the maturation of a sporocyte within the ovule.

Mendelian principles. Principles discovered by Gregor Johann Mendel.

menstruation. Sexual rhythm exhibited in the human female, accompanying the regular and periodic manufacture of ripe eggs.

mesophase. That stage in mitosis in which astral and spindle fibers are arranged in spindle fashion around the centrosomes, while the chromosomes have lined up in the center of the cell. *See also* mitosis.

metabolism. The sum total of the changes occurring in living matter, involving both the breaking down (catabolism) and the building up (anabolism) of protoplasm.

metaphase. The climax of mitosis, involving the longitudinal splitting of the chromosomes. *See also* mitosis.

microsporangium (*plural*, microsporangia). A capsule of immature male germ cells of a flower found on the anther of the stamen.

microspore. *See* pollen grain.

migraine. An allergy resulting in severe, persistent headaches.

mitochondria. Small rod-shaped granules in the cytoplasm of the cell.

mitosis (also known as karyokinesis). Indirect method of cell division in which can be recognized the following stages: prophase, mesophase, metaphase, anaphase, and telophase.

modifying genes. Factors which tend to modify the intensity of the expression of the characters arising from other genes.

monœcious. Having both male and female reproductive organs in one individual. The monœcious condition is the same as the hermaphroditic condition.

monohybrid. The result of a cross between two individuals differing in only one trait.

monozygotic condition. The single-zygote condition from which identical twins are produced.

moron. A feeble-minded individual who cannot develop in intellectual capacity beyond that of a normal person of twelve or fourteen years.

morphology. The branch of biology concerned with the form and structure of organisms.

morula. The stage of development of an ovum in which it has become completely segmented.

mosaics. Sex intergrades in whom part of one structure resembles one sex and its neighboring part the opposite sex.

multiple allelomorphism. The existence of more than two genes for a trait, any two of which may be allelomorphic to each other, within an individual. Each trait in such a series is really allelomorphic to all the others.

multiple individuals. Several individuals produced at a birth.

muscular tissue. The tissue which makes up the muscles.

mutant. A new type produced by discontinuous variation.

mutation (known also as discontinuous variation, saltation, or sport). A sudden, distinct variation, either large or small, which is inherited.

mutilation. A transformation in the normal structure or appearance of a bodily portion through physical means.

myopia. An abnormality of vision commonly known as nearsightedness.

myxedema. A disease caused by deficiency of the thyroid gland which affects normal metabolism.

natural selection. The central idea around which the Darwinian theory of evolution is built. It is the blind force existing in nature which automatically chooses the best-fitted organisms that present themselves for survival.

nature. Popular term used to describe one's inheritance, as contrasted with "nurture." *Compare with* nurture.

Neo-Lamarckian. One of that group of present-day biologists who are inclined to accept Lamarck's major premises regarding inheritance.

nervous tissue. Tissue which makes up the nervous system. It is specialized for responding to stimuli.

neurone. A nerve cell with all its processes and extensions.

night-blindness. Inability to see in faint light.

nondisjunction. Nonseparation of pairs of homologous chromosomes, so that both elements of the nonseparated pair wander into one of the resulting daughter cells. This may lead to the emergence of new expressions of characters.

nonfluctuating variations. *See* discontinuous variations.

nuclear sap. Liquid contained in the nucleus.

nucleus. The more condensed part of the cell which contains the chromatin, the heredity-bearing material.

nuptial pads. Pads on the first toes of the fore limbs of a frog, used for clasping the female during mating.

nurture. Popular term used to describe one's surroundings and training, as contrasted with "nature." *Compare with* nature.

odd chromosomes. *See* accessory chromosomes.

Œnothera lamarckiana. A species of evening primrose, used by De Vries in his studies on discontinuous variations.

œstrous cycle. Sexual rhythm exhibited in the female of the higher animals, accompanying the production of the ripe eggs. This cycle is comparable to menstruation in the female of the human species.

oögenesis. The process of the maturation of the female gamete, the ovum.

oögonium. An immature female germ cell in animals.

oösperm. *See* zygote.

oötid. One of the four cells formed during maturation of the immature female germ cell. *See also* polar bodies.

ophthalmoplegia. A condition in which some of the eye muscles become paralyzed.

organ systems. Groups of organs which carry on the necessary functions of the body.

organic evolution. The facts and principles responsible for the emergence of the different types of organisms which have existed in the past, those in existence now, and those which will emerge in the future.

orthogenetic variation. Spontaneous variation which continues to appear, proceeding in a definite direction, with the result that the modifications engendered may lead to the extinction of the species in question.

Orthoptera. The order of insects, which includes grasshoppers, locusts, cockroaches, katydids, crickets, mantids, walking sticks, and many others.

outbreeding (often called outcrossing). The crossing of two inbred individuals possessing similar characteristics but belonging to different strains of the same blood line, with beneficial results to the progeny.

outcrossing. *See* outbreeding.

ovariotomy. Removal of the ovaries.

ovary. In animals, one of the female reproductive organs; in flowers, the enlarged portion at the base of the pistil.

oviducts. Passages or tubes by which the ova are conducted from the ovary to the uterus.

ovist. A believer in the preformation theory who thought that the ovum rather than the spermatozoön held the miniature individual.

ovule (same as megasporangium). The structure containing the mature egg cell in a flower.

ovum. The female germ cell in an animal.

oxytocin. One of the components of pituitrin in the posterior lobe of the pituitary gland, which stimulates the smooth muscles of the uterus. *See also* pituitrin.

P. Parents in a cross; P_1, the immediate parents; P_2, the grandparents; P_3, the great-grandparents, and so on.

pancreas. A gland located in the first fold of the intestine. It manufactures digestive enzymes and insulin.

pangen (same as gemmule). One of the small particles which Darwin believed to be budded off from the cells of the body to become stored within the germ cells.

pangenesis theory. The theory propounded by Darwin to account for inheritance. It assumed that every somatic cell of an organism budded off representative particles (pangens or gemmules) and these collected in the mature germ cells.

parallel induction. The parallel modification of bodily structures and the germinal determiners responsible for their expression.

parallel inductionist. A believer in the parallel-induction view of heredity. *See also* parallel induction.

parathyroids. Four small glands, located near or imbedded in the thyroid, which are important for normal development. *See also* tetany.

paresis. A disease of the nervous system which brings about a general paralysis of the individual.

parthenogenesis. The development of eggs without the agency of fertilization.

partial dominance. The condition where the F_1 hybrids show partial or intermediate resemblances to the dominant parent.

pauperism. The condition of those dependent on charity.

pedigree breeding. The mating of individuals whose heredity has become fairly well established and recorded through experimental methods, for purposes of insuring the production of desirable offspring.

penis. The copulatory organ of the male.

permanent variations. Modifications that are germinal in origin and are inherited.

petals. Leaves in the second layer of a flower. The petals constitute the corolla.

Phaseolus vulgaris. The species comprising the common garden variety of bean.

phenotype. A class of individuals appearing alike externally regardless of germinal makeup. Organisms may be classified into the same phenotype and yet may be found to belong to a number of different genotypes. *Compare with* genotype.

Phylloxera. A group of insects used in research on sex determination.

physiology. The science which treats of the functions of organisms.

piebald condition. Spotting of the skin due to concentration of dark pigmentation in certain patches.

pigment granules. Minute particles of coloring matter.

pistil. The composite structure of a flower which includes the carpels, or female gamete-producing portions.

Pisum sativum. The species of garden pea used by Mendel in his experiments on heredity.

pituitary gland. A small endocrine gland located on the under surface of the brain. It affects growth. *See also* gigantism *and* dwarfism.

pituitrin. A hormone secreted by the posterior region of the pituitary gland. It consists of oxytocin and vasopressin. *See also* oxytocin *and* vasopressin.

polar bodies. The three smaller oötids (also called polocytes) formed at one pole of the large oötid during the process of the maturation of the female germ cell. The single large oötid forms the egg.

polled. Hornless.

pollen grain (same as microspore). A structure formed after the maturation of a male sporocyte of a flower.

polocytes. *See* polar bodies.

polydactyly. A condition in which more than five fingers or toes are produced.

population. A mixed group of individuals.

preformation theory. The view that the complete organism existed as a miniature model within the germ cell.

prenatal influences. Supposed influences during pregnancy by which, according to this erroneous belief, a child may be branded or influenced in certain directions by external stimuli, either physical or mental, which happen to impress the mother.

primary oöcyte. Immature female germ cell at the beginning of its maturation.

primary sexual characters. Those traits revealed by the reproductive glands, testes or ovaries, which give the organism its immediate stamp as male or female.

primary spermatocyte. Immature male germ cell at the beginning of its maturation.

Primates. The order of mammals to which apes and human beings belong.

prophase. That stage in mitosis where the cell is prepared for division. *See also* mitosis.

protoplasm. The viscid, semifluid substance that makes up the cells of living matter.

Protozoa. The first phylum of the animal kingdom, composed chiefly of unicellular animals.

pure-bred. Free from mixture with any other breed or strain. The factors for the traits exist in homozygous fashion.

pure line. The progeny of parents in all of whom the germinal determiners are identical with respect to the traits in question.

quagga. Dun-colored, zebra-like animal known as the wild ass of South Africa.

radioactive. Containing atoms which spontaneously disintegrate and emit alpha, beta, and gamma rays.

radium. A chemical element possessing great powers of radioactivity.

recessive character. That entity or trait which is covered over by the dominant character in a cross. *Compare with* dominant.

reduction division. That division during the maturation process of the germ cells in which the double or somatic (diploid) number of chromosomes is reduced to the single or germinal (haploid) number.

rejuvenescence. Renewal of youth.

retinal detachment. An eye defect in which the retina seems to become separated from its underlying membranes.

retinitis pigmentosa. An abnormality of the eye in which pigment is deposited in the blood vessels of the retina.

reversion. The reappearance of a character present in some remote ancestor but which has not manifested itself for a number of generations.

roan. A color between red and white, obtained when crossing red and white Shorthorn cattle.

salpingectomy. Operation for sterilization in the female, whereby portions of the oviducts are removed and the cut ends sealed.

saltation. *See* mutation.

scrubs. Inferior types of organisms.

scurs. Traces of horns in cattle.

secondary oöcytes. The cells formed following the reduction division in the maturation process of the female germ cells.

secondary sexual characters. Somatic characters of the different sexes which normally accompany primary and accessory characters.

secondary spermatocytes. The cells formed following the reduction division in the maturation process of the male germ cells.

self-fertilization. Method of propagation in which the male elements of an individual fertilize the female germ cells of the same individual. This may occur in monœcious, or hermaphroditic, organisms.

sepals. Leaves forming the outer layer of a flower. The sepals constitute the calyx.

serum. The clear liquid of the blood.

sex intergrade. *See* gynandromorph.

sex-limited trait. A character expressed in one sex only, dominant in one sex and recessive in the other; usually some secondary sexual character.

sex-linked factor. A factor which is carried in the sex chromosome.

sex-linked trait. A character associated with sex owing to the fact that its factor is located in the sex chromosome.

sexual selection. Selection by the sexes during the mating season.

Siamese twins (same as conjoined twins). Double monstrosity, in which the zygote fails to separate completely and produces two individuals joined somewhere in the middle.

simplex. *See* haploid.

sire. Male parent among mammals.

sociology. The science dealing with the problems facing society.

somatic. Referring to the body.

somatoplasm. The material of the somatic, or body, cells, in contradistinction to the germ plasm.

sperm nucleus. One of the two nuclei formed by the division of the generative nucleus of the pollen grain; the true male gamete in plants.

spermatids. The four ultimate cells formed during maturation of each of the immature germ cells of the male.

spermatogenesis. The maturation process of the male gamete, the spermatozoön.

spermatogonium. The immature male germ cell in animals.

spermatozoön. The mature male germ cell in animals.

spermist. A believer in the preformation theory who thought that the spermatozoön rather than the ovum held the miniature individual.

Sphærechinus. A genus of sea urchins.

spindle fibers. The elongated linear structures in a cell undergoing mitosis.

spireme. A coiled thread of chromatin appearing in the nucleus at the beginning of mitosis.

splitting. An asexual process of reproduction resorted to in the propagation of many plants.

sporocyte. An immature germ cell in plants, from which spores are produced.

sporophyte. The nonsexual generation in the life cycle of plants resulting in spore formation.

sport. *See* mutation.

stamen. The portion of a flower which bears male gametes.

statistical method. A method of studying biological problems by collecting and tabulating data on large numbers of individuals. *See also* biometry.

sterilization. Deprivation of power of reproduction.

stigma. The anterior portion of the pistil.

style. The slender middle part of the pistil.

supplementary genes. Factors, belonging to different allelomorphic pairs and effective in producing distinctive characters, which may on being combined in one zygote produce a distinctly different expression of the trait.

suprarenals. *See* adrenal glands.

sympathetic nervous system (same as autonomic nervous system). The branch of the nervous system that controls many of the activities going on in the body over which man has little or no conscious control.

sympnalangy. A condition in which some of the fingers become stiffened owing to a fusion of the bones at one of the joints.

synapsis (same as syndesis). The stage in the maturation process of the germ cells in which similar chromosomes line up in pairs for the reduction division.

syndactyly. A condition in which there is a fusion of the bony elements of the neighboring fingers or toes, thus giving a webbed appearance.

syndesis. *See* synapsis.

syphilis. A venereal disease caused by a microörganism.

telegony. A supposed phenomenon according to which a former sire may leave his permanent impressions on the reproductive cells of a female, so that when she is later mated to another sire, her offspring will continue to show the effects of this former union.

telophase. The last phase of mitosis, when the cell divides and the daughter nuclei are formed. *See also* mitosis.

tertiary sexual characters. Characters which are not obvious and are not associated with either sex but are usually predominant in one sex.

testis (*plural*, testes). One of the male reproductive glands.

tetany. A disease caused by deficient parathyroids, manifesting itself by nervous disturbances and diminution of the normal calcium content of the blood.

tetraploidy. The state in which the chromosome number of a species has been quadrupled.

thyroid gland. An endocrine gland located in the throat, exerting an influence on metabolism and growth. *See also* cretinism, exophthalmic goiter, goiter, myxedema.

thyroxin. The secretion of the thyroid gland.

tissue. A group of similar cells specialized for a particular function.

total dominance. The condition where the dominance of one character over another is absolute.

toxin. A poisonous substance.

transfusion. Injection of blood from one individual into the veins of another individual.

transitory variations. Modifications which appear during the life of an organism and pass out of existence at the time of its death.

translocation phenomenon. Attachment of a fragment of one chromosome to a nonhomologous chromosome, resulting in a new arrangement of genes.

trihybrid cross. A cross considering three traits in which the parents differ.

triploidy. The state in which the chromosome number of a species has been trebled.

tube nucleus. One of the two nuclei formed by the division of the nucleus of the pollen grain.

tuberculosis. A bacterial disease affecting lungs, glands, and bones or joints.

unidentical twins (same as fraternal twins). Twins each one of which has distinctive characteristics and has developed from a separate zygote.

unisexual. Of one sex. In unisexual organisms the sexes are separate; that is, male and female reproductive organs are produced in different individuals.

unit character. *See* gene.

urethra. The tube which conveys urine from the urinary bladder to the exterior.

use and disuse. The principle propounded by Lamarck to account for the inheritance of acquired characters. By use a structure is emphasized, by disuse it is minimized, so that in time the structure becomes either more or less efficient.

vacuole. A region within a cell occupied by fluid other than protoplasm.

vagina. The passage in the female leading from the uterus to the external orifice, the vulva.

variation. The difference exhibited by organisms related by descent.

vas deferens (*plural*, vasa deferentia). A duct in the male conveying spermatozoa from the testis to the urethra.

vascular tissue. Tissue comprising the vessels or ducts for conveyance of fluids in the body.

vasectomy. Operation for sterilization in the male, whereby portions of the vasa deferentia are removed and the cut ends are sealed.

vasopressin. One of the components of pituitrin in the posterior lobe of the pituitary gland, which causes the blood vessels to undergo contraction. *See also* pituitrin.

vegetative structures. Structures which play their part in the feeding, the transportation, the protection, and the responses of the organism.

vulva. The folds surrounding the entrance to the vagina.

W-chromosome. Sex chromosome accompanying the Z-chromosome in such forms as the domestic fowl and corresponding to the Y-chromosome.

Weismannian. A believer in the germ-plasm theory of heredity as enunciated by Weismann.

X-chromosome. Sex chromosome found in many organisms. In those species possessing it, the female has two such chromosomes, and the male has one.

xenia. The visible influence of pollen on tissues other than germinal ones, as noticed in seed plants, where the phenomenon of double fertilization occurs.

Y-chromosome. Sex chromosome accompanying the X-chromosome in many organisms and ordinarily found only in the male.

yolk. The substance in an ovum which provides nourishment for the developing embryo.

Z-chromosome. Sex chromosome in certain insects, birds, and perhaps fishes that corresponds to the X-chromosome.

zygodactyly. A fusion of the skin between neighboring fingers or toes, producing a webbed condition. This is the true webbed condition.

zygote (same as oösperm). The fertilized ovum, the initial start of the new organism.

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