GENETICS AND EUGENICS

A TEXT-BOOK FOR STUDENTS OF BIOLOGY AND A REFERENCE BOOK FOR ANIMAL AND PLANT BREEDERS

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PREFACE

This book is an attempt to present, in a form as simple and readily intelligible as possible, the subject of heredity, as related to man and his creatures, the domestic animals and cultivated plants. To write such a book has been with the author a long cherished ambition, but one which, as the years went by, seemed less and less likely of realization, as knowledge of the subject increased and took on more and more complicated forms. Each year, however, he has been forced by his responsibilities as a teacher, to make, for students having only an elementary knowledge of biology, an analysis and summary of our knowledge of this subject to date. The longer he has continued to do this, the more fully he has realized that a subject in a state of healthy growth can never assume a final and finished form. He makes no apology, therefore, for presenting the subject with very unevenly and incompletely developed parts. Such, it must be confessed, is the present state of our knowledge.

It would be a great service to the student to show him where in his subject positive knowledge stops and speculation, the useful servant but dangerous master in science, begins. This task, where possible, has been attempted in this book. But such attempts can of necessity succeed only partially and for the time being, for it often happens that the speculation of today becomes the verified theory of tomorrow. For having guessed right and proved the correctness of their guesses, we honor in this field the names of Lamarck, Darwin, Weismann, and Mendel. Others still living have made contributions of scarcely less importance but to name them would be invidious. Americans may take encouragement from the thought that all are not likely to be named from one side of the Atlantic and later enumerations are likely to include names from Pacific lands also. For advance in science never results merely from brilliant guesses by the few, but takes place chiefly through the patient, persistent efforts of numerous workers who test by observation and experiment every suggested explanation of the phenomena of nature. This is a task of such magnitude and such importance that in it the coöperation of all nations is needed and fortunately is not withheld. To promote the common good of all is the greatest honor of each.

The author has found that interest in the subject of heredity is not confined to college classes but is shared by people of intelligence everywhere, because it touches and affects the lives of all. The animal breeder and the plant breeder have an intensified interest in the subject because it vitally concerns the success or failure of their occupations. The needs of this wider public have been kept in mind in the preparation of this book, but it has not been thought necessary to omit on this account discussion of questions requiring thoughtful consideration for their full understanding. A discussion which evokes no independent thinking, or even opposition, is not likely to extend knowledge, the teacher's prime concern.

I am indebted to many friends and fellow biologists for assistance in connection with the illustrations, acknowledged in the legends of the figures, to Professor B. M. Davis for a critical revision of Chapter VI, and to Professor J. A. Detlefsen for assistance in revising the proofs. My best thanks are due to the publishers who have spared no effort to make their part of the work successful.

W. E. Castle.

Cambridge, Massachusetts,
December, 1916.

PREFACE TO SECOND EDITION

Rapid advance in our knowledge of the fundamental principles of genetics has made necessary a complete rewriting of several chapters as originally published and the addition of several others. The more important changes and additions relate to the subjects of blending inheritance, the pure line principle, the nature of genetic changes, their frequency and location in the germ-cells, linkage, inbreeding, and heterosis.

W. E. C.

March, 1920.

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GENETICS AND EUGENICS

INTRODUCTION

Genetics may be defined as the science which deals with the *coming into being* of organisms. It does not refer, however, to the first creation of organic beings, but rather to the present and every-day creation of new individuals or new races. It refers particularly to the part that parent organisms have in bringing new organisms into being and to the influence which parents exert on the characteristics of their offspring. In this sense it is nearly equivalent to the term heredity. But logically, though less immediately, it is concerned with all agencies which in any way affect, condition, or limit the coming into being of a new organism or a new race. All physical and chemical changes in the world outside the organism, or in a word the environment, vitally concern genetics, though they are the more immediate field of study of other branches of biology.

Eugenics, from its etymology, means *coming into being well.* It is used at present solely with reference to man, and means almost literally the *science of being well-born.* Since man is zoölogically merely one of the higher animals, it is evident that his reproduction is a very special case falling under the general laws of genetics, and before we can properly understand this special case we must know something of the general laws of genetics. We shall therefore turn our attention to genetics first and foremost, and to eugenics subsequently and secondarily.

The term *Eugenics* was proposed by Francis Galton who defines it thus: — " Eugenics is the study of agencies under social control that may improve or impair the racial qualities of future generations, either physically or mentally."

As thus defined it is purely an applied science, for it is concerned only with those agencies which are under social control and gives no attention to any agencies, however important, which are not under social control. Its scope therefore is much narrower than that of genetics. It is concerned with only so much of genetics as concerns man, and with only so much of that as is under social control. To determine what are the general principles of genetics and to what extent man is subject to them are primarily biological problems, but to determine how far these are socially controllable is a problem for the sociologist, and one which I shall not attempt to answer without help from sociologists.

The coming into being of a new organism is one of the least understood of all natural phenomena. Even to the trained biologist it is largely an unexplained mystery. To understand his viewpoint concerning it, and what definite facts he knows about it, and how he attempts to explain them, we must be familiar with certain of the generalizations of biology. Familiarity with the more important of these fundamental generalizations of biology will be assumed in the present work.

From the philosophical standpoint genetics is only a subdivision of evolution. For the evolution theory teaches that the organisms now existing have come into being through descent with modification from those which existed at an earlier time and, in general, that the world as we know it today is different from what it has been at any previous time; that all things, organic and inorganic, are constantly undergoing change, yet nothing wholly new comes into being, for everything new arises out of something which existed before. Thus no new matter is created, yet new creations constantly arise out of elements which before existed in different form.

It will be our first task to discuss the rise of the evolution theory and in particular its relation to the subject of genetics. Subsequently we shall discuss the known facts of genetics and the several ways in which biologists interpret them; and finally we shall discuss human evolution as a subdivision of genetics, and its social control, or eugenics.

PART I

GENETICS

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CHAPTER I

DARWIN'S THEORY OF EVOLUTION AND ITS EVIDENCES

The human mind is characterized above all else by curiosity, the source of all our wisdom as well as of our woes. This fact the ancients portray in the tale of Pandora's box. We instinctively seek an explanation of all the phenomena of nature, unless our natural curiosity has been repressed by convention or education (falsely so called). We demand a reason for everything, and if none is forthcoming from an outside source, we straightway construct one for ourselves out of our own imaginings. This is the attitude of mind of the child whose perpetual " why " and " what " are so distressing to perplexed parents. It is the attitude of mind in which all primitive peoples and original thinkers have regarded the phenomena of nature. It was this attitude of mind which led to the formulation of *the evolution theory, which is an attempt to explain the present condition of the world in terms of simpler pre-existing conditions.*

When evolution is mentioned, we think of Darwin as its originator, but in reality he did not originate it; the idea of organic evolution had often been suggested before his time, but he proved its reality. The principle of evolution had long been recognized in relation to inorganic things. In chemistry, physics, and astronomy, the constancy and indestructibility of matter were fully established. It was recognized for example that more complex states of matter, that is, " chemical compounds," may arise out of the simpler " elements " by their combination in definite proportions, and that out of such compounds the elements may by suitable means be recovered again unchanged and in the original proportions.

n geology, the work of Lyell had shown that the present dition of the earth's crust had come about gradually gh the action of causes still at work.

Accordingly in all the fundamental sciences which deal with the inorganic world the reign of natural law was acknowledged before the time of Darwin, and the principle of miraculous change was no longer offered as an explanation of existing conditions.

But in the realm of living things it was in Darwin's time very different. The animal kingdom was not supposed to have grown, but to have been made outright. The higher animals were not supposed to have originated from lower ones but to have been made in the form in which they exist today. It was Darwin's work which dispelled this outgrown idea, and established the principle of evolution as an explanation of the organic as well as of the inorganic world. In his time the idea was so novel as applied to animals and plants that it aroused the greatest opposition. But the idea was not wholly new to human thought; in forms more or less fanciful and incomplete it had been suggested in previous centuries from the days of the early Greek philosophers on. [1]

Darwin lived in a time peculiarly inhospitable to the idea of organic evolution, partly because of theological, and partly because of scientific dogma. Had the idea been brought forward centuries before accompanied by proofs such as Darwin advanced in its support, it undoubtedly would have met more ready acceptance than it found in the last century. As it was, Darwin had to make the discovery anew for himself, largely unaided by his predecessors, who, though they had formulated more or less clearly the same line of explanation which he adopted, had failed to put it to the test of long-continued and detailed observation and experiment, which alone sufficed firmly to establish it.

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[1] Professor H. F. Osborn ('94) has described in a most interesting book the various foreshadowings of the idea of organic evolution which appear in the writings of Darwin's predecessors, and the development of the idea in Darwin's own mind as evidenced by his letters and other writings. One interested in the historical and philosophical growth of the idea cannot do better than to consult Osborn's book.

Charles Darwin was born in 1809 and died in 1882. Both his father and his paternal grandfather were physicians; the grandfather, Erasmus Darwin, was also a naturalist and philosopher of note, who anticipated many of the evolutionary ideas of Lamarck and some of those of his own illustrious grandson.

On his mother's side, Darwin's grandfather was Josiah Wedgwood, the famous manufacturer of pottery. Francis Galton, the founder of Eugenics, was his cousin. Those who consider special tastes and talents hereditary find significance in these relationships. Thus one biographer, after noting that Darwin's father had originally intended him for the Church, continues " but hereditary tendencies toward natural history led him in another direction." It may fairly be questioned whether " tendencies toward natural history " are hereditary in the strict sense of the word any more than tendencies toward pottery, which Darwin does not seem to have manifested though his grandfather was Josiah Wedgwood. Such language as I have quoted is quite permissible on the part of a literary biographer (indeed Darwin speaks in like vein in his autobiography) but the student of eugenics must be on his guard against accepting it at its face value.

What Darwin probably inherited was not a " tendency toward natural history " but a good mind; what subjects engaged it was probably determined not by inheritance but by the subjects which came to his attention at the period of life when men do their best creative thinking. In Darwin's case, the thing which centered his attention upon the problem of the origin of species and held it there for the rest of his lifetime was the famous voyage of the *Beagle*.

In school Darwin was not a distinguished student. He attended Edinburgh University for two sessions and then the University of Cambridge, where he took the B.A. degree in 1831. Shortly after graduation he seized the opportunity to go as naturalist on the ship *Beagle* of the English navy, which was detailed on a voyage of exploration round the world. This voyage lasted almost five years, from December 27, 1831, to October 2, 1836. Much time was spent by this expedition in making surveys of southern South America, and of oceanic islands. For a large part of this time Darwin was brought into intimate daily contact with the animals and plants of an unexplored part of the world. What a post-graduate course in natural history this was! It is probably fortunate that his previous studies of natural history had not been more specialized and detailed, and that he had no master at hand to guide him in his studies during the voyage. Otherwise he would certainly have been hampered by preconceived ideas and have been less inclined to depart from accepted notions. But here he was face to face with a new world of animals and plants awaiting explanation, and his it was to study them without assistance or let up for three years. For an ordinary boy of twenty-two, what a perplexing and bewildering task, what a *fate*, sentenced to five years of seasickness, the effects of which were to last throughout his life! But for a Darwin, what an opportunity, to study at first hand the animals, the plants, the peoples of all lands and of all seas!

After Darwin had spent some three years on the *Beagle* he returned home with impaired health which forced him to live quietly at his country home in Downs, England. Here he devoted a part of each day to working up the scientific results of his journey, and published during the next twenty years an attempt to correlate, to unify and to explain the various observations which he had made, an attempt which finally found fruition in his theory of evolution through natural selection.

It had long been known to a number of Darwin's scientific friends that he was working on a theory of evolution when, in 1858, he received from A. R. Wallace, then in the East Indies, the manuscript of a paper containing precisely the same explanation of organic adaptations which he himself had reached. Darwin was naturally much embarrassed, but seemed willing to throw aside his own work and give precedence to Wallace's paper. On the advice of friends, however, he submitted to the Linnaean Society of London an abstract of his own conclusions, which was read and published simultaneously with the paper by Wallace. The work of each author was so manifestly independent of the other and each dealt so generously with the other that no rivalry arose between them, and both were to the last the best of friends. The essential points in their theory, which Darwin elaborated more fully the following year (1859) in his *Origin of Species*, have been summarized thus by Conn (p. 353):

" 1. *Overproduction.* All animals and plants tend to multiply more rapidly than it is possible for them to continue to exist. More offspring are produced by even the slowest breeding animals and plants than can possibly find sustenance in the world.

" 2. *Struggle for existence.* As a result of overproduction, the individuals that are born are engaged in a constant struggle with each other for the opportunity to live. This struggle is sometimes an active, sometimes a passive one; and sometimes it is a struggle with each other for food. It is a struggle in which only the victors remain alive, the vanquished being exterminated without living long enough to leave offspring.

" 3. *Variation, or diversity.* All animals and plants show a large amount of diversity among themselves, and, as a result, some must be better fitted for the struggle for life than others.

" 4. *Natural selection, or the survival of the fittest.* It is a logical result of the struggle for existence that only those individuals best fitted for the struggle will be the ones, in the long run, to win in the contest. Hence the " fittest " in the long run will survive, while those less fitted to exist will be exterminated.

" 5. *Heredity.* By the laws of heredity, individuals transmit to their offspring their own characters. Hence if one individual survives the struggle for existence by virtue of some special characteristic, it will transmit this characteristic to its offspring. The offspring will inherit it, and in the course of a few generations the only individuals left alive will be those that have developed it, while those that did not develop it will be exterminated by the law of natural selection."

This theory stands today in the main as Darwin left it, the chief advances since his time being concerned with one or other of the two factors, variation and heredity, concerning which our knowledge, though still incomplete, has made notable advances. But before we pass to the consideration of these, let us pause to inquire what were the lines of evidence upon which Darwin relied to establish his theory.

These have been well summarized by T. H. Huxley (1825–1895) who by his able championship of Darwin's views did more than any other one man to gain for these views general recognition and acceptance. As modified by Lock, Huxley's summary is as follows: —

" 1. *The Gradation of Organisms.* Both in the animal and vegetable kingdoms we may trace, in spite of certain gaps, a long series of gradations in complexity of structure, so that between the simplest and the most complicated of living things a great number of intermediate stages are to be found. When we pass to the lower end of the scale in either case, we come upon a group of creatures of comparatively simple organization. Among them we find members with regard to which we cannot definitely say that they are either animals or plants. Moreover, these unicellular organisms resemble in many ways the egg-cell from which every individual among the higher animals and plants originates.

"2. *Embryology.* All the members of a particular group of animals or plants as a rule resemble one another more closely in the early stages of their individual development than they do in the adult condition, and in the earliest stages of all they are often indistinguishable. These facts are explained if we suppose that such individuals have a common origin, that they are descended from a common ancestor, and that traces of their pedigree are still to be observed in the developmental stages through which each one passes. We do not find a complete parallelism between the development of the individual and the history of the race, nor should we expect to do so, since embryonic as well as adult stages may be modified in the course of evolution; what we should expect is a more or less vague historical sketch, and this is what is usually found remaining.

"3. *Morphology.* On comparing together the different members of one of the great groups or classes of animals or plants, we find the same fundamental plan of organization running through all of them. Series of corresponding organs are often to be made out which are built upon the same general scheme, although their functions may be quite dissimilar; so that, for instance, in the hand of a man, the paw of a dog, the wing of a bat, and the paddle of a whale, almost identically the same series of bones can be traced. An obvious explanation is to be found in the supposition that these parts have arisen by the divergent modification of parts which were originally identical.

"4. *Geographical Distribution.* Observation shows that groups of closely allied creatures are often found living in neighbouring districts, and that when such a barrier as an ocean or a range of lofty mountains is passed an entirely new fauna and flora are usually to be met with. These facts may be explained by the hypothesis that allied groups of species originated by a process of descent in the same countries which they now inhabit, and they can be explained by no other known hypothesis.

"5. *The Geological Succession of Organisms.* The general facts regarding the distribution of allied species of animals and plants in time point in precisely the same direction as those relating to their distribution in space. In a few cases, notably in that of the extinct horse of North America, a long chain of possibly ancestral types has been found leading back to a remote and very different progenitor. This supposed ancestor of the horse was a creature little larger than a moderate-sized dog. It had four separate toes to each fore-limb, and three to each hind-limb, and its teeth were much simpler and less specialized than those of existing horses. The general distribution of organisms throughout the geological strata agrees, moreover, in a remarkable way with what is to be expected on the evolution theory.

" 6. *Changes under Domestication.* Among domesticated animals and plants we know of numerous cases in which the actual origin of new forms has been observed. These have often differed from their predecessors by amounts quite comparable with the differences by which natural species or even genera are separated. A notable example of this process is afforded by the numerous breeds of pigeons known to have arisen under domestication from a single wild species. We have no reason whatever for supposing that domesticated species are more mutable than wild species, and there is consequently every reason to believe that changes of a similar character take place in Nature. The conditions of domestication, of course, afford much better opportunities of observing such phenomena.

" 7. *The Observed Facts of Mutation.* Nevertheless, individual specimens of particular wild species are frequently found showing modifications which, if they occurred constantly in an isolated group, would afford a basis for the description of new species. In a few cases the actual occurrence of similar changes has been observed in wild species of plants.

" We see, therefore, that the evidence in favour of the existing species of animals and plants, having arisen by a process of evolution, is of a most ample and convincing kind."

How some of these evidences first presented themselves to Darwin's mind and how he came later to value them, Darwin states in the closing pages of the Introduction to his *Variation of Animals and Plants under Domestication.*

> When I visited, during the voyage of H. M. S. *Beagle*, the Galapagos Archipelago, situated in the Pacific Ocean about five hundred miles from South America, I found myself surrounded by peculiar species of birds, reptiles, and plants, existing nowhere else in the world. Yet they nearly all bore an American stamp. In the song of the mocking-thrush, in the harsh cry of the carrion-hawk, in the great candlestick-like opuntias, I

clearly perceived the neighbourhood of America, though the islands were separated by so many miles of ocean from the mainland, and differed much in their geological constitution and climate. Still more surprising was the fact that most of the inhabitants of each separate island in this small archipelago were specifically different, though most closely related to each other. The archipelago, with its innumerable craters and bare streams of lava, appeared to be of recent origin; and thus I fancied myself brought near to the very act of creation. I often asked myself how these many peculiar animals and plants had been produced: the simplest answer seemed to be that the inhabitants of the several islands had descended from each other, undergoing modification in the course of their descent; and that all the inhabitants of the archipelago were descended from those of the nearest land, namely America, whence colonists would naturally have been derived. But it long remained to me an inexplicable problem how the necessary degree of modification could have been effected, and it would have thus remained for ever, had I not studied domestic productions, and thus acquired a just idea of the power of Selection. As soon as I had fully realized this idea, I saw, on reading Malthus on Population, that Natural Selection was the inevitable result of the rapid increase of all organic beings; for I was prepared to appreciate the struggle for existence by having long studied the habits of animals.

Before visiting the Galapagos I had collected many animals whilst travelling from north to south on both sides of America, and everywhere, under conditions of life as different as it is possible to conceive, American forms were met with — species replacing species of the same peculiar genera. Thus it was when the Cordilleras were ascended, or the thick tropical forests penetrated, or the fresh waters of America searched. Subsequently I visited other countries, which in all their conditions of life were incomparably more like parts of South America, than the different parts of that continent are to each other; yet in these countries, as in Australia or Southern Africa, the traveller cannot fail to be struck with the entire difference of their productions. Again the reflection was forced on me that community of descent from the early inhabitants of South America would alone explain the wide prevalence of American types throughout that immense area.

To exhume with one's own hands the bones of extinct and gigantic quadrupeds, brings the whole question of the succession of species vividly before one's mind; and I found in South America great pieces of tesselated armour exactly like, but on a magnificent scale, that covering the pigmy armadillo; I had found great teeth like those of the living sloth, and bones like those of the cavy. An analogous succession of allied forms had been previously observed in Australia. Here then we see the prevalence, as if by descent, in time as in space, of the same types in the same areas; and in neither case does the similarity of the conditions by any means seem sufficient to account for the similarity of the forms of life. It is notorious that the fossil remains of closely consecutive formations are closely allied in structure, and we can at once understand the fact if they are closely allied by descent. The succession of the many distinct species of the same genus throughout the long series of geological formations seems to have been unbroken or continuous. New species come in gradually one by one. Ancient and extinct forms of life are often intermediate in character, like the words of a dead language with respect to its several offshoots or living tongues. All these facts seemed to me to point to descent with modification as the means of production of new species.

The innumerable past and present inhabitants of the world are connected together by the most singular and complex affinities, and can be classed in groups under groups, in the same manner as varieties can be classed under species and sub-varieties under varieties, but with much higher grades of difference. These complex affinities and the rules for classification, receive a rational explanation on the theory of descent, combined with the principle of natural selection, which entails divergence of character and the extinction of intermediate forms. How inexplicable is the similar pattern of the hand of a man, the foot of a dog, the wing of a bat, the flipper of a seal, on the doctrine of independent acts of creation! How simply explained on the principle of the natural selection of successive slight variations in the diverging descendants from a single progenitor! So it is with certain parts or organs in the same individual animal or plant, for instance, the jaws and legs of a crab, or the petals, stamens, and pistils of a flower. During the many changes to which in the course of time organic beings have been subjected, certain organs or parts have occasionally become at first of little use and ultimately superfluous; and the retention of such parts in a rudimentary and useless condition is intelligible on the theory of descent. It can be shown that modifications of structure are generally inherited by the offspring at the same age at which each successive variation appeared in the parents; it can further be shown that variations do not commonly supervene at a very early period of embryonic growth, and on these two principles we can understand that most wonderful fact in the whole circuit of natural history, namely, the close similarity of the embryos within the same class — for instance, those of mammals, birds, reptiles, and fish.

It is the consideration and explanation of such facts as these which has convinced me that the theory of descent with modification by means of natural selection is in the main true. These facts as yet received no explanation on the theory of independent Creation; they cannot be grouped together under one point of view, but each has to be considered as an ultimate fact. As the first origin of life on this earth, as well as the continued life of each individual, is at present quite beyond the scope of science, I do not wish to lay much stress on the greater simplicity of the view of a few forms or of only one form having been originally created, instead of innumerable periods; though this more simple view accords well with Maupertuis's philosophical axiom of " least action."

In considering how far the theory of natural selection may be extended; that is, in determining from how many progenitors the inhabitants of the world have descended, — we may conclude that at least all the members of the same class have descended from a single ancestor. A number of organic beings are included in the same class, because they present, independently of their habits of life, the same fundamental type of structure, and because they graduate into each other. Moreover, members of the same class can in most cases be shown to be closely alike at an early embryonic age. These facts can be explained on the belief of their descent from a common form; therefore it may be safely admitted that all the members of the same class are descended from one progenitor. But as the members of quite distinct classes have something in common in structure and much in common in constitution, analogy would lead us one step further, and to infer as probable that all living creatures are descended from a single prototype.

I hope that the reader will pause before coming to any final and hostile conclusion on the theory of natural selection. The reader may consult my "Origin of Species" for a general sketch of the whole subject; but in that work he has to take many statements on trust. In considering the theory of natural selection, he will assuredly meet with weighty difficulties, but these difficulties relate chiefly to subjects — such as the degree of perfection of the geological record, the means of distribution, the possibility of transitions in organs, etc., on which we are confessedly ignorant; nor do we know how ignorant we are. If we are much more ignorant than is generally supposed, most of these difficulties wholly disappear. Let the reader reflect on the difficulty of looking at whole classes of facts from a new point of view. Let him observe how slowly, but surely, the noble views of Lyell on the gradual changes now in progress on the earth's surface have been accepted as sufficient to account for all that we see in its past history. The present action of natural selection may seem more or less probable; but I believe in the truth of the theory, because it collects, under one point of view, and gives a rational explanation of, many apparently independent classes of facts.

In his earlier statements of his theory, Darwin does not seem to have paid much attention to the source of variations or to the manner of their inheritance, but these subjects receive much attention in his great work on the *Variation of animals and plants under domestication*, from which we have just quoted. He seems to have come more and more to hold views similar to those of Lamarck, his great French predecessor, regarding the direct effect of environment as a cause of variation, and the inheritance of effects so produced. Concerning the general nature of Lamarck's views we should therefore inform ourselves.

CHAPTER II

CONTRIBUTIONS OF LAMARCK, WEISMANN, AND HERBERT SPENCER TO THE THEORY OF EVOLUTION; DARWIN'S THEORY OF PANGENESIS

Lamarck (1744–1829), the greatest evolutionist before Darwin, was, according to his biographer, a man of great physical and moral courage. He distinguished himself by a deed of singular bravery in the French army, and, receiving an injury, re-entered life as a doctor. He was first attracted to botany by the rich flora near Monaco observed during his military service. Going to Paris he gained the attention of the great naturalist, Buffon, under whose direction he published a "Flora of France," written in six months, which passed through many editions. He seems to have possessed powers of exceptionally rapid observation, with great facility in writing and with unusual powers of definition and description. At the age of forty-nine (1793) he was transferred to a Zoölogical chair in the *Jardins des Plantes*, being placed in charge of invertebrate zoölogy, while at the same time Geoffroy Saint-Hilaire was placed in charge of vertebrate zoölogy. Being at this time in his fiftieth year, Lamarck took up the study of zoölogy with such zeal and success that he almost immediately introduced striking reforms in classification, and developed (after having reached middle life) the conception of the mutability of species and of the origin of new species by descent. His relation to the evolution idea was thus very different from Darwin's. It came to Darwin almost in his boyhood and he spent a lifetime working it out, not publishing anything upon it until he was fifty years old. To Lamarck the idea seems scarcely to have come before the age of fifty, and he rapidly developed it into a system, sufficiently elaborate to explain evolution, if his basic principle is true, viz.

the inheritance of acquired characters. This we shall consider further.

Regarding Lamarck's later life, Osborn (p. 158) says:

> His devotion to the study of the small forms of life, probably with inferior facilities for work, for he was extremely poor, gradually deprived him of the use of his eyes, and in 1819 he became completely blind. The last two volumes of the first edition of his *Natural history of invertebrated animals*, which was begun in 1816 and completed in 1822, was carried on by dictation to his daughter, who showed him the greatest devotion; after Lamarck was confined to his room, it is said she never left the house. Lamarck was thus saddened in his old age by extreme poverty and by the harsh reception of his transmutation theories, in the truth of which he felt the most absolute conviction.

Lamarck's Theory

The factors recognized by Lamarck as concerned in evolution may be summarized as follows: —

1. *The direct effect of environment.* We know that a plant in rich soil grows large and luxuriant, but that the same plant in poor soil would remain small and stunted. This is a direct effect of the environment. Lamarck supposed that such effects of environment are cumulative from generation to generation so that long-continued growing in rich soil would produce a more luxuriant race, while continued growing in poor soil would produce a different and smaller race. In the case of animals Lamarck does not think that the action of environment is quite so direct, but that animals are changed indirectly through changes in their habits. Buffon considered the action of environment direct in both animals and plants, and this view Darwin seems to have adopted rather than Lamarck's slightly different one. Darwin in his *Variation* adopts this factor, the direct effect of environment, as one of the causes, if not the *chief* cause of variations. He says (p. 6):

> If then organic beings in a state of nature vary even in a slight degree, owing to changes in the surrounding conditions, of which we have abundant geological evidence, or from any other cause, — then the severe and often-recurrent struggle for existence will determine that those variations, however slight, which are favorable shall be preserved or selected, and those which are unfavorable shall be destroyed.

2. Lamarck regarded *new physical needs* as a second factor or cause of variations. He supposed that the *need* of an organ caused the organ to be produced, that *need* of horns to fight with or of teeth to chew with would cause the production of horns and teeth respectively. Darwin never adopted this view.

3. A third Lamarckian factor however Darwin did regard as a genuine cause of variation, viz., *use and disuse.* The use of an organ, as the arm or leg, causes it to increase in size and strength; conversely disuse causes decrease in size and efficiency.

4. *Inheritance of acquired characters.* As regards heredity, Lamarck believed that variations of every sort are inherited. Those which result from direct action of the environment or from use and disuse, we now call *acquired characters*, and Lamarck supposed that *acquired characters are inherited.* Indeed he supposed that all variations are of this nature. Darwin shared Lamarck's view in part; he too probably did not clearly distinguish between variations which we should class as acquired characters and those of other sorts. Certainly Lamarck did not make this distinction, for on his view all variations are what we should call *acquired.*

In illustration of Lamarck's views concerning the causes of variations and of consequent evolution, it may be well to quote a few passages largely in his own words, as given in translation in Osborn, pp. 164–171.

> In considering the natural order of animals, the very positive gradation which exists in their structure, organization, and in the number as well as in the perfection of their faculties, is very far removed from being a new truth, because the Greeks themselves fully perceived it; but they were unable to expose the principles and the proofs of this evolution, because they lacked the knowledge necessary to establish it. In consideration of this gradation of life, there are only two conclusions which face us as to its origin : — *The conclusion adopted up to today :* Nature (or its Author) in creating animals has foreseen all possible sorts of circumstances in which they would be destined to live, and has given to each species a constant organization, as well as a form determined and invariable in its parts, which forces each species to live in the places and climates where it is found, and there to preserve the habits which we know belong to it. *My personal conclusion:* Nature, in producing successively all the species of animals, and commenc-

> ing by the most imperfect or the most simple to conclude its labour in the most perfect, has gradually completed their organization ; and of these animals, while spreading generally in all the habitable regions of the globe, each species has received, under the influence of environment which it has encountered, the habits which we recognize and the modifications in its parts which observation reveals in it.
>
> All that Nature has caused individuals to acquire or lose by the influences of environment to which they have been long exposed, and consequently by the influence of the predominant employment of a certain organ, or by that of the continued lack of use of the same part, — all this Nature conserves by generation to the new individuals which arise, provided that these acquired variations (changements) are common to both sexes, or to those which have produced these new individuals.
>
> But great changes in environment bring about changes in the habits of animals. Changes in their wants necessarily bring about parallel changes in their habits. If new wants become constant or very lasting, they form new habits, the new habits involve the use of new parts, or a different use of old parts, which results finally in the production of new organs and the modification of old ones.

Darwin's later views concerning variation and heredity, as compared with those of Lamarck, may be briefly stated thus:

1. Variation was thought to be due either to the two Lamarckian factors, direct action of the environment and use or disuse, or to other as yet unknown causes, the results of which Darwin refers to as "chance variations."

2. As regards heredity, Darwin seems to have thought with Lamarck that variations of all sorts are inherited, though some doubtless were inherited more strongly and persistently than others.

Weismann (1834–1914). The first great advance, after Darwin, in our knowledge of variation and heredity was made by Weismann, a German zoölogist, who within two years after Darwin's death (viz. in 1883) brought forward a new classification of variations and a new theory of heredity.

He showed that some variations are congenital (*i. e.*, are *born with us*), are in the blood so to speak, while others are acquired through the action of environment, use or disuse. Regarding acquired characters, he showed that these, in all probability, are not inherited. This was a wholly new idea and called forth a hot debate which has not yet ended, but gradually biologists have been coming to the view that Weismann is right. The consequences of this view are very important not only as regards evolution in general, but also as regards education, for if Weismann is right scholarship is not inherited, but only capacity to learn. The son must begin in his education, not where his father left off, but at the alphabet, and he will not learn any faster because his father was educated. I think the experience of educators justifies this view. Children growing up in cultured homes have a certain educational advantage due to their environment, but not to heredity. Thus Darwin's attention was directed toward natural history, by the home environment in which he grew up. The same is true in even greater degree of his sons, three of whom have become distinguished scientists. It is very improbable that he *inherited a taste for natural history*, as he supposed. More likely he *acquired* such a taste.

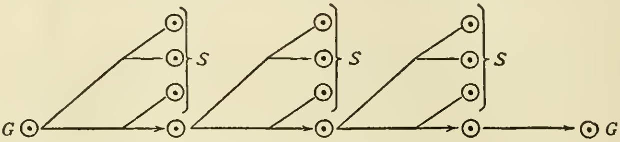

Fig. 1. Diagram showing the relation of the body or soma (*S*) to the germ-cells (*G*) in heredity. (After E. B. Wilson.)

Besides showing that there is no sufficient evidence that acquired characters *are* inherited, Weismann pointed out anatomical and physiological reasons why we should not expect them to be inherited. In the higher animals and plants reproduction takes place not by division of the body but by the development of special reproductive cells, eggs, spores, and the like. The fertilized egg-cell of an animal begins its development by dividing into two cells; these divide into four, and so on. Sooner or later we notice that these cells are not all alike. Some of them develop into muscles, others into bone, or nervous tissue; in short they become differentiated to form the various parts and tissues of the body, all except some few which remain undifferentiated like the original egg-cell itself. These undifferentiated cells will in fact

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

Fig. 7

Results of ovarian transplantation in guinea-pigs. Ovaries from a small black guinea-pig (Fig. 2) were transplanted into an albino (Fig. 3) which, mated with another albino (Fig. 4), produced black young (Figs. 5–7).

give rise to egg-cells or sperm-cells rather than to muscle, bone, or any other part of the body proper. Weismann called the cells which collectively make up the body the *soma* (Greek for body); whereas those undifferentiated cells destined for reproduction he called *germ-cells* or collectively the *germ-plasm.* Now Weismann maintained that the germ-cells, since they are not descended from body-cells but only from the fertilized egg-cell, have no way of transmitting *body-modifications, i. e.,* acquired characters. The germ-cells are guests in the body, but not members of the household. They feed at the common table but have no share in the other activities

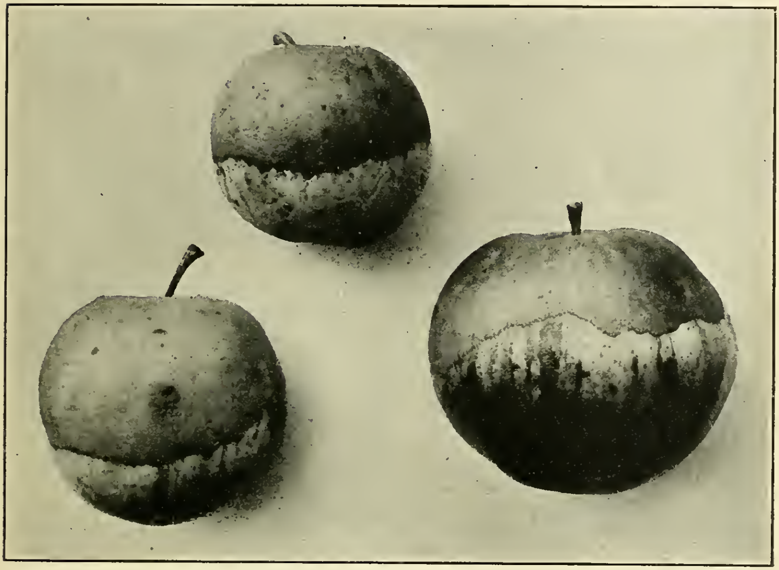

Fig. 8. Fruits of an apple "graft-hybrid" or "chimera." Two distinct varieties are represented in one fruit. The stem-end of the apple is russet and sour; the blossom-end is smooth-skinned, red-striped and sweet. A sharp line of division separates the two portions. Such fruits are borne on a tree produced by grafting one variety on another, the tree-trunk having grown from a bud which arose just where stock and scion join, and which included cells derived from both sources. But the two kinds of cells and all their descendants have retained their original distinctness, as the composite fruits show. Hence, not only may the body and germ-cells be of unlike character (as Figs. 2–7 show), but even the body may be composite and yet each part retain its original character. By grafting tadpoles, Harrison has produced a frog which anteriorly was of one species and posteriorly of another. If such a frog produced eggs, their character would depend upon which part of the body furnished the eggs. "Graft-hybrids" between the tomato and black nightshade (Solanum nigrum) produced by Winkler and studied by him and by Baur were found to produce as seedlings either pure tomato plants or pure nightshade plants, depending on which species made up that part of the "chimera" from which the germ-cells arise.

of the home, and are themselves unmodified by those activities. To show the biological soundness of Weismann's conclusion that soma and germ-plasm are anatomically and physiologically distinct, I may cite an experiment performed by Dr. John C. Phillips and myself:

> A female albino guinea-pig (Fig. 3) just attaining sexual maturity was by an operation deprived of its ovaries, and instead of the removed ovaries there were introduced into her body the ovaries of a young black female guinea-pig (Fig. 2), not yet sexually mature, aged about three weeks. The grafted animal was now mated with a male albino guinea-pig (Fig. 4). From numerous experiments with albino guinea-pigs it may be stated emphatically that normal albinos mated together, without exception, produce only albino young, and the presumption is strong, therefore, that had this female not been operated upon she would have done the same. She produced, however, by the albino male three litters of young, which together consisted of six individuals, all black. (See Figs. 5–7.) The first litter of young was produced about six months after the operation, the last one about a year. The transplanted ovarian tissue must have remained in its new environment therefore from four to ten months before the eggs attained full growth and were discharged, ample time, it would seem, for the influence of a foreign body upon the inheritance to show itself were such influence possible.

Since, then, germ-cells and body are distinct, heritable variations cannot have their origin in body-cells but only in the germ-plasm. The problem of evolution, therefore, on Weismann's view, becomes this — how are changes in the germ-plasm brought about?

Darwin's theory of pangenesis.

Before Weismann's time, Darwin, in common with biologists in general, had come to recognize that the germ-cells (*i. e.*, the egg and sperm-cells) are the sole vehicles of inheritance. Darwin therefore realized that if acquired characters are inherited, as everyone then supposed, bodily modifications must in some way be registered in the germ-cells, and he framed an hypothesis to explain how this could come about. This hypothesis, which he called *Pangenesis*, is put forward in the closing chapters of his book on *Animals and plants under domestication.* Darwin himself was not sure of its correctness and advanced it as he says " tentatively " only. We are very sure that it was *not* correct, but it has for us an historical interest because it had much influence upon biological investigation and theory at that time and subsequently. Logically, Darwin's theory of pangenesis may be regarded as a modification of one of Herbert Spencer's speculations upon biology.

Herbert Spencer (1820–1903) was the champion of evolution from the standpoint of philosophy, as Huxley was from the standpoint of comparative anatomy and embryology. His ideas had much influence on the development of evolutionary thought down to our own time. (See Delage and Goldsmith, 1912.) Spencer tried to explain the structure of living substance (protoplasm) in harmony with the chemical explanation of lifeless substance then current. He supposed that there are structural units of protoplasm comparable with the molecules of chemical compounds, each kind of protoplasm within the body being composed of a different kind or kinds of units. These he called *physiological units.*

Darwin adopting this same line of thought, but with a more intimate knowledge of the facts of inheritance, saw that every kind of physiological unit must be supposed to exist in the germ-cell, since out of the germ-cell an entire body develops. In his theory of *pangenesis,* he supposes that every part of the body is constantly giving off its particular kinds of units into the blood, just as a fungus gives off spores into the air. These given off units Darwin called "gemmules," or little buds. He supposed further that these gemmules are carried through the body in the blood stream, and accumulate in the germ-cells, in which they multiply as the germ-cell develops. Thus out of one germ-cell comes an entire body with its various parts, because each part was represented in the germ by a gemmule. No one today holds this theory, as Darwin stated it, but the underlying idea of preformed determining particles existing in the germ-cell reappears a little later in Weismann's theory of heredity, and has wide acceptance today in the chromosome theory of inheritance.

We shall come to these later, but for the present let us go back to Darwin's theory of *pangenesis.* Darwin's method of reaching this theory was inductive and beyond criticism. He first collected all the facts obtainable about inheritance and then attempted to frame an hypothesis which would account for them all, which would bring them all under one point of view. Where he erred was in accepting as facts some things which we know are not facts. In fitting a theory to them, he framed a false theory, simply because the assumed facts were false.

Darwin's cousin, Francis Galton, showed the unsoundness of pangenesis by a simple experiment. He reasoned thus. If, as Darwin assumes, gemmules circulating in the blood determine the character of the germ-cells, then blood of one animal transfused into blood-vessels of another should carry into the germ-cells of the second animal gemmules derived from the first animal. Consequently offspring subsequently produced by an animal into which blood has been transfused should show characteristics of the animal from which the blood was taken. Galton performed this experiment on rabbits but with results wholly negative. The experiment, however, cannot be regarded as altogether conclusive because (1) blood transfused from one individual to another probably does not long persist, but is replaced by new blood formed by the individual into which transfusion occurred. Therefore the effects of transfusion would at most be of short duration. (2) Supposing that modifications were induced in the germ-cells by transfusion, it is not to be expected, in the light of our present knowledge, that such modifications would in all cases appear in the first generation offspring, but rather in the second or later generations of offspring, but Galton did not carry the experiment so far. Galton's experiment therefore cannot be regarded as a complete refutation of pangenesis, but such a refutation has become unnecessary through the development of biological knowledge along other lines.

The theory of pangenesis was an attempt to explain the mechanism of the inheritance of acquired characters. If acquired characters are not inherited, as we now have reason to think, the hypothesis of pangenesis is unnecessary and should accordingly be discarded. This in fact is what has actually happened. The theory as Darwin stated it has no supporters at present. Those who now hold, in a modified form, that acquired characters are inherited, have adopted other ways of explaining their inheritance, or else, with Delage, admit the inadequacy of Darwin's explanation and state that no satisfactory substitute has yet been found, but entertain the hope that one will yet be discovered.

CHAPTER III

ARE ACQUIRED CHARACTERS INHERITED?

Evidence from ovarian transplantation experiments with guinea-pigs has been cited to show that body and germ-cells are morphologically and physiologically distinct and that germ-cells may be lodged in a foreign body during their development without losing their distinctive character. But this by no means proves that germ-cells are immune from modification by influences which reach them through the body. The evidence cited is negative evidence. It creates a presumption against the inheritance of acquired characters but does not prove a universal negative, which is impossible. The question whether acquired characters are or are not inherited is therefore a question to be decided only by the careful weighing of evidence. It is possible that some categories of supposed acquired characters are more readily capable of an alternative interpretation than are others. Several of these may now be discussed briefly.

1. *Mutilations.* It is now all but universally admitted that somatic modifications due to mutilation are not inherited. Nevertheless "cases" are from time to time reported, in which a man or a domesticated animal which by accident had lost a limb has produced offspring similarly defective. One of the most frequently recurring of these stories has come to me at first hand. A cat which had accidentally lost her tail gave birth to kittens part of which were short-tailed. It is not necessary to suppose that the report is inaccurate. Certain races of cats are naturally short-tailed, and a cat might produce offspring short-tailed by inheritance quite irrespective of any injury to either parent. On the other hand where docking of the tail has been followed up systematically for many generations and on a large scale, as is the case in sheep, no racial shortening of the tail is observ-

able. Finally, we have the direct experimental evidence of Weismann, who cut off the tails of mice for nineteen generations in succession without however observing any inheritance of the mutilation. We have also the evidence furnished by long-continued mutilations practiced by man upon his own person, such for example as tatooing and circumcision. The effects of such mutilations, as is well known, are not inherited in the slightest degree.

Notwithstanding all this negative evidence, Semon, who like a drowning man catches at every straw, cites Kammerer as having recently shown that a soft-bodied marine animal (Ciona, an ascidian) after its siphons are cut off regenerates new ones longer than normal, and he maintains that the young of such animals have siphons of abnormal length. In view of all the negative evidence furnished by other animals this case, as yet incompletely published, seems highly improbable. The unsupported claim throws more light upon the credibility of Kammerer as a witness (and he has brought forward many cases in recent years) than upon the general question of the inheritance of mutilations.

2. *Congenital diseases.* Cases of disease acquired by a parent and by him transmitted to his offspring are frequently reported. But all these cases are capable of other explanations than that of inheritance of an acquired character.

(*a*) In some cases a disease-producing organism may be present in the body of the parent and may pass directly into the reproductive cell. Thus in silkmoths, the organism which causes "pebrine" is transmitted as an infection within the egg, as Pasteur showed. The same is true of Texas fever in cattle. This disease is caused by a protozoön which is introduced into the blood of cattle by a tick which harbors the disease. The protozoan parasite is present in the egg-cell of the tick, so that the young tick which develops out of such infected eggs cannot fail to contain the parasite; but the disease is no more *inherited* than a grain of sand placed within the egg would be inherited. In a similar way in man syphilis may be transmitted, but it is in no true sense inherited. Yet the practical outcome is very similar; an individual once infected with syphilis is racially condemned; his seed is as truly bad as if the syphilis germ were an essential part of the germinal substance.

(*b*) The intimate relationship of parent to child may give unusual opportunities for post-natal infection, as in the case of tuberculosis. Thus the children of tuberculous parents are more liable to infection with tuberculosis, other things being equal, than the children of non-tuberculous parents. But we are not justified for that reason in speaking of tuberculosis as hereditary. It is probably in all cases acquired by the patient, individually, and not inherited. Whether some individuals are more susceptible than others is a wholly different question. Susceptibility may well be inherited.

(*c*) Just as a disease-producing organism may be received into the egg or the embryo while it is still within the body of the mother, so chemical substances in the mother's blood may enter the egg or embryo and affect its subsequent character. Thus it has been shown that in guinea-pigs immunity acquired by the mother (which is known to be due to the presence of specific substances in the blood) may be transmitted to her offspring, though the father has no such influence, the reason being that the sperm-cell is too small to carry an effective quantity of antitoxin, *i. e.*, of immunity producing substance. In such cases as I have just mentioned of transmitted immunity, the immunity does not last beyond a single generation. It has not become hereditary, it has simply been passively received by the embryo.

On the whole, we must conclude that disease transmission furnishes no evidence in favor of the transmission of acquired characters. The most debatable case is that of acquired disease transmitted in the germ-cell. For practical purposes this *is heredity*. For truly hereditary characters are often as detachable and separate from the germ-cell as foreign bodies, as we shall see when we come to study Mendelian inheritance.

3. *Induced epilepsy.* A famous case cited in all discussions of this subject is the case of Brown-Sequard's guinea-pigs.

From 1869 to 1891 Brown-Sequard experimented on thousands of guinea-pigs, developing methods by which a certain form of epilepsy could be induced through injury to different parts of the nervous system, such as the spinal cord or the sciatic nerve. In some cases the young of animals thus rendered epileptic were themselves similarly affected. Some persons who have repeated Brown-Sequard's experiments confirm his results, notably Romanes; others have failed to confirm them.

Weismann has suggested that some pathogenic organism may have got into the wounds and, migrating into the central nervous system, have caused the epilepsy, and this same organism may have infected the young. There is no evidence that such was the case, however.

Guinea-pigs are said to be strongly predisposed to epilepsy, and so the results of Brown-Sequard's experiments may be pure coincidences, or due to the transmission of a chemical substance. In some cases reported by Brown-Sequard the animals gnawed off one or more toes after the sciatic nerve had been cut. Certain of their young are reported to have done the same. This is almost certainly pure coincidence, since the evidence as regards the inheritance of mutilations is unmistakable.

4. *Acclimatization.* It is well known that animals or plants taken from one climate to another undergo changes of form. The same plant divided into two parts and planted one part upon an exposed mountain side, the other in a sheltered, fertile valley, assumes forms very different in the two places. The mountain form is short, compact and dwarfed; the valley form is tall, spreading and luxuriant. It is assumed by Lamarckians that these direct effects of the environment are to some extent inherited, that if they are repeated through a long series of generations they at last become *habitual*, so to speak, and appear spontaneously even when the external cause is lacking. In this way it is explained why mountain species in general are dwarfed, and lowland species are tall and luxuriant, even when the two are grown side by side

under identical conditions. Lamarckians assume that the direct effects of the environment have accumulated and become hereditary. Selectionists, on the other hand, maintain that dwarf species were dwarfs originally and by nature, and that they have found their way to the mountains because they alone can survive under the harsh conditions there obtaining, whereas the more luxuriant forms were better adapted to lowland conditions and have there crowded out the dwarfs. It is evident that both explanations are logically sound, though both cannot be true. Many experiments have been tried to determine which best accords with fact, but the results are not entirely conclusive because they are usually capable of alternative interpretations, and each one interprets them in accordance with the general theory which he favors. A few typical experiments may be enumerated.

(*a*) *To altered salinity.* Paul Bert, many years ago, attempted to acclimatize some Daphniae (small fresh-water crustacea) to salt water by gradually adding salt to the aquarium. At the end of forty-five days, when the water contained 1.5 per cent of salt all the adults had died; but the eggs in their brood-chambers survived, and the new generation arising from these flourished well in the salt medium. This case has been cited as a case of inherited modification, but such it clearly is not, because the parents did not succeed in becoming acclimatized; they died without becoming modified sufficiently to exist in the salt water. But their egg-cells did become so modified, and the animals developing out of them were acclimatized, through direct response to the environment, not through inheritance.

Ferronière transferred a worm (*Tubifex*) from fresh water into sea water. The animal lived there and underwent certain changes of form (loss of bristles, etc.), which became more deeply marked in later generations. After several generations the animals were unable to live in the original medium. This case is cited as showing inheritance of an acquired modification. But it can with equal propriety be interpreted as showing power of direct adaptation to changed environment. It is doubtful whether any inheritance occurred at all, for these animals usually reproduce by fission and Ferronière's " several generations " probably represent merely regenerated fragments of one and the same original individual. Had the transfer back to fresh water been gradual enough there can be little doubt that it would have been accomplished successfully.

(*b*) *To a shorter season.* Corn or other grain taken from a southern to a northern latitude adapts itself to a shorter growing season, maturing earlier. The change is not immediate, but progressive, the period required for maturity growing shorter through several generations. This at first sight looks like a good Lamarckian effect, but selectionists regard it as equally good evidence in support of their view. For it is evident that the shorter growing season in northern latitudes would act as a selecting agency, killing off all variations requiring a long growing season, so that earlier maturity would become a racial character.

5. *Effects of changed food supply.* Kellogg and Bell (1903) fed larvae of the silkmoth on a reduced quantity of mulberry leaves or on a diet partly of lettuce, partly of mulberry leaves. A decrease in size of the adult moths resulted which persisted through two subsequent generations, even when normally fed. In this way a race of dwarf moths was produced which however died out at the end of three generations. This is not a clear case of inherited modification, but of direct weakening of the organism through mal-nutrition or disease, the cause whatever it was being probably transmitted in the egg like "pebrine."

Similar but more extensive experiments were performed by Pictet (1910–1911) upon larvae of the gipsy-moth. These larvae feed by preference on oak leaves. Pictet fed some on walnut leaves and thus obtained moths of modified, paler coloration. These modifications became accentuated after several generations had been reared on walnut leaves. In one experiment the modified coloration persisted in spite of a return to normal diet. The first generation was fed on walnut leaves and presented the paler coloration; the second and third generations were fed on oak leaves but retained the modified coloration. In the third generation, however, the female showed partial return to normal coloration.

Pictet observed some cases in which moths became so completely accustomed to the diet of walnut leaves that their coloration became normal. Delage regards this as greatly weakening the case for inherited modification. He interprets the case thus. Walnut leaves are in general a poor diet for gipsy-moth larvae. They weaken the animal. This weakness persists through one or more generations, doubtless because of impaired constitution of the egg, but is not certainly transmitted as an acquired character. Indeed the race may recover from the weakening produced by the changed diet.

6. *Temperature experiments.* Many experiments have been performed with moths and butterflies in which the pupae were subjected to abnormally low or abnormally high temperatures. The effects of both extremes are in many cases similar. In general extremely low or extremely high temperatures produce darker adults. Fischer reared adults from pupae of Arctia caja exposed to a very low temperature, 8° C. Abnormally dark adults were obtained in this way. Some of the darkest of these, produced under normal conditions unusually dark offspring. Fischer considers that the induced modifications were transmitted. But this is far from certain for (1) the moths vary in darkness of coloration under normal conditions. It is not established that the supposedly induced variations lie outside the range of normal variation. (2) Fischer's treatment served to show what animals were naturally inclined to become dark, for these under treatment would become darkest, and from such Fischer bred. The supposed transmission of an acquired characteristic may be regarded in this case as nothing but the transmission of a natural or inborn characteristic, the treatment serving as a guide to selection.

Weismann, however, influenced by studies of his own upon variation in color of butterflies in northern and in southern

Europe, is willing to accept at full face value such cases as this brought forward by Fischer, and to allow that the race may become darker through long-continued subjection to lower temperatures. He supposes not that the body effects are *transferred* to the germ-cells, but that the low temperatures act simultaneously on the body and on the germ-cells, producing in them similar changes, the changes in the germ-plasm affecting the hereditary character of the race permanently. This view under the name of *parallel-induction* now has many adherents. It is a practical admission for a particular case of the Lamarckian principle of evolution guided in its course by environmental action. Whether, however, Weismann is right in his interpretation may still be regarded as an open question.

In this country, W. L. Tower (1896) has carried on extensive experiments upon potato beetles and related insects, in which variations in temperature and humidity of the environment have been followed by variations in pigmentation of the insects, similar to those observed by Fischer in the case of butterflies. Tower interprets his observations, as would Weismann, as showing, not inheritance of acquired characters but direct modification of the germ-cells, independently of the soma. For, he claims to have obtained modification of the germ-plasm, which accordingly resulted in inherited variations, where no parallel modification of the body of the parent had occurred. Inheritance of an acquired character is accordingly excluded because no modification was acquired. His strongest evidence for this claim consists of cases in which the same parents were subjected to periods of heat or cold, alternating with periods of normal temperature, each being of several weeks' duration. It was found that when a batch of eggs was produced in or immediately following a period of heat, characteristic color variations were likely to occur among the offspring which may be called heat variations and these proved hereditary. But when eggs were produced by these same parents at normal temperatures, no such variations occurred. Similar effects were obtained in cold periods, as contrasted with normal temperatures. While the bodies of the parents remained unaffected, the coloration of their offspring varied with conditions of temperature and moisture during the growth and fertilization of the eggs which produced those offspring. Tower therefore concludes that the germ-plasm was directly and permanently affected by variations in the environment during a particular sensitive growth period of the egg. This work is therefore no argument for the inheritance of acquired characters; nevertheless it is an argument for evolution directly guided by the environment, which after all is the essence of Lamarckism. There are several reasons why we should accept Tower's conclusions with some reservation.

1. In the first place his experiments are not reported in sufficient detail to enable us to form a critical opinion as to their conclusiveness.

2. If the supposed temperature and moisture effects are due solely to those conditions, they should appear equally in all eggs subjected to the same conditions, but this is not the case. Only certain individuals are modified. Since this is so, it is evident that all the eggs were not alike at the outset, for some were more sensitive than others to temperature and moisture changes in the environment, if indeed these were the agencies which caused the changes observed. A good argument could therefore be made for considering the temperature and moisture changes as merely selective agencies exerted on a collection of germ-cells already inherently variable in their potentialities. For Tower maintains that the variations once obtained are perfectly stable for an indefinite number of generations. His claim, therefore, is that by direct action of the environment for a comparatively brief period permanent changes in the germ-plasm may be brought about. It would seem that if the germ-plasm is thus directly modifiable, the action ought to be reversible. Changes of environment should *unmake* species as readily as they make them, yet such a result would scarcely harmonize with Tower's

theory, or with the known stubborn and persistent nature of heritable variations, when once they have arisen.

Kammerer of Vienna has published in the last five years the results of a long series of experiments with salamanders and lizards designed to show the inheritance of acquired characters. In this connection we will consider his experiments with temperature. The coloration of several species of lizard, with which Kammerer experimented, changes with changes of temperature. Kammerer kept lizards at abnormally high or abnormally low temperatures, and found that the induced changes of coloration persisted to some extent even after the animals were returned to normal conditions. Further, while they were thus altered, the offspring which they produced, inherited in some degree the supposedly induced changes. The evidence for this case, as for many similar cases which might be cited, is quite insufficient. Undoubtedly individual differences in coloration occur among the lizards quite independently of external temperatures. Further some probably change more readily and extensively than do others in consequence of changed temperatures. A corresponding variation among the offspring, plus and minus, as compared with their parents, would then account for such plus variations in pigmentation as Kammerer observed among the offspring and which he ascribes to inheritance of changes induced in the parents.

Sumner (1915) kept white mice, some in a cold room, some in a warm room, where they multiplied. The mice which grew up in the cold room had shorter tails and feet than those which grew up in the warm room. Animals reared in each room were now transferred to a common room of ordinary temperature and allowed to produce offspring there. In three out of four such lots of offspring studied, the cold-room parents had young with shorter tails and feet, but in a fourth lot these relations were reversed. It seems doubtful, therefore, whether the agreement between parents and offspring in three of the four cases studied is anything but a coincidence. But even supposing it to have statistical significance, it may be due, as Sumner suggests, to differences directly impressed upon the germ-cells while they were contained within the body of the parent and the parent itself, being very young, varied in body temperature with the room in which it was born. If so, there can be no question of a transfer of an effect from body to germ-cells, but only of simultaneous modification of the two.

7. *Pressure effects.* It is well known that pressure has direct effects upon the parts of the body. The skin on the soles of our feet is thickened where our weight rests upon it, and callouses form on the hand when it is used at hard work. A long illness, during which the person does not stand upon his feet causes the thickenings on the feet in part to disappear. They are undoubtedly due directly to pressure. Yet all previous generations of man have been subjected to the same action, and if acquired effects are inherited this should be. In fact, it is found that in the foetus of man, long before birth (from five months on) the skin is thicker on the sole of the feet than on the back of the foot. If this is not to be regarded as an inherited effect of use (pressure), it will be necessary to explain how the skin came to be thickened originally in those particular regions where use induces thickening.

The camel's hump has been cited as a character acquired by pressure, carrying loads on its back. But this is a less fortunate example for the Lamarckians, for the camel's hump is not due probably to pressure at all. It represents rather a reserve food organ, like special accumulations of fat in most animals. For not all animals which carry loads on their backs acquire humps, for example the ass, the horse. Further, animals may acquire humps without carrying loads, as the American bison and the humped cattle of India.

8. *Light effects.* Kammerer has experimented with the European spotted salamander (" fire salamander ") which is mottled with black and yellow areas. He finds that if salamanders are kept on a yellow background, the yellow areas become more extensive, while if the animals are kept on a

black background, their black areas become more extensive. Thus there is an automatic control of the color-pattern adapted for concealment, such as is known to occur in many fishes. Now Kammerer bred from animals, thus rendered extremely yellow, and reared part of the young on a yellow background, part of them on a black background. Both lots developed yellow spots but these were more extensive in those animals kept on a yellow background. In some of them the yellow was more extensive than in the parents. This result Kammerer ascribes to inheritance of the acquired yellow coloration added to the direct effect of the yellow background on the young. This conclusion is a fallacious one. Spotted animals are extremely variable in pattern, even when the environment does not change. If a particular kind or degree of spotting is selected in the parent animals, it may be expected that offspring will be obtained both darker and lighter than the parents. In this way the race can by selection be made either darker or lighter, quite irrespective of any change in the environment. Kammerer has obtained nothing beyond such effects as these. There is no reason to think that a change of illumination induced them to any greater extent in the second generation than it did in the first.

Another light experiment carried out by Kammerer seems to me to have more weight. This was concerned with the degeneration of the eyes in cave animals. It is a well-known fact that cave animals have bodies nearly or quite colorless and possess degenerate eyes. In animals pigment formation is an oxidation process, which frequently does not take place in the absence of light. Therefore many animals which develop in complete darkness are unpigmented. The human skin, to be sure, develops pigment even in darkness, but it develops much more of it in direct sunlight. The skin of a European is fair if he stays indoors, but darkens quickly if he spends much time outdoors in the direct sunlight. The darkest races of mankind are those which live where the sunlight is strongest and the skies are clear; the fairest races live where the sun's rays are less intense and the skies are often overcast. This signifies to the Lamarckian that the effects of the sun's rays on the human skin are inherited; but to the selectionist it means only that men vary in depth of pigmentation and that each race has migrated to that climate which it is best fitted to endure.

As regards the origin of cave animals the same diversity of opinion exists. Some consider that animals which found their way into caves lost their pigmentation and transmitted this condition to their offspring; others hold that such animals as were able to survive when by chance they made their way into caves were probably animals with little pigmentation, which could not very well exist elsewhere.

As regards the vision of cave animals, the Lamarckians hold that the eyes have degenerated because no longer used, whereas the selectionists hold that the animals which have taken to living in caves have been driven to this course by the degeneration of their eyes, and they point out that the nearest relatives of cave animals are those with poorly developed eyes, which live in semi-darkness.

Kammerer, very commendably, has put these alternative views to an experimental test. He has reared in daylight the young of the cave salamander, Proteus anguinius. Under these circumstances the skin became pigmented and the eye did not degenerate, as normally; but if the animals were kept in strong light continuously the skin became so heavily pigmented, including that in front of the eye where the transparent cornea forms in ordinary animals living in the light, that in consequence the eye itself degenerated. To overcome this difficulty Kammerer kept the animals in red light, which is less favorable than daylight to pigment formation, but suffices nevertheless to stimulate the eyes to development. The red-light treatment was given for one week out of three during the first eighteen months of the animals' lives. In this way the eye, which in cave-inhabiting individuals is very small and rudimentary, was brought to full development, with a transparent cornea and all other parts necessary for vision.

This result leaves no doubt that light is a necessary stimulus for full development of the eye in Proteus, and it is the absence of this stimulus which has led in part to the present degenerate condition of the eye. Whether or not the degeneration has advanced from generation to generation is of course conjectural, but seems highly probable. Weismann indeed considered the evidence for the progressive degeneration of disused organs so strong that he framed a special hypothesis, that of germinal selection, to account for it. To this matter we shall return later.

9. *Instincts.* Instincts are among the most vital possessions of animals, but the same difference of opinion exists as regards their origin as concerning the origin of other adaptive characteristics of organisms. Without being taught, animals do generation after generation the same acts in the same way. They seem to know, without individual experience or education, exactly what to eat, and how to secure it; how to prepare a nest or burrow of a very definite pattern; how to care for young, though they have never seen young cared for before; what to do as the seasons change; and numberless other vital and necessary things. Some say this is inherited memory, nothing less; the ancestors have learned, their descendants remember. Just as brain cells, after receiving a variety of sensations one after another, are able to reproduce them again in the same order and complexity through memory, so the reproductive cells become storehouses of racial experience or habit which they transmit as instincts. This easy way of accounting for instincts as habits registered like phonograph records in the germ-plasm has even been extended to all inheritance by a number of writers, represented at the present time by Richard Semon. This idea had great influence in America in the last quarter of the last century, when a strong school of modern Lamarckians, or neo-Lamarckians, flourished here. Many still hold to this view, but the neo-Darwinians, or followers of Weismann, have of late been rather in the ascendancy. In their view, instincts arise because the structure of the germ-plasm neces-

sitates a particular response when certain external stimuli are operative, not at all because such a response has before been made by the ancestors. Having denied that action of the individual can affect the germ-plasm within it, they can conceive of no mechanism for the transmission of habits formed by the individual, and so deny the existence of such transmission.

On the neo-Lamarckian view a hen sits on eggs because her ancestors have formed the habit of incubating eggs; on the Weismannian view the hen sits on eggs because she cannot help doing it; when she is in a certain physiological state and the nest of eggs is there, she sits, and that is all there is to it. Neither of these views is very satisfying. On one hand the neo-Lamarckian fails to explain how the first hen came to incubate, which the Weismannian glibly states is just because she is built that way; her germ-plasm necessitates it. On the other hand, the Weismannian can give us no suggestion as to how structural conditions of the germ-plasm can cause a hen to sit rather than to crow, when a nest of eggs is before her, but the well-established effects of internal secretions come here to his rescue.

The whole question of the relation of instincts to inheritance is very perplexing. At present we can make very little out of it, yet there can be no doubt that it concerns vitally our fundamental theories of evolution and such applied fields as Eugenics.

The correct attitude in the study of instincts is maintained by those who are seeking to learn how much each instinct involves, and to what extent imitation and education supplement or modify it. So far as possible each instinct should be resolved into terms of response to external chemical or physical changes, or to internal physiological states. For example it was observed many years ago that certain small crustacea instinctively swim toward a light. More careful study showed that they do so only under particular conditions. If the temperature of the water is raised, or its salinity increased, the animal may reverse its response and swim away from the source of light. These are changes of external conditions which modify the instinctive response. Internal or physiological states of the animal may also modify the instinctive responses. Thus, if the crustacean has been subjected to mechanical stimulation (repeated touching with a solid object) its response may be altered.

Again larvae of a barnacle for a few minutes after hatching swim toward the light, then they turn and swim away from it, a series of responses calculated to bring them to suitable spots for attachment. The response has been modified through some internal physiological change. Larvae of the brown-tail moth, after their winter fast, are strongly positively phototropic. They migrate up to the tips of the branches to feed on the opening buds. If at this time they are brought into the laboratory and placed in a test tube, they go toward the window and will remain at the end of the tube toward the window until they die, even if food is at the opposite end of the tube a few inches away. After the larvae have fed they are no longer phototropic. Digestion has probably destroyed the substance in their bodies on which their phototropism depended. (Loeb, *Yale Review*, July, 1915.)

By such methods of studying the instincts of animals the problem of instinct formation and inheritance may be simplified, through the elimination from it of all non-essential and outside elements.

As intelligence increases in the animal kingdom, we find that instinct sinks more and more into a subordinate position. In man there is very little inherited knowledge, if instinct may so be regarded; nearly everything has to be learned from the beginning. Nevertheless it is an open question whether intelligence has not increased through use, whether we do not learn more easily for the reason that our ancestors have for a million generations been learners. Of course I do not refer here to formal education, but only to the exercise of such intelligence as distinguishes man from other animals. May not this have been evolved in part through use ?

Summary. Notwithstanding the fundamental nature of the problem of the inheritance of acquired characters, and all that has been said and done to solve it, it still remains an unsolved problem. So far as the inheritance of mutilations, disease, and induced epilepsy are concerned, the evidence is negative or inconclusive. Acclimatization, the effects of changed food supply, and temperature effects can be explained quite as well on other grounds as on that of the inheritance of acquired characters. Pressure and light effects are somewhat more easily explained as cumulative from generation to generation, *i. e.*, as inherited acquired characters, than as due merely to germinal variation. The same is true of instincts, which, if interpreted as inherited habits, afford the strongest outstanding evidence for the inheritance of acquired characters. Nevertheless even here an alternative explanation is possible.

The Lamarckian view has been shown by the critical work of Weismann and his followers to be inapplicable to many groups of cases to which it had previously been applied. This is a real service on the part of Weismann. Nevertheless, in fields where the Lamarckian principle has not yet been disproved, viz., as regards the effects of use and disuse, it affords an easier and fuller explanation of progressive evolution and of adaptation in particular than does the selectionist view. Further, Weismann and his followers have been forced practically to concede the existence of Lamarckian evolution, that is evolution the course of which is guided in adaptive directions by the environment. For Weismann admits that the environment may cause *parallel* modifications of soma and germ-plasm. For practical purposes this is just as effective in guiding evolution as if the soma first developed modifications and then handed them on to the germ-cells. That a mechanism for the transmission of acquired characters from soma to germ-cells has as yet not been demonstrated, does not of course disprove the existence of such a mechanism. Such phenomena as memory, having its basis in the nervous system, and as the control of development and of behavior through internal secretions, give us grounds for believing that an adequate basis will be found when our knowledge of the organism becomes more complete.

The problem of acquired characters, after all, concerns only the higher animals. In the lower animals and in plants no such sharp distinction exists between body and germ-cells as we find in the higher animals. We may reproduce the entire plant from a cutting of root, stem, or even a leaf in some cases. Hence there is more chance in such cases of direct modification of the cells capable of reproduction, for most of the cells of the plant retain this capacity. In the lowest organisms (*protozoa, bacteria*) there is no distinction whatever between body and germ-cells. Every cell is capable of reproduction; and modifications produced in a cell by the environment are handed on directly to the next generation. For example medical men have learned how to decrease the virulence of diseases at will by heat or chemicals acting directly on the disease germs. They are thus able to confer immunity to a virulent disease by first producing and then introducing into the body a feeble form of the same disease.

If in the lower organisms the potentialities of living substance can thus be altered, it seems reasonable to suppose that the same possibility may exist in the higher animals and plants, provided agencies capable of producing change are allowed to act on the germinal substance. It is the sheltered position of the germ-cells which seems ordinarily to exempt them from direct modification, but we cannot safely assume that they are in all cases free from such modification. Experiments of Stockard show that in guinea-pigs repeatedly intoxicated with alcohol, the germ-cells are enfeebled so that offspring of such parents, whether male or female, are more likely to be feeble and sickly, and so to die. Experiments of Hertwig show that similarly the germ-cells of frogs are capable of being injured by emanations of radium in consequence of which enfeebled or abnormal offspring may be produced.

If the germ-cells are thus capable of modification, evolution guided by the environment must be in some measure at least a reality. The truth then lies neither in the extreme Lamarckian view that all acquired characters are inherited nor in the extreme Weismannian view, that no extraneous influences modify the germ-plasm, but somewhere in between.

CHAPTER IV

WEISMANN'S THEORY OF HEREDITY

Weismann believed that a new type of organism arises only in consequence of the origin of a new type of germ-cell. If he had been asked the ancient riddle, " which was created first, the egg or the hen," he would undoubtedly have answered, " the egg." He would have explained that the first bird came from a new type of egg laid by a reptile-like ancestor. Changed structure of the germ-plasm must result, he thought, in changed structure of the organism developing from it; and he would scarcely have admitted that a new sort of organism might arise in any other way. But the experimental study of the development of organisms has shown that the germ-plasm forms only *one* of two complementary sets of agencies which determine what the adult organism shall be. It is true that the character of the germ-cell determines in part what the character of the adult organism shall be, but so also does the environment. If we plant beans, we must expect to harvest beans not corn, but whether the harvest is large or small will depend upon the soil and the season. Sunlight, moisture, a suitable temperature, and proper chemical substances in the soil are all indispensable conditions to the production of any crop at all, and they control within limits the size, vigor, and productiveness of the plants grown. Both internal and external agencies influence the form of organisms. These are summarized in the two words, heredity and environment. Weismann emphasized the first almost to the neglect of the second. Lamarck had previously gone to the opposite extreme, emphasizing the importance of the environment not only in directly adapting the organism to its surroundings but also in controlling its heredity. It is coming to be recognized that the truth lies somewhere between these extreme views.

What in general were Weismann's views and how did he arrive at them ?

Weismann's Method

Weismann's method of constructing an hypothesis to account for heredity differed fundamentally from Darwin's. Darwin reasoned inductively, Weismann deductively. Darwin tried first to ascertain what characteristics are inherited and then to imagine a mechanism which might explain their inheritance. The result was "pangenesis." Weismann, on the other hand, first inquired what is the mechanism of inheritance and, having answered this to his own satisfaction, proceeded to the conclusion that only such characters are inherited as have their basis in this mechanism. The result was the chromosome theory of inheritance. It has this feature in common with "pangenesis," the inherited characteristics are supposed to be determined in advance and to be represented in the germ-cell by material bodies. These are the "gemmules" of Darwin, the "determiners" of Weismann. Darwin supposed that the "gemmules" migrate from all parts of the body into the germ-cells and so make it inevitable that the organism which develops out of the germ-cell shall have the same parts and properties as the parent. As regards the origin of variations, pangenesis might be called a *centripetal* theory, since determiners are supposed by it to migrate centrally toward the germ-cells.

Weismann's theory, on the other hand, is *centrifugal*; he supposes that the "determiners" originate solely in the germ-plasm and migrate thence out into the various parts of the developing body and that thus differentiation is produced. There is on his view no centripetal movement of determiners whatever; they never pass from soma to germ-cells, but only in the reverse direction.

Weismann's Mechanism of Heredity

Weismann had this advantage over Darwin; in his time knowledge of the structure of the germ-cells had considerably increased over what it was when Darwin conceived the hypothesis of pangenesis.

Weismann identified his " determiners " with certain conspicuous structures of the germ-cell called chromosomes (unknown in Darwin's time), and supposed that the nature of these determines and controls the nature and activity of the cell containing them.

It is the theoretical importance which Weismann and others have assigned to these structures that has given them their great prominence in the study and description of cell phenomena in the last thirty years. In reality the chromosomes make up a part only of the germ-cell and we have no certain knowledge that they form the more important part. Nevertheless a majority of biologists, probably, at the present time believe with Weismann that heredity is due to material substances or determiners which are located in the chromosomes. The principal reasons for so thinking are:

1. The conspicuousness of the chromosomes at the time of cell division and the very exact manner in which as a rule each of them divides into two equal parts, which pass into different cell-products.

2. The constancy of the number of the chromosomes in the same species of animal or plant. The number is different in different species but within the same species it is very constant. The only known exceptions to this rule are such as may be cited in support of the general idea that chromosomes are determiners of heredity.

(*a*) The two sexes within the same species frequently differ as regards the number of chromosomes in their germ-cells. When this is the case the male has the smaller number of chromosomes, and it is assumed that the chromosome or chromosomes which the male lacks determine femaleness.

(*b*) It has been shown in the case of the evening primroses (Oenothera) that a particular heritable type of variation

(" lata mutant ") contains one more chromosome than the parent species from which it has been observed repeatedly to arise. Another type of mutant in this same group of plants contains twice the ordinary number of chromosomes (" gigas mutant," Gates, 1915). The fact that visible characters of the organism vary simultaneously with variation in the chromosomes creates a presumption that the relationship is a causal one.

3. The experimental evidence shows that in general the father is just as influential as the mother in determining the inheritance of the children. But the egg-cell is vastly larger than the sperm-cell. Therefore much of the substance of the egg cannot be concerned in heredity. What the egg and sperm-cell have in common *consists more largely of chromatin than of any other substance.* This makes it seem probable that chromatin is concerned in heredity.

4. There exists a parallelism between the behavior of the chromosomes in the development of the germ-cells and that of certain characteristics in heredity. It is supposed, therefore, that the chromosomes actually contain chemical substances necessary for the development of these inherited characters and in this sense are determiners of heredity.

The assumption of Weismann that heredity is due to determiners contained in the germ-cell, like the pangenesis theory of Darwin, has encountered many difficulties. Consequently numerous supplementary hypotheses have been found necessary to enable it to feature as a general explanation of the facts of inheritance.

DIFFICULTIES ENCOUNTERED BY WEISMANN'S THEORY

1. *Development* (ontogeny). The first difficulty encountered lay in the explanation of the development of the individual from the egg. Weismann assumed that each cell owes its peculiar form and activities to the determiners which it contains, these being located in its chromosomes. Since the cells composing the different parts and tissues of the body differ in their forms and activities, it was necessary to assume

further that the different kinds of cells contain different determiners and consequently that as the egg divides up into cells which form the different parts of the body, these cells must receive different determiners. But microscopic examination of the cells of the body reveals no such differences; it shows differences in pretty much everything *except chromosomes,* which remain remarkably constant.

Boveri (1887) has described one case which seems to support the idea that changes in the chromatin occur, as body-cells become distinguishable from germ-cells. In the parasitic worm, Ascaris, the chromosomes are seen partially to break up and disintegrate in those cells of the embryo from which the *body* arises, whereas the original ovarian structure remains unmodified in the germ-cells. No similar case, however, has been described in other organisms, so that it seems very doubtful whether the observed changes have the significance originally attached to them by Boveri.[1] There are good reasons for believing that the chromatin content of each cell of the body is like that of every other cell of the same body, and that differentiation results either (*a*) from the position of a cell in relation to other cells, which will accordingly regulate its intake and output, or (*b*) from an original difference in substance contained in the cytoplasm of the cell (the extranuclear part). Such cytoplasmic differences between cells arise, during development, from the fact that the egg cytoplasm, at the beginning of development, is not homogeneous, and consequently the cells into which the egg divides are not alike in cytoplasmic content.

2. *Regeneration.* A man who loses a leg or an arm is deprived of the same for the remainder of his life, but many of the lower animals can restore lost parts by a process which we call regeneration. If a young salamander, a crab or a lobster is deprived of a leg, a new leg grows out again from

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[1] It is true that Hegner (1914), confirming Kahle (1908), has also observed "diminution of chromatin" occurring in the differentiation of somatic cells in an insect, Miastor, but in numerous other animals studied by Hegner he has found no such diminution of chromatin but has observed the germ-cells to be differentiated solely by cytoplasmic changes.

the stump of the old one. Such facts as these compelled Weismann to assume that, in cases of leg regeneration, not all the leg determiners pass out during development into the leg, but a supply is also held in reserve in the adjacent parts of the body; these being latent or inactive ordinarily, but becoming active when the leg is removed.

Experimental studies of regeneration made by Morgan, Child, and others scarcely support Weismann's view. They indicate that *any* undifferential cell of the body, if placed at the stump of an amputated leg, might function in leg regeneration, and so that specific leg regenerators do not exist. It is true that, in many animals, particular groups of cells have the ability to produce only a particular kind of structure, no matter where they are placed in the body, in a transplantation experiment. But in such cases it is pretty clear that we are dealing, not with the effects of specific determiners, but with the consequences of cytoplasmic differentiation which, in many cases at least, arose in the undivided egg when no nuclear difference existed within the organism, since it contained only a single nucleus.

3. *Polymorphism.* In many species of animals and plants the form of the adult differs fundamentally according to the environment in which it is placed. In certain amphibious plants (*e. g.*, Ranunculus aquatilis) the plant when growing in the air develops flat broad leaves, but when growing under water develops leaves dissected into numerous hairlike appendages. Weismann supposed that in such cases there exist alternative sets of determiners in the germ-plasm, one for the land form of leaf, one for the water form, conditions of dryness or dampness during development calling one or the other set into activity. If intermediate conditions were shown to produce intermediate effects, he would doubtless assume a joint and partial activity of both sets. In animals more complicated conditions of polymorphism occur. Many species of butterfly have spring and summer generations of offspring (broods as they are called), quite different in appearance, corresponding to different external conditions of tem-

perature or food supply. The gall insects of oak and willow trees have summer and winter generations very different in character. The summer generation usually feeds upon the soft tissues of the growing leaf and produces winged adults of both sexes; whereas the winter generation feeding on the woody tissues produced by a stem or metamorphosed bud, may consist of wingless females only, which lay unfertilized, *i. e.*, parthenogenetic eggs. In such cases Weismann supposes that alternative sets of determiners exist in the germ-plasm, which are activated by summer or by winter conditions respectively.

The case of the social insects (bees and ants) is still more complicated; here there may exist four or five different adult forms as drones (males) queens (egg-laying females) and workers or soldiers of various sorts. The workers and soldiers are all imperfectly developed females, not producing eggs ordinarily but merely taking care of the rest of the colony. Experiment has shown that the same egg, in the case of the honeybee, may produce either a queen or a worker, depending upon the amount and quality of the food supplied to the developing larva. The same is undoubtedly true of the various sorts of soldiers, among other social insects, these being alternative forms of the female. Weismann supposes that there are as many distinct sets of determiners in the egg as there are different forms into which it may develop. This line of explanation assigns to determiners located within the nucleus of the egg, influences which demonstrably lie outside the egg. As an explanation of polymorphism the theory of alternative nuclear determiners is not only superfluous but also positively erroneous.

4. *Variation.* Weismann supposed that all variations originate in the germ-plasm, and subsequently find expression in the body of the offspring, reversing the idea of Lamarck and Darwin, who supposed that variations first originate in the body and are thence transferred to the germ-cells. To account for adaptive variation, Weismann framed two supplementary hypotheses. 1. To account for the origin of

inherited variations *similar* to those which the environment directly produces in the body, he invented the hypothesis of *parallel modification* of germ-plasm and soma, to which reference has already been made. 2. To account for the apparent inheritance of the effects of use and disuse, he invented the hypothesis of *germinal selection*. On this view the various determiners which compose the germ-plasm are competing with each other in a struggle for nourishment, just as animals and plants struggle with each other for existence in the world at large. Sometimes one determiner gets more nourishment, sometimes another; but whichever one gets most nourishment, grows largest, and would consequently give rise to a plus variation of a corresponding part or organ of the body. When one determiner gets more nourishment, that is, produces a plus variation, some other determiner gets less and so produces a minus variation. Thus there is perpetual variation in the parts and organs of the body, which affords abundant material for natural selection to act upon. For if any essential organ gets too small, its possessor is eliminated. But if the organ which undergoes minus variation is a useless one, no disadvantage results to the organism; on the contrary, there is more nourishment left for essential organs, which therefore grow at the expense of the useless ones. Thus through natural selection useless organs tend to diminish and ultimately to disappear altogether, while essential organs (those most used) grow in size and activity. An *apparent* inheritance of the effects of use and disuse results.

Modern research supports Weismann's theory of nuclear determiners to this extent. It appears highly probable that special chemical substances necessary for the production of particular variations are located in particular parts of the cell, possibly in chromosomes. It is also conceivable that these substances may vary from cell to cell in amount or quality, and that under a constant environment variation in particular organs affected may thus result. But it is not necessary to suppose, as Weismann did, that these groups of substances are engaged in a struggle of any sort, with each other.

CHAPTER V

ATTEMPTS TO CLASSIFY AND MEASURE VARIATION: BIOMETRY

The period from 1880 to 1900, following Darwin's death, was marked by extreme speculation concerning evolution rather than by inductive study of its phenomena. This speculative tendency found its culmination in Weismann's brilliant essays, but his ideas, notwithstanding their brilliancy, failed to win acceptance among such biologists as insisted on having a substantial basis of well-ascertained facts on which to rest their theories. Weismann's theories were accordingly distinctly on the wane when in 1900 they received support from an unexpected source, the rediscovery of Mendel's law of heredity, which now fully established seems to require for its explanation some such system of determiners as Weismann had hypothecated and located in the chromosomes.

During this period of speculation about evolution, biologists had been looking in various directions for new tools with which to attack the study of evolutionary problems. The facts of development were more carefully studied and accurately described than ever before, and more precise information was sought about the influence of environment upon development and growth. Thus experimental embryology and experimental morphology were born, to be followed a little later by experimental breeding. Meantime, Bateson was attempting to classify variations on morphological grounds without reference to their causation, and Pearson was seeking to measure variability so as to determine its direction and rate of progress.

Darwin had throughout nearly a lifetime collected all obtainable facts about variation in animals and plants as a basis for his generalizations concerning evolution and heredity. Much of his data is contained in his work on the

Variation of Animals and Plants under Domestication. Bateson took up this work after Darwin's death and collected a large number of facts concerning variation, which he attempted to classify, but without great success. His results are found in a book entitled *Materials for the Study of Variation,* published in 1894. The most important conclusion reached by Bateson, was one which Francis Galton had already stated with great clearness in 1889 (*Natural Inheritance*), viz., that variations fall naturally into two classes, continuous and discontinuous. *Continuous variations* are those which are *graded,* the extremes being connected by a complete series of intermediate conditions; *discontinuous variations* are such as are separated by gaps in which no intermediate stages occur. Bateson believed that discontinuous variations are more important in species formation than are continuous ones, because, where variations are discontinuous, the action of natural selection is greatly simplified. In discontinuous variation selection determines the survival of one or the other of two distinct groups, since intermediates do not occur and it is unnecessary to assign selectional value to each plus or minus gradation of an organ. Galton had earlier expressed the same idea, suggesting that evolution may be like the behavior of a polyhedron when pushed. If pushed or tipped a little, it returns to its former position of equilibrium, merely oscillating back and forth on the same face as before. But if it is pushed hard enough, it rolls over on to a new face coming to rest in a new position of equilibrium. Galton suggested that discontinuous variations may be *species forming* variations, stable from the start, whereas slight or graded variations may have no lasting effect, like the oscillations of the polyhedron on one and the same face. This view was strongly supported a few years later by the botanist De Vries in his theory of mutation (1900–1903).

Meanwhile variation was being studied from a new point of view, which we may call *biometry.* Francis Galton (1889) was the founder of biometry but its full development has been due chiefly to the valuable work of Karl Pearson. The underlying idea in biometry is to apply to the study of evolution the precise quantitative methods followed in the study of physics and chemistry with such signal success.

Biometry is the statistical study of variation and heredity. It deals with masses, not with individuals, differing in this respect from the method of Darwin and Bateson. It seeks to obtain a quantitative estimate, as precise as possible, of variation in one generation, and to compare with this a similar quantitative estimate of the next generation and then by comparing these to learn in what direction evolution is taking place and at what rate. In some cases it has attempted to discover the direction of evolution from the character of the variation within a single generation.

Biometry is best adapted to deal with continuous variation, but it has its uses also in dealing with discontinuous variations. Its ideal, to make biological investigation more accurate and comprehensive, is wholly commendable. But mere collection and compilation of biological statistics will not advance knowledge unless brought into relation with other facts about living things, and it is in this respect chiefly that biometricians have sometimes erred, drawing unwarranted conclusions from their statistical data.

Biometry means literally the *measurement of living things*. It is obvious that it can deal only with characteristics which are measurable, such as linear dimensions, volume, weight, or number of parts. One of the cases most carefully studied by Galton was human stature. This case illustrates very well the methods and results of biometric study.

Measurements made at the Harvard gymnasium of the height and weight of one thousand students of ages eighteen to twenty-five are classified in Table 1. In order that the number of classes may not be too great for convenient statistical treatment, height classes are formed of 3 cm. each. Thus students measuring 155, 156, or 157 cm. are all placed in a common class, whose middle value is 156 cm. In dealing with large numbers, the probability is that each of the three

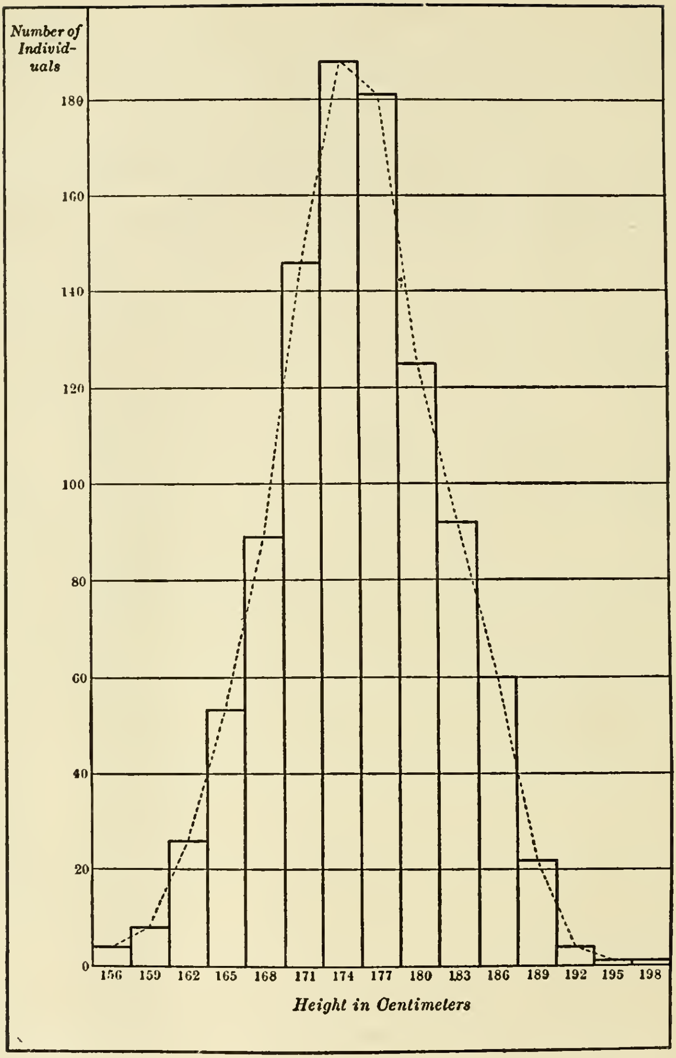

FIG. 9. Frequency-polygon and curve showing variation in height of one thousand Harvard students of ages 18–25.

measurements would occur as frequently as either of the others, so that the middle value would be a fair representative of the class and could be used in statistical computations as the class value with entire propriety and accuracy. Weight classes are also formed of three kilos extent in classifying the weights. The numbers of individuals found in each height class are shown in the totals at the bottom of Table 1. The largest number of individuals is found in the class, 173–175 cm., viz., 188. On either side of this class the numbers of individuals (called *frequencies*) fall off steadily reaching a frequency of four in the shortest class and of one in the tallest class. In Fig. 9 the relative frequencies of the height classes are shown graphically, each column of the figure being proportional in altitude to the frequency of the class which it represents. This method of representing variation is called the " method of loaded ordinates." By joining the tops of the several columns of the figure, as in the dotted line, a so-called variation curve is obtained.

The class with greatest frequency in a group of variates is called the *mode, i. e.*, the fashionable class. It has, of course, the *tallest* ordinate in the variation figure (class 174, Fig. 9).

A classification of the same one thousand students as regards weight is given in the totals at the right of Table 1, and a graphic presentation of the same data in Fig. 10. The modal class is that which has as its middle value sixty-three kilos. This has a frequency of one hundred and fifty-four with the two adjacent classes almost as large and more remote classes diminishing in frequency to minima in classes forty-five and one hundred and five. The falling off is more rapid to the left than to the right of the modal class, so that in all there are only six classes below the mode but there are fourteen classes in the range of variation above the mode. This results in a " skew " or asymmetrical curve obtained by joining the tops of the ordinates (dotted line, Fig. 10). The variation curve for the height measurements (Fig. 9) was also slightly skew, but its skewness was much less than that of the curve for weight.

A variation curve which is free from skewness resembles what mathematicians call a " frequency of error " curve or simply a " curve of error " or " normal curve " (Fig. 11).

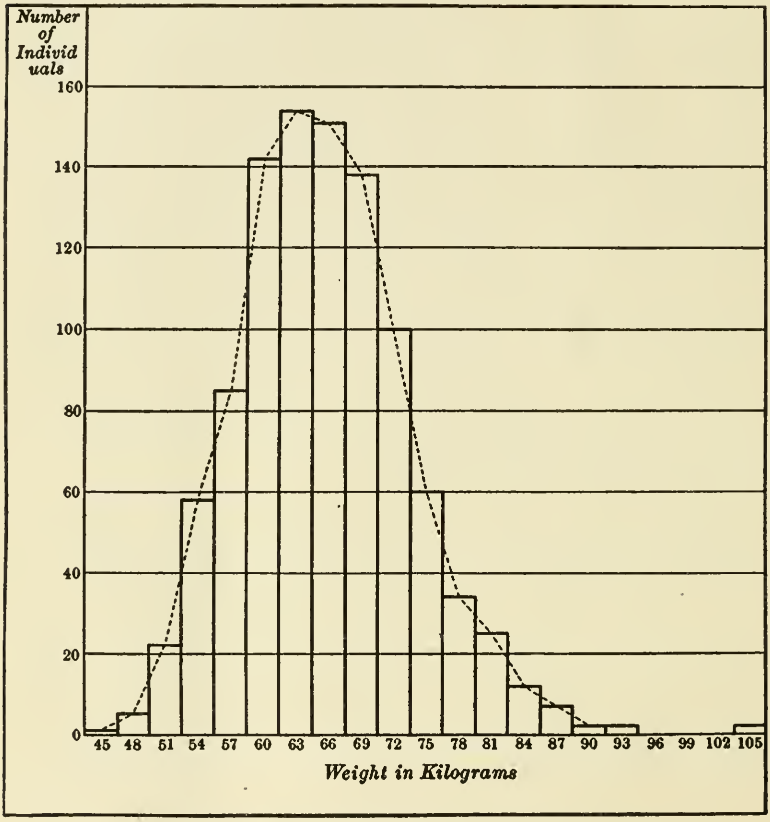

Fig. 10. Frequency-polygon and curve showing variation in weight of one thousand Harvard students of ages 18–25.

TABLE 1

Showing the Variation in Height and Weight and the Correlation between Height and Weight among 1000 Harvard Students of Ages 18–25 Measured at the Harvard Gymnasium in the Years 1914–1916

Weight in Kilos.	Height in Centimeters															Totals
	155–157	158–160	161–163	164–166	167–169	170–172	173–175	176–178	179–181	182–184	185–187	188–190	191–193	194–196	197–199	
44– 46	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	1
47– 49	1	..	3	1	..	..	..	..	..	..	..	..	..	..	..	5
50– 52	1	2	1	6	4	6	2	..	..	..	..	..	..	..	..	22
53– 55	1	4	8	15	12	8	7	2	..	..	1	..	..	..	..	58
56– 58	..	1	4	10	15	19	20	11	3	2	..	..	..	..	..	85
59– 61	..	1	5	8	22	43	25	21	11	4	2	..	..	..	..	142
62– 64	1	..	2	8	9	31	39	29	21	10	2	2	..	..	..	154
65– 67	..	..	1	2	10	21	25	39	30	18	4	..	1	..	..	151
68– 70	..	..	1	1	9	6	30	27	32	16	13	2	..	1	..	138
71– 73	..	..	..	2	4	5	18	20	12	18	15	4	2	..	..	100
74– 76	..	..	..	..	1	4	11	15	6	7	9	6	..	..	1	60
77– 79	..	..	..	..	1	2	2	8	5	7	4	4	1	..	..	34
80– 82	..	..	..	..	..	..	4	6	3	4	6	2	..	..	..	25
83– 85	..	..	..	..	..	..	2	1	2	3	2	2	..	..	..	12
86– 88	..	..	..	..	2	1	2	..	..	2	..	..	..	..	..	7
89– 91	..	..	..	..	..	..	..	..	..	1	1	..	..	..	..	2
92– 94	..	..	..	..	..	..	1	1	..	..	..	..	..	..	..	2
95– 97	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
98–100	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
101–103	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
104–106	..	..	..	..	..	..	..	1	..	..	1	..	..	..	..	2
Totals	4	8	26	53	89	146	188	181	125	92	60	22	4	1	1	1000

Mean height = 175.33 cm. (5 ft. 9 in.)
Mean weight = 65.66 kilos. (144.75 lbs.)
σ height = 6.58 cm.
σ weight = 7.84 kilos.

CV height = 3.76 %
CV weight = 11.94%
r height-weight = .54

It expresses the result of the simultaneous action of several independent causes, or contingencies. If, for example, I toss ten coins in the air simultaneously, it is certain that each one will show uppermost on landing either a head or a tail, but the landing of one coin does not affect that of the others. The landing of each coin is a separate contingency. If the coins are thrown several times and a count made of the number of heads following each throw and these results are then combined and plotted we shall get a frequency of error curve about the number five which will be the most *frequent*, *i. e.*, the modal result, heads being of the same frequency as tails. See Fig. 12 and Table 2.

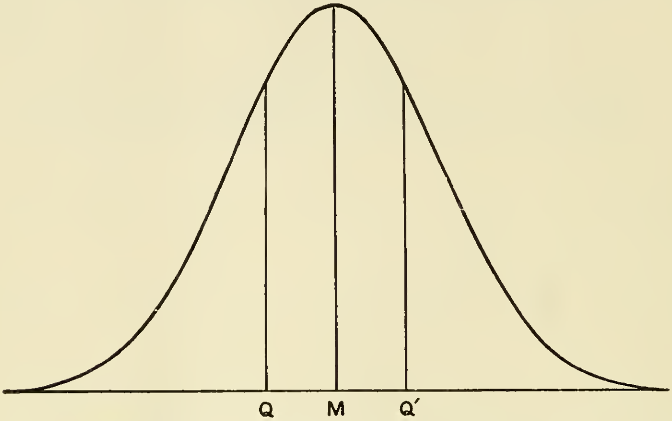

Fig. 11. "Frequency of error" or "normal" curve M, mode. Q, Q′, quartile; one-half the area of the figure lies between Q and Q′. After Lock.

Biometry has established the fact that biological variation, when measurable, is commonly of the frequency of error type, which means that it must be the result of several independent contingencies or causes. Some of these causes are doubtless environmental, others are due to heredity. Their combined action is to produce variation of the frequency of error type.

TABLE 2

Probable Results of Tossing Ten Coins Simultaneously. (After Lock)

Heads		Tails	Relative Probability	Heads		Tails	Relative Probability
10	and	0	1	4	and	6	210
9	"	1	10	3	"	7	120
8	"	2	45	2	"	8	45
7	"	3	120	1	"	9	10
6	"	4	210	0	"	10	1
5	"	5	252				

The action of several heredity factors which are independent of each other produces a curve of the same sort; and so do several environmental factors independent of each other; in most cases of variation agencies of both sorts are at work. But in some cases the causes which tend to produce plus variation may be stronger or weaker than those which tend to produce minus variation. The result is an unsymmetrical or " skew " variation curve. Thus among Harvard students the causes which tend to produce variation in weight above the normal are apparently stronger than those causes which tend to produce weight below the normal, as is indicated by Fig. 10. The same was found to be true still more emphatically of adult males in England, according to data tabulated by Yule.

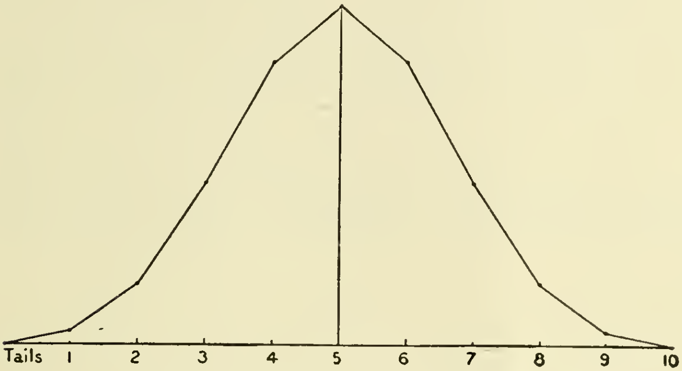

Fig. 12. A graphic presentation of the data contained in Table 2. After Lock.

In some cases, biological variation is exclusively in one direction from the mode, *i. e.*, all the causes of variation which are operative tend in one direction. Thus the common buttercup varies in number of petals from five upward but very rarely in the reverse direction. Five is the commonest or modal number, but the observed variation curve is one-sided. See Fig. 14, H 1887.

It is evident that to describe the character of variation in any case it will not suffice to name the mode; we must also state whether the variation is symmetrical about the mode, how extensive is its range, and whether the majority of the variates cluster closely about the mode or are widely scattered. To express these various features of the variation, special statistical coefficients have been devised. It will suffice for our purposes to discuss only the more important of these.

1. The *mean*, or *average*, is in a case of symmetrical variation, identical with the mode. Thus the average height of the thousand Harvard students (Table 1) is close to 174 mm., the mode. But their average weight lies outside and above the modal weight class, because their variation in weight is decidedly skew, more men exceeding 66 kilos in weight than fall below that weight. To find the *average*, *multiply the value of each class by the number of individuals contained in it, add the products, and divide by the entire number of individuals.*

2. *Average Deviation* and *Standard Deviation.* Two sets of variates having the same mode and mean may nevertheless differ widely in their variability, one being more scattered than the other.

To express the greater *spread* of one curve as compared with another, the *average deviation*, may be employed. That is, we may estimate how far, on the average, an individual taken at random differs from the *mean*. This is computed as follows: *Find the deviation of each class from the mean, multiply this by the frequency of that class, add the products, and divide by the entire number of variates.* The quotient is the average deviation. Formula $A\,D = \frac{\Sigma\, D f}{n}$ in which Σ signifies that the *sum* is to be taken of the products indicated, D means the *deviation* of each class value from the mean of all variates, f means the frequency (number of individuals) of each class, and n means the total number of variates (individuals). This measure of variability is improved, mathematicians tell us, by the method of least squares, *i. e.*, by *squaring* the deviation of each class, and *extracting the* *square root* of the final quotient. To distinguish it from the average deviation, this is called the *standard* deviation. Its formula is $\sigma = \sqrt{\frac{\Sigma D^2 f}{n}}$. It forms a measure of the degree of *scatter* of the variates. This measure is expressed in the same units as were employed in measuring the variates.

3. To compare one case of variation with another as regards degree of scatter of the variates, another expression has been devised which is called the *Coefficient of Variation.* It is obtained by dividing the standard deviation by the mean. Formula, $C\,V = \frac{\sigma \times 100}{M}$. It is an abstract number expressing the variability in *per cent* of the mean.

Judged by their coefficients of variability, Harvard students are found to be more variable in weight than in height, the respective coefficients ($C\,V$) for height and weight being 3.76 and 11.94. See Table 1.

4. Another important tool of the biometrician should be mentioned, viz., the *coefficient of correlation*, which is a measure of the extent to which one character varies in agreement with another.

In order to obtain a coefficient of correlation a set of observations may be classified simultaneously as regards two characteristics. Thus we might inquire is there any correlation between the height and the weight of men, and if so how much ? Are tall men on the whole heavier than short ones or *vice versa* ? To determine this matter we must first obtain observations on the height and weight of the same individuals. The observations may then be classified in a correlation table (as in Table 1), which is made by ruling paper into squares and entering the observations on height in vertical columns, and the observations on weight in horizontal rows, or *vice versa.* An individual 156 cm. in height and weighing 48 kilos will be entered in the square at which column 156 and row 48 intersect; an individual of the same height but ten kilos heavier will be recorded in the third square below, and so on. When all the observations have been entered in the table, we may proceed to calculate[1] a coefficient of correlation which will be a measure of the extent to which men vary in weight as they vary in height. Its numerical value will lie between 0 and 1.

It is evident that the correlation would be most complete if men invariably increased in weight as they increase in height. The entries in the table would then be distributed in a single diagonal row running across the table from its upper left-hand corner to its lower right-hand corner. We should infer that in such a case the two completely correlated phenomena were due to the same causes or contingencies exactly. Our numerical coefficient of correlation would in such a case be + 1.

In reality such correlation as this rarely, if ever, occurs in biological material. We know that men of the same height vary in weight and *vice versa.* For weight does not depend upon height alone but also upon width and thickness and specific gravity. It does however depend *somewhat* upon height, and so our table would show *incomplete* correlation, which would be expressed by a coefficient less than 1 but greater than 0.

---

[1] The coefficient of correlation is calculated by the formula

$$r = \frac{\Sigma\, D_x\, D_y\, f}{n\, \sigma_x\, \sigma_y}.$$

in which r is the coefficient of correlation, D_x and D_y are the deviations of each observed group of individuals from the respective means of height and weight, Σ signifies that the *sum* of the products indicated is to be taken, n is the total number of individuals observed, and σ_x and σ_y are the standard deviations for height and weight respectively. To express in the form of a *rule* the procedure to be followed in calculating the coefficient of correlation between (say) height and weight: First find the *average height* and the *average weight* of all individuals observed, then their standard deviation in height and their standard deviation in weight. Next determine for each square of the table its deviation from the *average* height and *average* weight respectively. Find the product of these two deviations (regarding signs) and multiply it by the number of individuals recorded in the square under consideration. After such a product as this has been found for *every square in the table,* the products are to be added (regarding signs) and this sum is to be divided by the product of the two standard deviations times the total number of individuals observed. There are several short-cuts by which the calculation as here described may be shortened or simplified. For a description of these the reader is referred to the special works of C. B. Davenport (1904), Eugene Davenport (1907), and Yule (1912).

In the table the entries would show a *tendency* to group themselves about the diagonal, but there would be a considerable scattering of entries in squares not lying in the diagonal. Compare Tables 1 and 3.

If men in general did *not* increase in weight as they increase in height, but actually grew lighter as they grow taller, then we should find a *negative* value for the coefficient of correlation. Cases of this kind are occasionally met with, but they are of no importance since by rearrangement of the correlation table (as by reversing the order of the grades for one character) a negative result may always be converted into a positive one of like magnitude. The essential thing, which a coefficient of correlation does, is to show whether two observed phenomena are or are not causally related to each other. Any result other than 0 indicates that the two sets of phenomena are so related, and the *size* of the coefficient indicates the *extent* to which they are causally related, up to a value of + 1 which would indicate that they are due to identical causes.

In biometry the correlation table has found two principal uses (1) to show what parts or processes of an organism vary in unison and to what extent they so vary and (2) to measure heredity. Examples of the first use are the relation between height and weight in man already discussed and the relation between one skeletal dimension and another, as skull length and femur length, which in rabbits have a correlation of 0.76, or the lengths of femur and humerus, which in rabbits show a correlation of 0.86. See Table 3. The correlation values for corresponding bone measurements in men are very similar. If the correlation between two parts is known, it is possible from a knowledge of the magnitude of one of them to predict the magnitude of the other, with an accuracy indicated by the coefficient of correlation. If for instance the correlation between femur and humerus is 0.86 and I know the femur length of an individual, I can estimate his humerus length with an accuracy of about 86 per cent.

The second use of the correlation coefficient is still more important, viz., to measure the strength of heredity. It affords a means of comparing the strength of a character in successive generations and of thus measuring its heredity. Thus the amount of white on the body of piebald rats is a variable character (Fig. 125) to some extent inherited. The resemblance between parents and offspring in grade of whiteness as shown in Table 4 is about 23 per cent, the correlation coefficient in this case being 0.233. Pearson found, for his human data, the height of father and son to have a correlation of 0.514; between brother and brother he found the correlation to be 0.511, figures which indicate the strong inheritance of size differences in man.

TABLE 3

Correlation Table showing the Relation between Femur-length and Humerus-length in 370 Rabbits. $r = 0.857$

From MacDowell, Appendix, Table 16.

Humerus, Length in mm.	Femur, Length in mm.										Totals
	76–77	78–79	80–81	82–83	84–85	86–87	88–89	90–91	92–93	94–95	
60–61	1	2	1	..	..	..	..	..	..	..	4
62–63	2	16	13	4	..	..	..	..	..	..	35
64–65	..	9	51	32	4	..	..	..	..	..	96
66–67	..	..	13	52	47	4	..	..	..	..	116
68–69	..	..	1	10	29	29	4	..	..	..	73
70–71	..	..	..	..	3	13	13	4	..	..	33
72–73	..	..	..	1	..	1	4	1	3	..	10
74–75	..	..	..	..	..	..	..	..	2	..	2
76–77	..	..	..	..	..	..	..	..	.	..	..
78–79	..	..	..	..	..	..	..	..	..	1	1
Totals	3	27	79	99	83	47	21	5	5	1	370

Probable error is a measure of the reliability of a statistical conclusion. The need of such a measure rests on the fact that the number of observations on which the conclusion rests is finite, that is the number of observations is smaller than the class concerning which generalization is made. For example, if I knew the height of each member of a college class I could calculate the absolute average height of the class without any possible inaccuracy, if the arithmetical operations were free from mistakes. But if I want to know the average height of students in the entire college and have only the measurements of a particular class on which to base an opinion, it is obvious that my conclusion is possibly erroneous. Perhaps I have not a fair sample of the students of the college as regards height. Obviously the larger my class the less probable is any error in my conclusion. If my class included half or more than half of all the men in the University (unselected as to size) the probability of an error through random sampling would be small; and if it included *all* men in the University, the probability of error would disappear.

TABLE 4

Correlation Table used as a Measure of Heredity. The Character Studied is the Relative Amount of White in the "Hooded" Pattern of Piebald Rats. $r = 0.233$.

From Castle and Phillips, Table 11.

Grade of Parents	Grade of Offspring										Totals
	$2\frac{3}{4}$	3	$3\frac{1}{4}$	$3\frac{1}{2}$	$3\frac{3}{4}$	4	$4\frac{1}{4}$	$4\frac{1}{2}$	$4\frac{3}{4}$	5	
$3\frac{3}{4}$	..	..	..	2	7	2	..	..	..	..	11
$3\frac{7}{8}$	2	7	17	87	162	41	11	3	3	..	333
4	..	3	2	25	87	65	24	6	1	1	214
$4\frac{1}{8}$	..	3	3	16	49	27	8	2	2	..	110
$4\frac{1}{4}$	..	..	..	2	13	5	3	1	1	..	25
$4\frac{3}{8}$	..	..	..	..	1	3	..	..	..	..	4
Totals	2	13	22	132	319	143	46	12	7	1	697

What statisticians call the *probable error* is a pair of values one larger than the calculated value, one smaller, the chances being *even* that the true value lies inside or outside the limits of these values.

To understand the significance of this statement, consider for a moment the *normal* curve or curve of error (Fig. 11). On either side of its mean and mode (M) we may draw a line

(Q, Q') so placed that between the two lines half the area of the figure will be included. It is obvious that an individual taken at random may fall in any part of the figure, but the chances are *even* that it will fall inside or outside of the probable error (Q, Q') since *half* the group occurs in each position. The probable error of a determination of the *mean* equals $\pm\ 0.6745 \frac{\sigma}{\sqrt{n}}$. Notice in accordance with this that the more individuals one observes the more accurate his conclusion, *i. e.*, the less the probable error, but not in direct proportion to the number observed but to its square root.

The probable error of the standard deviation is expressed by the equation,

$$E_\sigma = \pm\ 0.6745 \frac{\sigma}{\sqrt{2n}}$$

The probable error of the coefficient of variability is expressed by

$$E_c = \pm\ 0.6745 \frac{CV}{\sqrt{2n}}$$

The probable error of the coefficient of correlation is expressed by

$$E_r = \frac{\pm\ 0.6745\ (1 - r^2)}{\sqrt{n}}.$$

The probable error of a determination of the cross-over percentage between two linked characters is

$\pm\ .6745\sqrt{\frac{P\ (1 - P)}{n}}$ in which P is the observed cross-over percentage. (Haldane, 1919.)

CHAPTER VI

THE MUTATION THEORY

The theory that new races and species originate discontinuously and not gradually, has received its strongest support from the work of the Dutch botanist, Hugo de Vries, who was one of the pioneers in the recent revival of the study of evolution by experimental methods.

De Vries began studying the variation of species of plants in the field, transferring these variations to his garden and there subjecting them to selection. He found that garden conditions, *i. e.*, cultivation and improved nutrition, increased variability as regards minor differences in size, luxuriance and productiveness. Such variations, which Bateson calls continuous, De Vries speaks of as fluctuating. They depend, he thinks, wholly upon nutrition but do not permanently affect the specific type. This is stable, like Galton's polyhedron resting securely on one of its faces. Its fluctuations due to nutrition are like the oscillations of the polyhedron. No permanent change results from them. De Vries indeed appears to think that selection acting upon fluctuations (*i. e.*, upon continuous variations) may change the average condition of the race, but that such changes will not persist unless maintained by rigorous selection. As soon as selection ceases, he thinks, the race begins a gradual return to its former condition.

De Vries supported this view both with data from the history of cultivated plants and with direct experiments of his own. He showed for example that in the history of the cultivation of the sugar beet, the unimproved race contained (about sixty years ago) from 7 to 14 per cent of sugar. Vilmorin after two generations of selection of the sweetest beets for seed obtained beets with 21 per cent of sugar. Since then the choice of individual seed beets according to sugar-content has become general. Often hundreds of thousands of beets are tested at a single factory. De Vries has plotted a variation curve for forty thousand beets tested in 1896 at a factory in Holland. The result (Fig. 13) was a beautiful frequency of error curve with its mode at 15.5 per cent. The upper limit of variation was 21 per cent, or the same per cent as

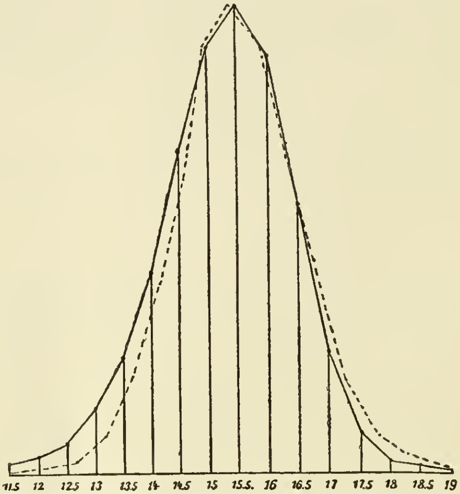

FIG. 13. Graph showing the variation in sugar-content of 40,000 sugar beets tested at a factory in Holland. (After De Vries.) The data are as follows:

Percent sugar	12	12.5	13	13.5	14	14.5	15	15.5	16	16.5	17	17.5	18	18.5	19
Number	340	635	1,192	2,205	3,597	5,561	7,178	7,829	6,925	4,458	2,233	692	133	14	5

The broken line shows the theoretical curve for $(a + b)^{20}$.

Vilmorin obtained after two generations of selection. The general average, to be sure, is considerably higher than when the selection began, but De Vries believes that this is due in part to improved methods of cultivation and more accurate methods of determining the sugar-content. He believes that whatever real improvement has taken place is due largely to the elimination of the poorest sorts through selection, and that these would speedily become reëstablished if the selection were discontinued.

The fact has only recently come to light that sugar beets are regularly cross-pollinated by a minute insect, a species of thrips, the plant being scarcely capable of self-pollination. This explains why constant selection is required to maintain a high standard. Hybridization constantly occurs and for this reason fully stable types cannot be obtained.

De Vries is also led to adverse conclusions concerning selection as an agency in producing racial changes by experiments of his own, one of the most extensive of which was an attempt to increase by selection the number of petals in the common meadow buttercup (*Ranunculus bulbosus*). This regularly has five-petaled flowers, but an occasional flower contains one or more extra petals. See Fig. 14. When this plant was cultivated in his garden, De Vries found the average number of petals to be 5.6. After five successive selections the average was raised to 8.6, the upper limit of variation from eight to thirty-one, and the mode (or commonest condition) from five to nine. De Vries concludes that the change thus produced could be maintained only by continued selection, and that further progress could probably not be made. This conclusion seems to me unwarranted, but I state it as illustrative of the general view of De Vries, who maintains that when a permanent racial change occurs it is due to something different from fluctuating variability, viz., to a discontinuous variation or *sport*, a process which De Vries

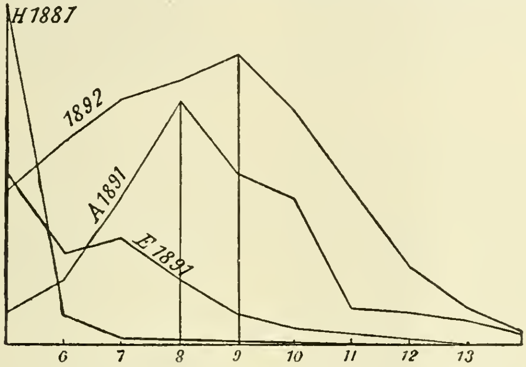

FIG. 14. Variation of the buttercup (Ranunculus bulbosus) in number of petals preceding and following selection. H 1887, variation curve of unselected race. E 1891 and 1892, curves for successive generations of the selected race. A 1891, curve for parent plants of the 1892 generation. (After De Vries.)

calls *mutation*. Mutation, he believes, involves a change in the nature of the germ-cells, whereas fluctuation involves only effects due to environment. These latter may indeed modify the soma, and also the germ-plasm temporarily, but not permanently. Weismann, as we have seen, admits for certain cases a direct modification of the germ-cells by the environment, and believes that such modifications when once produced are permanent. De Vries on the other hand is much more ready to admit modification of the germ-plasm by the environment, but maintains that these modifications are not permanent. Permanent changes in the germ-plasm, according to De Vries, have no relation to the action of the environment. They arise spontaneously out of internal conditions and are not necessarily adaptive in nature. Most of them perish because not adaptive (*i. e.*, beneficial) in character; only those mutations survive in a state of nature which chance to be adaptive. The environment does not cause mutations, according to De Vries, but only determines what ones may survive. Evolution is thus due primarily to internal causes; but its course is guided by the environment, which *selects* those mutations which are capable of survival.

The Evidences of Mutation

Two lines of evidences in favor of mutation may be cited, one general, the other special.

1. *The occurrence of elementary species.* Among many wild species of plants there occur varieties quite distinct and breeding true, but differing from each other by such minor characteristics as ordinarily escape notice. Thus in the common dandelion a considerable number of varieties may be distinguished. Some have narrow leaves, some broad leaves; on some the leaves are deeply notched, on others almost entire. If we save the seeds of any of these peculiar individuals and plant them we find that the characteristics of the parent plant are inherited. They breed true like distinct species, indeed they may be regarded as little species within the dandelion species. De Vries calls them " elementary "

Fig. 15. Lamarckiana.

Fig. 16. Gigas.

Fig. 17. Lamarckiana.

Fig. 18. Gigas.

Fig. 19. Oblonga.

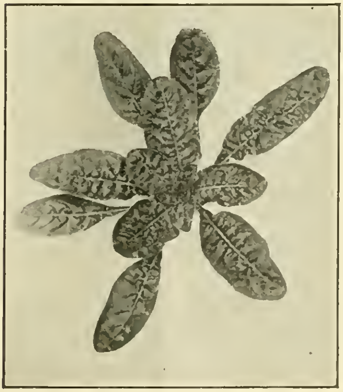

Fig. 20. Lata.

Oenothera Lamarckiana and Some of its Mutants
Fig. 15, late in season; 16, at mid-season; 17–20, in rosette stage (wintering-over stage).
From cultures and photographs by Professor B. M. Davis.

species. The same thing may be observed in the case of violets; many distinct varieties or elementary species may be recognized within the commonly recognized species, and experiment has shown that these breed true.

Among cultivated plants a similar diversity of forms occurs, especially among such as are self-fertilized, as for example wheat, beans and peas. Varieties differ in shape of leaf, hairiness, color of seed, fruit or flowers, and many other characteristics. Varieties of the same species may in many cases be grown together in the same field without mixing, and even if artificially crossed may not produce an intermediate character but one which is distinctive of one parent or the other. The same thing is true of our domesticated animals. Varieties are often discontinuous, intermediates being unknown. De Vries joins with Bateson in urging a discontinuous origin for such variations and brings forward much experimental evidence in support of this idea. He supposes that discontinuous variations arise through internal causes, that is by mutation.

2. "*Mutation*" *in Oenothera.* For proof of discontinuity in variation De Vries relies principally upon a specific case which he has studied for many years, that of Lamarck's evening primrose (*Oenothera Lamarckiana*). See Figs. 15–26. This plant is supposed to be of American origin. It is cultivated in Europe (and to some extent in America) in parks and gardens, for its showy yellow flowers. Here and there it has escaped from cultivation and grows wild. In this condition De Vries found it in an abandoned potato field near Amsterdam. But the plant has not been found growing wild in the western hemisphere, original home of the *oenotheras.* For this reason some naturalists are inclined to regard it as of hybrid and old-world origin.

The plant is a biennial, five or six feet high when fully grown, with a stout branching stem bearing at the ends of its branches spikes of bright yellow flowers. They open towards evening, as the name, evening primrose, indicates and are pollinated by bees and moths. On bright days their duration is confined to one evening and the following morning, but in cloudy weather they may remain open longer.

When De Vries discovered this plant growing wild in 1886 he was struck by its variability. It seemed to be producing, in the isolated spot where he found it, new species, the thing for which De Vries had long been looking. He says:

> I visited [the spot] many times, often weekly or even daily during the first few years, and always at least once a year up to the present time [eighteen years later]. This stately plant showed the long-sought peculiarity of producing a number of new species every year. Some of them were observed directly in the field, either as stems or as rosettes [young plants in their first year's growth]. The latter could be transplanted into my garden for further observation, and the stems yielded seeds to be sown under like control. Others were too weak to live a sufficiently long time in the field. They were discovered by sowing seed from plants of the wild locality.

By these means over a dozen new types were discovered never previously observed or described. De Vries has given to these distinctive names; some of them he regards as true species, others merely as varieties; the basis of his distinction, an arbitrary one, does not concern us. The peculiarity of the case is, not that a group of undescribed species or varieties was found growing together, but that they were produced year after year from the seed of the parent species, and from their first origin bred true (in most cases) to their distinctive characters.

TABLE 5

Some Mutants of Oenothera Lamarckiana

1. Smooth-leaved (*laevifolia*)	Retrogressive or Loss variations.
2. Short-styled (*brevistylis*)	
3. Dwarf (*nanella*)	
4. Giant (*gigas*)	Progressive or Gain variations.
5. Red-veined (*rubrinervis*)	
6. Pale-leaved (*albida*)	Feeble mutants.
7. Oblong-leaved (*oblonga*)	

One of the mutants was distinguished by its smooth slender leaves (*laevifolia*); another by the short style of its flowers (*brevistylis*); a third by its dwarf habit (*nanella*, Fig. 26), one-fourth the height of the parent species. All three bred true to these peculiarities which De Vries considers due

Fig. 21. Lamarckiana.

Fig. 22. Gigas.

Fig. 23. Oblonga.

Fig. 24. Scintillans.

Fig. 25. Lata.

Fig. 26. Nanella.

Oenothera Lamarckiana and Some of its Mutants

Figs. 21–24, inflorescence and leaf from base of main stem; 25, inflorescence only; 26, entire plant. (From Davis.)

to loss of something the parent possessed. For this reason he calls them " retrogressive varieties."

Two very vigorous mutants the *giant* (*gigas*, Figs. 16, 18, 22) and the *red-veined* (*rubrinervis*) De Vries considers to have acquired additional characters not present in the parent, and for this reason he regards them as genuine " elementary species " (having attained a new progressive characteristic). The giant is no taller than its parent species but much stouter, with larger leaves and flowers. Its cells contain twice as many chromosomes as those of the parent species, which fact is considered very important by some cytologists. A wide-leaved mutant (*lata*, Figs. 20, 25) has one extra chromosome in its nucleus ($14 + 1 = 15$).

The red-veined mutant (*rubrinervis*) has more red on its leaves and stems than has the parent species; its stems are also more brittle, the bast fibres having thinner walls.

Two other mutants are naturally feeble, not strong enough to survive in a wild state. They are *albida* (the pale whitish mutant), and *oblonga* (having oblong leaves on feeble plants, about half as tall as the parent species). See Figs. 19 and 23.

" These seven new forms," says De Vries, " which diverge in different ways from the parent type, were absolutely constant from seed. Hundreds or thousands of seedlings may have arisen, but they always come true and never revert to the original *O. Lamarckiana*-type." Several other mutants have been described by De Vries, among them scintillans, but they are less constant in character than those already mentioned. Their behavior need not here be considered.

A fact deserving especial attention in connection with De Vries' experiments is the repeated occurrence of the same mutation year after year in pedigree cultures from self-fertilized plants, showing that these particular variations occur with some regularity.

Starting with nine plants transplanted from the field De Vries carried a culture through seven subsequent generations, always planting seed of Lamarckiana parents, with the results shown in Table 6.

TABLE 6

AN EIGHT-GENERATION PEDIGREE CULTURE OF LAMARCK'S EVENING PRIMROSE

Generation	Gigas	Albida	Oblonga	Rubrinervis	Lamarckiana	Nanella	Lata	Scintillans
1	..	..	..	..	9	..	..	..
2	..	..	..	..	15,000	5	5	..
3	..	..	..	1	10,000	3	3	..
4	1	15	176	8	14,000	60	73	1
5	..	25	135	20	8,000	49	142	6
6	..	11	29	3	1,800	9	5	1
7	..	..	9	..	3,000	11	..	..
8	..	5	1	..	1,700	21	1	..

The giant mutant was obtained only once, but all the others in at least three different generations, from *Lamarckiana* parents.

Without going into the details of the case, to which De Vries has devoted an entire volume, we may notice what deductions or " laws " De Vries bases upon it.

1. *New elementary species appear suddenly and attain full constancy at once.*
2. *The same new species are produced in a large number of individuals.*

This would, of course, give them a better chance and fuller test in the struggle for existence than if they appeared but once.

3. *Mutability is something fundamentally different from fluctuating variability.* All organs and all qualities of *Lamarckiana* fluctuate and vary in a more or less evident manner, and those which I had the opportunity of examining more closely were found to comply with the general laws of fluctuation. But such oscillating changes have nothing in common with the mutations. Their essential character is the heaping up of slight deviations around a mean, and the occurrence of continuous lines of increasing deviations, linking the extremes with this group. Nothing of the kind is observed in the case of mutations. There is no mean for them to be grouped around and the extreme only is to be seen, and it is wholly unconnected with the original type. It might be supposed that on closer inspection each mutation might be brought into connection with some feature of the fluctuating variability. But this is not the case. The dwarfs are not at all the extreme variants of structure, as the fluctuation of the height of the *Lamarckiana* never decreases or even approaches that of the dwarfs. There is always a gap. The smallest specimens of the tall type are commonly the weakest, according to the general rule of the relationship between nourishment and variation, but the dwarfs according to this same rule are of course the most robust specimens of their group.

Fluctuating variability, as a rule, is subject to regression. The seeds of the extremes do not produce an offspring which fluctuates around their parents as a center, but around some point on the line which combines their attributes with the corresponding characteristic of their ancestors, as Vilmorin has put it. No regression accompanies mutation, and this fact is perhaps the completest contrast in which these two great types of variability are opposed to each other.

The offspring of my mutants are, of course, subject to the general laws of fluctuating variability. They vary, however, around their own mean, and this mean is simply the type of the new elementary species.

4. *The mutations take place in nearly all directions.*

Some are larger, others smaller than the parent species; some more vigorous and productive, others less so; some are more heavily pigmented, others less so; some can survive in competition with the parent form, others cannot. There is no evidence of adaptive modification, or modification controlled by the environment for the benefit of the species. The variation is in all directions.

The facts upon which De Vries bases these generalizations have been verified in the main by a number of workers in different parts of the world, notably in this country where several botanists have studied the seedlings of Lamarck's evening primrose. But the facts are not interpreted in the same way by all observers.

One view accepts the facts at their face value, including the regularity of the occurrence of the same mutation in successive generations, and its entire distinctness from the parent form, but maintains that *O. Lamarckiana* is a hybrid plant, not a pure species, and that the so-called mutation is only a new illustration of the splitting up of a hybrid into new forms, many of which are constant, a thing which is known frequently to occur following hybridization.

In support of this view it may be said that *O. Lamarckiana* has not been found growing wild in this country, its supposed place of origin, though careful search has been made for it. On the other hand *O. Lamarckiana* has for many years been growing wild in certain English stations, notably on the sand hills north of Liverpool, and there are good reasons for believing that the *Lamarckiana* first brought out by seedsmen about the year 1860 may have come from some English locality. The fact that several species of *Oenothera* are known to have been in England previous to this date suggests that *Lamarckiana* may have arisen through the crossing of other forms.

In this connection it is of interest to note that a hybrid has been synthesized by Davis from a cross of *O. franciscana* with *O. biennis,* which is essentially indistinguishable in its systematic characters from *O. Lamarckiana.* Furthermore this hybrid behaves like *Lamarckiana* in producing two classes of progeny when crossed with certain wild species as described in the next paragraph. This *Lamarckiana*-like hybrid, which has been given the name of *neo-Lamarckiana,* in the fourth generation bred true for about one-third of its progeny and therefore gave a very much larger percentage of variants than *Lamarckiana,* but its seed fertility was very much higher, which may account for the fact. At this stage in the investigation *neo-Lamarckiana* presents a breeding behavior at least similar to that of *Lamarckiana* and it will be a matter of interest to see whether in later generations the resemblance may not become more marked.

Another adverse view of De Vries' theory, with less concern as to the origin of *O. Lamarckiana,* maintains that however it originated it is clearly not pure genetically; if not actually a hybrid of recent origin, it at least has the genetic character of a hybrid and hence the regularity of its mutations. For hybridization, as we shall see, is a sure means of producing new and stable varieties. Hybridization experiments made by De Vries and repeatedly confirmed by others show that in every generation *O. Lamarckiana* produces different kinds of fertile gametes. In particular, it forms two classes of hybrids, " twin hybrids," in approximately equal numbers, in crosses with certain wild species, as do several of the wild species in crosses with each other, so that it is evident that *O. Lamarckiana,* as well as some wild species of *Oenothera,* have the variability characteristic of hybrids. Even those which seem to breed true, and which do breed true when self-pollinated, may give a variable progeny in crosses, and they *seem* to breed true merely because certain classes of their progeny are too feeble to survive. For in some cases only a fractional part of the seeds produced contain embryos capable of survival.

According to the views expressed above, *Oenothera Lamarckiana* is best interpreted as an impure or hybrid species which only breeds true in a relatively high degree because of extensive sterility, which eliminates large numbers of gametes and zygotes that differ from the germinal cells which reproduce the *Lamarckiana* type. The " mutants " come from occasional seeds of different types that survive the heavy mortality which renders sixty per cent or more of the seeds infertile and about fifty per cent of the pollen grains abortive. If this is the correct explanation of the peculiar breeding behavior of *Lamarckiana*, this plant is very far from being representative of a pure species, as De Vries assumed it to be, and is hardly suitable material for experiments designed to give evidence of mutation.

Even if we reject this explanation and consider that the mutability of the evening primrose has no causal relation to its hybridity, it by no means follows that mutation is a general method of origin of new varieties and species among animals and plants, which is the thesis of De Vries. In recent years the expression "mutation theory" has been used in a sense very different from that in which De Vries originally used it, and implying merely the origin of new and stable organic forms by change in single inheritance factors (genes), whether these produce striking variations (sports) or variations so minute as to be scarcely observable. This form of mutation theory will be discussed in a later chapter. To the mutation theory of De Vries, as a *general theory* of evolution, it seems to be a fatal objection that such mutation as it recognizes is not *general* in occurrence. Crosses of species or varieties as found in the wild state more often reveal the existence of numerous minute genetic differences than a single or a few striking differences.

CHAPTER VII

THE PIONEER PLANT HYBRIDIZERS: THE DISCOVERY AND REDISCOVERY OF MENDEL'S LAW

While De Vries was engaged in his studies of the evening primrose he hit upon an idea far more important, as most biologists now believe, than the idea of mutation, though De Vries himself both then and since has seemed to regard it as of only minor importance. He called this the "*law of the splitting of hybrids.*" The same law, it is claimed, was independently discovered about the same time by two other botanists, Correns in Germany, and Tschermak in Austria. Further, historical investigations made by De Vries showed that the same law had been discovered and clearly stated many years previously by an obscure naturalist of Brünn, Austria, named Gregor Mendel, and we have now come to call this law by his name, Mendel's law. Mendel was so little known when his discovery was published that it attracted little attention from scientists and was soon forgotten, only to be unearthed and duly honored years after the death of its author. Had Mendel lived forty years later than he did, he would doubtless have been a devotee of biometry, for he had a mathematical type of mind and his discovery of a law of hybridization was due to the fact that he applied to his biological studies methods of numerical exactness which he had learned from algebra and physics. In biology he was an amateur, being a teacher of the physical and natural sciences in a monastic school at Brünn. Later he became head of his monastery and gave up scientific work, partly because of other duties, partly because of failing eyesight.

The subject of plant hybridization had received considerable attention from botanists for a century before it was taken up by Mendel and the law of the *splitting* of hybrids which was discovered by Mendel and rediscovered by De

Vries had narrowly escaped discovery at the hands of their predecessors. There was lacking only the numerical exactness of a Mendel or the clear-sighted analysis of a De Vries to bring to light the rule governing the splitting of hybrids.

By a hybrid we understand an organism produced by the crossing of two distinct species or varieties of plant or animal, *i. e.*, an organism which has an individual of one species or variety as its mother and an individual of a different species or variety as its father. At times and by certain naturalists a distinction has been made between the offspring of a species cross and that of a variety cross, the term hybrid being limited to the progeny of a species cross, and the term mongrel being used to designate the progeny of a variety cross. But it has been found quite impossible to distinguish species from varieties sharply, for Darwin showed that varieties may be only incipient species, and that no definition can be framed of variety which will not also include species and *vice versa*. Accordingly at present we use the terms *species* and *variety* in a relative sense only. The differences which exist between species are supposed to be either more *numerous* or *greater* in degree than those which exist between varieties. The terms to the majority of biologists imply nothing more than this. If we cannot distinguish species from varieties, it is obvious that we cannot distinguish the products of a species-cross from the products of a variety-cross, and so at present all cross-bred offspring, whether of species or varieties, are called hybrids. The same law of splitting applies to all, as we shall see.

The pioneer plant hybridizer was Joseph (Gottlieb) Kölreuter (1733–1806) who between the years 1760 and 1766 carried out the first series of systematic experiments in plant hybridization which had ever been undertaken. The more important features of Kölreuter's work have been thus summarized by Lock, pp. 150–155.

> These experiments not only established with certainty for the first time the fact that the seeds of plants are produced by a sexual process comparable with that known to occur in animals, but also led to a knowledge

of the general behaviour of hybrid plants, which was scarcely bettered until Mendel made his observations a century afterwards.

Kölreuter found that the hybrid offspring of two different plants generally took as closely after the plant which yielded the pollen as after that upon which the actual hybrid seed was borne. Indeed, he found that it made little or no difference in the appearance of the hybrid which of the parental species was the pollen-parent (male), and which the seed-parent (female) — that is to say, in the case of plants the result of reciprocal crosses is usually identical. Thus, for the first time it was definitely shown that the pollen-grain plays just as important a part in determining the characters of the offspring as does the ovule which the pollen-grain fertilizes. This was a wholly novel idea in Kölreuter's time, and the fact was scarcely credited by his contemporaries.

Kölreuter had no means of discovering that the contents of a single pollen-grain unite with the contents of a single ovule in fertilization. But he ascertained by experiments that more than thirty seeds might be made to ripen by the application of between fifty and sixty pollen-grains to the stigma of a particular flower, so that, if he had had any hint of the actual microscopic processes of fertilization, he would have been quite prepared for the more fundamental discovery.

Kölreuter, indeed, believed that the act of fertilization consisted in the intimate mingling together of two fluids, the one contained in the pollen-grain, and the other secreted by the stigma of the plant. The mingled fluids, he supposed, next passed down the style into the ovary of the plant, and arriving at the unripe ovules, initiated in them those processes which led to the formation of seeds. In this belief Kölreuter simply followed the animal physiologists of his time, who looked upon the process of fertilization in animals as taking place by a similar mingling of two fluids. Now that we know that fertilization consists essentially in the intimate union of the nuclei of two cells, one of which, in the case of plants, is the ovum contained within the ovule, whilst the other is represented by one of a few cells into which the contents of the pollen-grain divide, we can understand more clearly the bearing of Kölreuter's observation. And it is greatly to this eminent naturalist's credit that he succeeded in carrying out his observations with so much accuracy, when the full meaning of those observations was of necessity hidden from his comprehension.

Kölreuter was the first to observe accurately the different ways in which pollen can be naturally conveyed to the stigma of a flower. This may take place either by the pollen-grains falling directly upon the stigma, or by the agency of the wind, or, lastly, the pollen may be carried by insects visiting the flowers. And he recognized many features characteristic of flowers apt to be fertilized in one or other of these ways in particular. Thus he was aware, for example, of the nature and use of the nectar which so many flowers produce — namely, that it is the substance from which the bees — by far the most diligent visitors of flowers — obtain their honey.

Curiously enough, Kölreuter was not aware of the existence of any natural wild hybrid plants. But he was quite right in contending that

FIG. 26*a*. The first artificially produced plant hybrid and its parents. A, Nicotiana paniculata; B, N. rustica var. humilis; C, F_1 hybrid between A and B; D, individual flowers of the hybrid (middle), of N. paniculata (right), and of N. rustica (left). Photographs by Prof. E. M. East, from his repetition of Kölreuter's pioneer experiment.

supposed examples of such hybrids required for their substantiation the experimental proof, which could only be afforded by making actual artificial crosses between the putative parent species.

The first hybrid made artificially by Kölreuter was obtained in 1760 by applying the pollen of *Nicotiana paniculata* to the stigma of *Nicotiana rustica*. The hybrid offspring of this cross showed a character intermediate between those of the two parent species in almost every measurable or recognizable feature, with a single notable exception. This exception was afforded by the condition of the stamens and of the pollen grains produced by the hybrids. These organs were so badly developed that in all the earlier experiments, self-fertilization of the hybrid plants yielded no good seed at all, nor were the pollen grains of the hybrid any more effective when applied to the stigmas of either of the parent species. On the other hand, when pollen from either parent was applied to the stigmas of the hybrid plants, a certain number of seeds capable of germination was obtained, although this number was much smaller than in the case of normal fertilization of either parent species. This partial sterility, affecting in particular the stamens and the pollen which they produce, is a feature common to the majority of hybrids between different natural species. Many such hybrids, indeed, are altogether sterile, so that a further generation cannot in any way be obtained from them. On the other hand, the members of different strains or varieties which have arisen under cultivation yield, as a rule, when crossed together offspring which are perfectly fertile.

In subsequent years Kölreuter was able to obtain a very few self-fertilized offspring from hybrids of the same origin as the above. The resulting plants were described as resembling their hybrid parent so closely as to be practically indistinguishable from it.

The offspring obtained by crossing the hybrid plants with pollen from either parent showed in each case a form more or less intermediate between that of the original hybrid and that of the parent species from which the pollen was derived. But the plants were not all alike in this respect, some of them being much more like the parent species than others, and some, again, varying in other directions. There were also considerable differences between the different individuals in respect of fertility, so that some of the plants were more and some less sterile than the original hybrids. Also, there was some tendency to the production of malformations of the flowers and other parts.

One of the most noted of Kölreuter's experiments was that which consisted in repeatedly crossing a hybrid plant with one of the parent species from which the hybrid was derived. By continuing to pollinate the members of one generation after another with the pollen of the same parent species, plants were at last arrived at which were indistinguishable from the parent in question. We shall return to this fact later on, when the reader will be in a position to appreciate its importance more fully.

Kölreuter found that the result of reciprocal crosses is usually identical — that is to say, the offspring obtained by fertilizing a plant A with pollen from a plant B are not to be distinguished from those obtained when B is fertilized with the pollen of A. But the two opposite processes of fertilization are not always equally easy to carry out. An extreme instance of this circumstance was met with in the case of the genus *Mirabilis*. *Mirabilis jalapa* was easily fertilized with pollen from *M. longiflora*. During eight years Kölreuter made more than two hundred attempts to effect the reverse cross, but without success.

It was shown by Kölreuter that hybrids between different races or varieties of the same species are usually much more fertile than hybrids obtained by crossing distinct species. Indeed, he believed that varieties of a single species were in all cases perfectly fertile together, whilst hybrids between species always showed some degree of sterility. But in this case Kölreuter based his definition of a species upon the very point at issue, and when he found forms, which other botanists regarded as good species, to be perfectly fertile together, he immediately regarded them as being only varieties of a single species.

One curious point is worth noting in this connection. Five varieties of *Nicotiana tabacum* were found to be perfectly fertile with one another, but when crossed with *Nicotiana glutinosa* one of them was found to be distinctly less sterile than the rest.

Another interesting point observed by Kölreuter was the fact that hybrid plants often exceed their parents in luxuriance of growth. Upon this fact, as we shall see later on, Knight and afterwards Darwin based theoretical conclusions of considerable importance in connection with the problem of sex.

To pick out the salient features of the foregoing account we may notice:

1. That Kölreuter established the occurrence of sexual reproduction in plants by showing that hybrid offspring inherit equally from the pollen plant and the seed plant.
2. He showed that hybrids are commonly intermediate between their parents in nearly all characters observed, such for example as size and shape of parts.
3. Many hybrids are partially or wholly sterile, especially when the parents are very dissimilar (belong to widely distinct species). Such hybrids often exceed either parent species in size and vigor of growth.
4. Kölreuter did not observe the regular *splitting* of hybrids which Mendel and De Vries record, but some of his successors did, particularly Thomas Knight (1799) [1] and John Goss (1822) [1] in England who were engaged in the crossing of garden peas with a view to producing more vigorous and

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[1] For a fuller account of the work of these early plant hybridizers, see Lock.

productive varieties, and Naudin (1862) in France who made a comprehensive survey of the facts of hybridization in plants and came very near to expressing the generalization which Mendel reached four years later. He pointed out the significance of the fact first observed by Kölreuter that hybrids may be brought back to the form of either parent by repeated crossing with that parent. Naudin supposes that the potentialities of each species are contained in its pollen and ovules and the potentialities of both species are present together in the hybrid. If species A is fertilized by species B, the hybrid contains potentialities AB. Naudin supposes that these potentialities may segregate from each other in the pollen grains and ovules of the hybrid plant. An ovule A of such a hybrid plant, if fertilized by pollen of the pure species A, will form a plant of exactly the same nature as pure species A. This idea of the segregation of potentialities in the germ-cells of the hybrid was adopted by Mendel. He added to it the conception that the segregation applies to *single* potentialities or characteristics rather than to all the potentialities of a species at once, and the result is what we call Mendel's law. Like all great discoveries it was not made out of hand, nor as the result of one man's work alone. Mendel added one final touch to the work of his predecessors as summarized by Naudin, and the result was that hybridization became for the first time an orderly and understandable process, capable of throwing light on normal heredity.

CHAPTER VIII

MENDEL'S LAW OF HEREDITY ILLUSTRATED IN ANIMAL BREEDING

Mendel's law may best be explained with the aid of examples, which will be chosen, for convenience, from the heredity of guinea-pigs. If a guinea-pig of pure race with colored fur (say black) is mated with a guinea-pig having uncolored (white) fur, a so-called albino, the offspring will all have colored fur, none being albinos. See Figs. 27–30. To use Mendel's terminology, colored fur dominates in the cross, while albinism recedes from view. Colored fur is, therefore, called the *dominant* character; albinism, the *recessive* character.

But if now two of the colored individuals produced by this cross are mated with each other, the recessive (albino) character reappears on the average in one in four of their offspring (Fig. 30). The reappearance of the recessive character, after skipping a generation, in the particular proportion, one fourth, of the second generation offspring, is a regular feature of Mendelian inheritance. It may be explained as follows (see Fig. 30*a*): the gametes which united in the original mating of a pure colored individual with an albino must have transmitted, one color (C), the other albinism (c). The contrasted characters were then associated together in the offspring. But color from its nature dominated, since albinism is due apparently to the lack of something necessary to the formation of color, which the other gamete would supply.

But when the young produced by this cross have become adult and themselves form gametes, the characters, color and albinism, will separate from each other and pass into different gametes, since, as regards the transmission of alternative

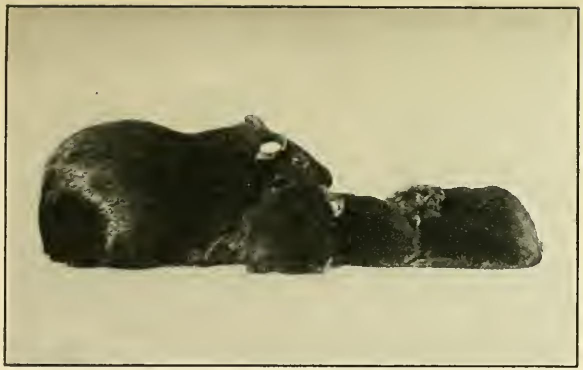

FIG. 27. Pure-bred black mother and young.

FIG. 28. Albino sire.

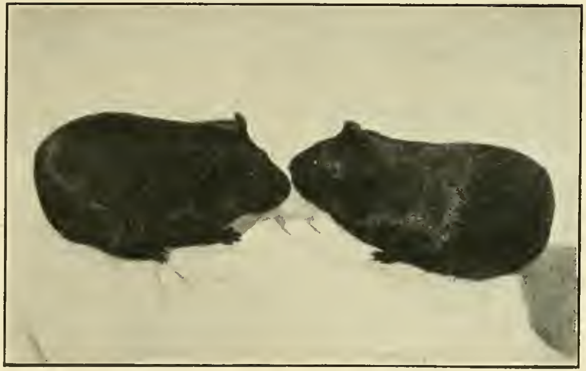

FIG. 29. Young grown to maturity.

FIG. 30. Second generation young.

characters like color and albinism, a gamete is able to transmit only one, its nature being simplex.

Accordingly a female hybrid will transmit the character, color (C), in half its eggs, and the contrasted character, albinism (c), in half its eggs. A male hybrid will also transmit color (C) in half its sperm, and albinism (c) in the other half.

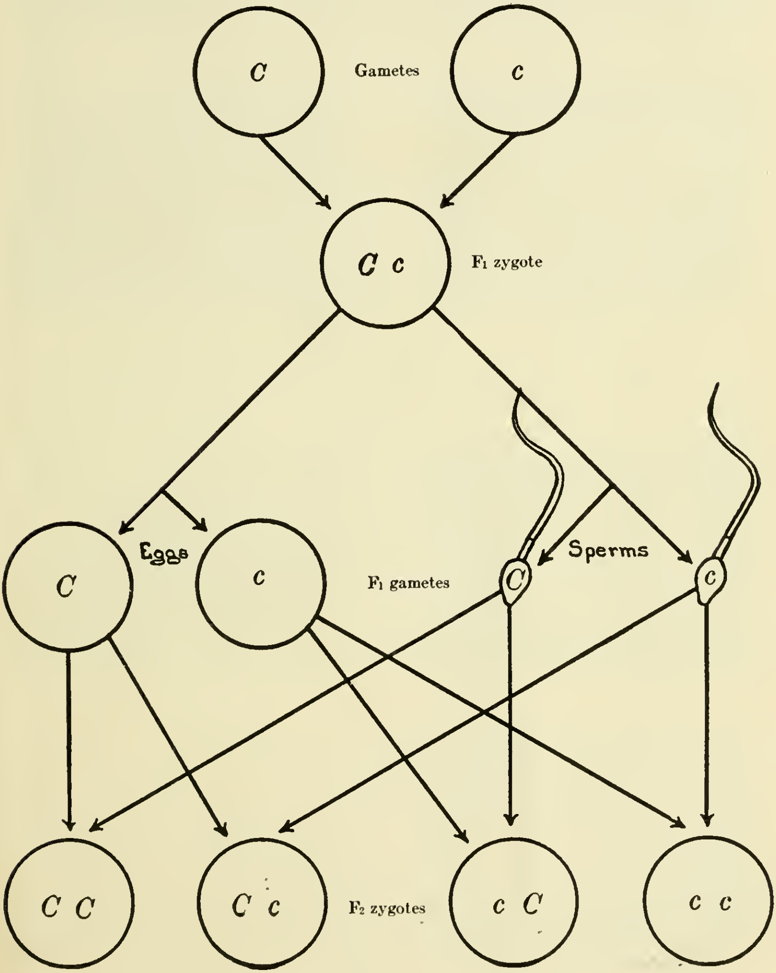

Fig. 30*a*. Diagram to explain the inheritance of color (*C*) and albinism (*c*) in the cross shown in Figs. 27–30.

If the type of egg which transmits color (C) is fertilized as readily by one type of sperm as by the other, combinations will result which are either CC or Cc in character. And if the type of egg which transmits albinism (c) is also fertilized as readily by one kind of sperm as by the other, combinations will result which are either Cc or cc in character. Putting together the results expected from the fertilization of both types, we get 1 CC : 2 Cc : 1 cc, *i. e.*, one combination of color with color, two combinations of color with albinism, and one combination of albinism with albinism; or three combinations which contain color (and so will show it) to one combination which lacks color and so will be white. This agrees with the observed average result.

The albino individual may be expected to transmit only the albino character (c), never color (C), which it does not possess. Experiment shows this to be true. Albino guinea-pigs mated with each other produce only albino offspring. But the colored individuals are of two sorts, CC and Cc in character. The CC individual is pure, so far as its breeding capacity is concerned. It can form only C gametes. But the Cc individuals may be expected to breed exactly like the first generation hybrids, which had the same composition. They will transmit color (C) in half their gametes, albinism (c) in the other half. Experiment justifies these expectations also. The test of individual animals may readily be made by mating them one by one with albinos. The pure colored individuals (CC) will produce only colored offspring, since they transmit color (C) in all their gametes. But the other and more numerous class of colored individuals (Cc) will produce offspring part of which will be colored (Cc) and the remainder albino (cc). The two kinds of dominant individuals, those which breed true and those which do not, we may call *homozygous* and *heterozygous*, following the convenient terminology of Bateson. A *homozygous* individual is one in which *like* characters are joined together, as CC or cc; a *heterozygous* individual is one in which *unlike* characters are joined together, as Cc. It goes without saying that reces-

10


Fig. 31


Fig. 32


Fig. 33


Fig. 34

Figs. 31–34. Results of a cross between two varieties of guinea-pig differing in two unit-characters, color and roughness of fur. Fig. 31, a colored and smooth-coated guinea-pig.

Fig. 32. An albino and rough-coated guinea-pig. Fig. 33. One of the F_1 young, colored and rough.

Fig. 34. A smooth-coated albino, one of the four varieties occurring among the F_2 young. The other three varieties of F_2 young are like the parents and grandparents respectively (Figs. 31–33).


Fig. 35


Fig. 36


Fig. 37


Fig. 38

Figs. 35–38. Results of a cross between two varieties of guinea-pig differing in the two unit-characters, color and length of fur. Fig. 35, a colored and short-haired guinea-pig. Fig. 36, an albino and long-haired guinea-pig. The F_1 young were colored and short-haired like the parent shown in Fig. 35. Fig. 37, a colored and long-haired guinea-pig, one of the new F_2 varieties. Fig. 38, an albino and short-haired guinea-pig, the other new F_2 variety. The two other F_2 varieties were like the grandparents (Figs. 35 and 36).

sives are always homozygous. For they do not contain the dominant character; otherwise they would show it.

It will be observed that, in the cross of colored with albino guinea-pigs, color and albinism behave as a pair of alternative units which may meet in fertilization but separate again at the formation of gametes.

Mendel's law as illustrated in this cross includes three principles: (1) The existence of *unit-characters*, (2) *dominance*, in cases where the parents differ in a unit-character, and (3) *segregation* of the units contributed by the respective parents, this segregation being found among the gametes formed by the offspring.

The principles of dominance and segregation apply to the inheritance of many characteristics in animals and plants. Thus in guinea-pigs a rough or rosetted coat (Figs. 32 and 33) is dominant over the ordinary smooth coat. If a pure rough individual is crossed with a smooth one, all the offspring are rough; but in the next generation smooth coat reappears in one-fourth of the offspring, as a rule. Again, in guinea-pigs and rabbits a long or angora condition of the fur (Figs. 36, and 37) is recessive in crosses with normal short hair. All the immediate offspring of such a cross are short haired, but in the next generation long hair reappears in approximately one-fourth of the offspring.

In cattle, the polled or hornless condition is dominant over the normal horned condition; in man, two jointed fingers and toes are dominant over normal three-jointed ones.

In each of the cases thus far considered a single unit-character is concerned. Crosses in such cases involve no necessary change in the race, but only the continuance within it of two sharply alternative conditions. But the result is quite different when parents are crossed which differ simultaneously in two or more independent unit-characters. Crossing then becomes an active agency for the production of new varieties.

In discussing the crosses now to be described, it will be convenient to refer to the various generations in more precise terms, as Bateson has done. The generation of the animals originally crossed will be called the parental generation (P); the subsequent generations will be called filial generations, viz., the first filial generation (F_1), second filial (F_2), and so on.

When guinea-pigs are crossed of pure races which differ simultaneously in two unit-characters, the F_1 offspring are all alike, but the F_2 offspring are of four sorts. Thus, when a smooth colored animal (Fig. 31) is crossed with a rough albino (Fig. 32), the F_1 offspring are all rough and colored (Fig. 33), manifesting the two dominant unit-characters, — colored coat derived from one parent, rough coat derived from the other. But the F_2 offspring are of four sorts, viz., (1) smooth and colored, like one grandparent, (2) rough and albino, like the other grandparent, (3) rough and colored, like the F_1 generation, and (4) smooth and albino, a new variety (Fig. 34). It will be seen that the pigmentation of the coat has no relation to its smoothness. The dark animals are either rough or smooth, and so are the white ones. Pigmentation of the coat is evidently a unit-character independent of hair direction, and as new combinations of these two units the cross has produced two new varieties, — the rough colored and the smooth albino.

Again, hair-length is a unit-character independent of hair-color. For if a short-haired colored animal (either self or spotted, Fig. 35) be crossed with a long-haired albino (Fig. 36), the F_1 offspring are all short-haired and colored, but the F_2 offspring are of four sorts, viz., (1) colored and short-haired, like one grandparent, (2) albino and long-haired, like the other, (3) colored and long-haired, a new combination (Fig. 37), and (4) albino and short-haired, a second new combination (Fig. 38).

Now the four sorts of individuals obtained from such a cross as this will not be equally numerous. As we noticed in connection with the simple cross of colored with albino guinea-pigs, dominant individuals are to the corresponding recessives as three to one. Therefore, we shall expect the short-haired individuals in F_2 to be three times as numerous as the long-haired ones, and colored ones to be three times as numerous as albinos. Further, individuals which are *both* short-haired and colored should be 3 × 3 or nine times as numerous as those which are neither short-haired nor colored. The expected proportions of the four classes of F_2 offspring are accordingly nine short colored : three long colored : three short albino : one long albino, a proportion which is closely approximated in actual experience.

The Mendelian theory of independent unit-characters accounts for this result fully. No other hypothesis has as yet been suggested which can account for it. Suppose that each independent unit has a different material basis in the gamete. Let us represent the material basis of hair-length by a circle, that of hair-color by a square; then combinations and recombinations arise as shown in Fig. 39. The composition of the gametes furnished by the parents is shown in the first line of the figure; that of an F_1 zygote, in the second line; that of the gametes formed by F_1 individuals in the third line. S meets s and C meets c in fertilization to form an F_1 individual duplex and also heterozygous as regards hair-length and hair-color, but these units segregate again as the gametes of the F_1 individuals are formed, and it is a matter of chance whether or not they are associated as originally, S with C and s with c, or in a new relationship, s with C and S with c. Hence we expect the F_1 individuals to form four kinds of gametes all equally numerous: SC, sc, sC, and Sc. By chance unions of these in pairs nine kinds of combinations become possible, and their chance frequencies will be as follows:

Short Colored	Long Colored	Short Albino	Long Albino
1 SSCC	1 ssCC	1 SScc	1 sscc
2 SSCc	2 ssCc	2 Sscc	
2 SsCC			
4 SsCc			
9	3	3	1

Four of these combinations, including nine individuals, will show the two dominant characters, short and colored; two classes, including three individuals, will show one dominant and one recessive character, viz., colored and long; two more classes, including three individuals, will show the other dominant and the other recessive character, viz., short and albino; and lastly, one class, including a single individual, will show the two recessive characters, long and albino. The four *apparent* classes, or, as Johannsen calls them, *phenotypes*, will accordingly be as 9 : 3 : 3 : 1.

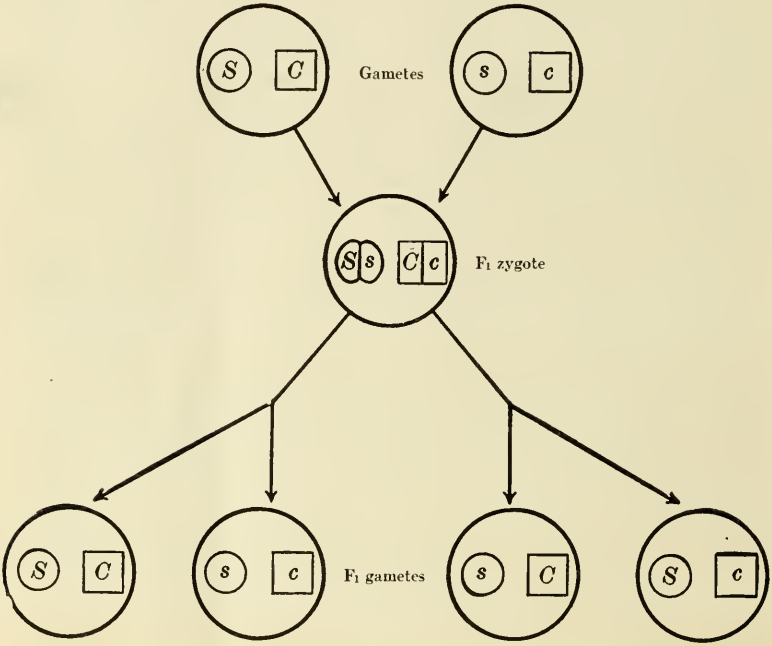

Fig. 39. Diagram to explain the simultaneous and independent inheritance of colored fur (*C*) and short hair (*S*) in the cross shown in Figs. 35–38.

One individual in each of these four classes will, if mated with an individual like itself, breed true, for it is homozygous, containing only like units. The double recessive class, long albino, of course contains *only* homozygous individuals, but in each class which shows a dominant unit, heterozygous individuals outnumber homozygous ones, as 2 : 1, or 8 : 1.

Now the breeder who by means of crosses has produced a new type of animal wishes, of course, to "fix" it, — that is,

Fig. 40

Fig. 41

Fig. 42

Fig. 43

Fig. 44

Fig. 45

Fig. 46

Fig. 47

Figs. 40–47. Results of a cross between varieties of guinea-pig differing in three unit-characters, color, length and roughness of fur. Fig. 40, the colored, short-haired and smooth parent. Fig. 41, the albino, long-haired and rough parent. Fig. 42, one of the F_1 young, colored, short-haired and rough. Figs. 43–47, five new varieties occurring among the F_2 young. Fig. 43, colored, long-haired and rough. Fig. 44, colored, long-haired and smooth. Fig. 45, albino, short-haired and rough. Fig. 46, albino, long-haired and smooth. Fig. 47, albino, short-haired and smooth. Three other F_2 varieties were like the parents and grandparents respectively (Figs. 40–42).

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

We may next discuss a cross in which three unit-character differences exist between the parents, instead of two. If guinea-pigs are crossed which differ simultaneously in three unit-characters, color, length, and direction of the hair, a still larger number of phenotypes is obtained in F_2, namely, eight. A cross between a short-haired, colored, smooth guinea-pig (Fig. 40) and one which was long-haired, albino, and rough (Fig. 41) produced offspring in F_1 which were short-haired, colored, and rough (Fig. 42), these being the three dominant characters, two derived from one parent, one from the other. The F_2 offspring were of eight distinct types, two like the respective grandparents, one like the F_1 individuals (parents), and the other five new, shown in Figs. 43–47. The largest of the eight apparent classes (*phenotypes*) was the one which manifested the three dominant characters, short, colored, and rough, which had been the exclusive F_1 type (Fig. 42); the smallest class was the one which manifested the three recessive characters, long, albino, and smooth

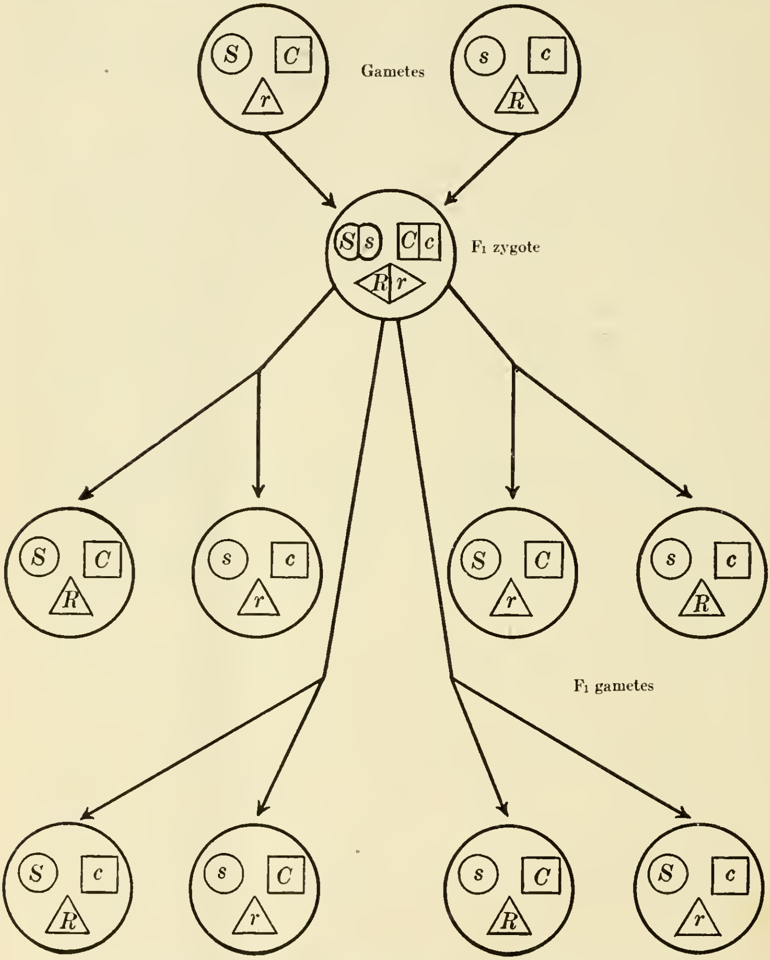

FIG. 48. Diagram to explain the simultaneous and independent inheritance of short (*S*) colored (*C*) and rough (*R*) fur in the cross shown in Figs. 40–47.

(Fig. 46). Theoretically these two classes should be to each other as 27 : 1. Of the twenty-seven triple dominants, twenty-six should be heretozygous. The triple recessive would of course be fully homozygous.

A comparison of this case with the one just previously described shows what an increasingly difficult thing it is to fix types obtained by crossing, as the number of dominant characters in the selected type increases. On the theory of unit-characters the gametic combinations and segregations in this cross are as shown in Fig. 48. The nature of the gametes formed by the parents crossed is shown in the first row; the composition of the F_1 individuals, immediately below. In the two lower rows are shown four different sorts of gametic splittings which may occur in F_1 individuals, producing thus eight different kinds of gametes.

If, as suggested, the F_1 individuals produced in this cross form eight different kinds of gametes, each of these kinds should, when united with a gamete having the same constitution as itself, produce a homozygous and so true-breeding zygote of a different variety, making in all eight true-breeding varieties. Experiment has shown that in reality eight such varieties are produced in F_2. It is therefore evident that the crossing of varieties which differ from each other by unit-characters becomes, under the operation of Mendel's law, a ready means of producing other new varieties different from those crossed, and that the number of such new varieties capable of production in this way increases rapidly with every additional unit-character difference between the parent varieties which are crossed.

CHAPTER IX

SOME MENDELIAN TERMS AND THEIR USES

In describing Mendelian heredity it is convenient for brevity to use technical terms, some of which are already in general use among biologists, but others of which have been framed to meet needs not previously existing. The significance of these the reader must keep clearly in mind, for which reason it seems best briefly to define them.

A *gamete* is a reproductive cell capable of uniting with another reproductive cell to form a new individual. In all the higher animals and plants the gametes which are capable of union in pairs are of two unlike sorts, eggs and sperms.

An *egg-cell* (capable of fertilization) is the larger, non-motile gamete, produced by the female parent, when the parents are sexually different.

A *sperm* is the smaller gamete, commonly motile, and produced by the male parent, when the parents are sexually different. Exceptions to the motility of sperms occur in the crustacea among animals and in all but the lowest of the flowering plants. In the lowest flowering plants motile sperms are found in the pollen-tube, but in the ordinary flowering plants the two gametes which are produced in the pollen-tube are non-motile. The pollen-tube itself transports them by its growth toward the egg-cell of the plant.

A *zygote* results from the union of two gametes in fertilization, an egg with a sperm. It is, potentially or actually, a new individual produced by a sexual process (union of gametes).

A *homo-zygote* results from the union of gametes which transmit the same Mendelian character, as black joined with black, or white joined with white.

A *hetero-zygote* results from the union of gametes which transmit alternative Mendelian characters, as black united with white.

Mendelian characters exist in contrasted pairs which are alternatives of each other, as black and white, rough and smooth, long and short. A gamete may from its nature transmit only *one* of a pair, either black or white, but not both. Its nature is *simplex*. A zygote is *duplex* in nature; it may contain a character twice represented (when it is a homozygote), or contain both a character and its alternative (when it is a heterozygote). The same zygote may be a homozygote as regards one character (say hair-color) and a heterozygote as regards another (say hair-length).

Unit-character or unit-factor or gene. Such characters of animals and plants as follow Mendel's law in heredity, *i. e.*, are inherited as independent units, are often called *unit-characters.* But it has been shown in numerous cases that an independent factor, which follows Mendel's law in transmission, may affect or condition the inheritance of a supposed unit-character, without itself producing any other discoverable effect. Thus the agouti (or yellow-ticked) character of the fur of rodents is not developed unless along with the other genetic factors which produce a black or a brown coat, a particular "agouti" factor is present; yet we have no other evidence of the existence of this factor, except the form which the black or brown coat assumes when this factor is inherited. But it can be shown unmistakably that the inheritance of this unseen factor is that of an independent Mendelian character.

Some have sought to avoid the difficulty presented by such cases by making a distinction between *unit-characters* and *unit-factors*, the former being the recognized morphological or physiological parts or properties of the organism, the latter their hypothetical determiners. But this distinction is of doubtful utility, since the only objective evidence which we possess that unit-characters exist is the occurrence of classes among the F_2 individuals and their numerical frequencies. But this same evidence also forms our only indication that determiners exist. In fact the "unit-characters" about which we talk are the hypothetical determiners. For no one familiar with Mendelian phenomena would venture to classify the anatomical parts or physiological processes of an organism as unit-characters in heredity merely because they are distinct anatomical parts or distinct physiological processes.

The head, the hand, the stomach, stomach-digestion, — these are not unit-characters so far as any one knows. But if a race without hands were to arise and this should Mendelize in crosses with normal races, then we should speak of a unit-character or unit-factor for "hands," loss of which or variation in which had produced the abnormal race. But in so doing we should refer not to the hand as an anatomical part of the body nor to the thousand and one factors concerned in its production but merely to *one hypothetical factor* to which we assign the failure of the hand to develop in a particular case. It is immaterial whether we call this a *unit-character* or *unit-factor* or use both terms inter-changeably, but it would be a mistake to suppose that they refer to different things or that one is less abstract than the other. Historically the term unit-character has priority, though factor seems better to express the abstract and purely hypothetical nature of the conception involved. The application of the term unit-character at first to certain agencies which were later found to be complex led to the coining of a new term (unit-factor) to apply to the newly recognized simpler agencies. If this process were to be continued indefinitely we should have to invent a new set of terms for every step in advance in Mendelian analysis. It seems better to discard earlier and imperfect analyses as knowledge advances but not to multiply technical terms needlessly when no new conception is involved.

Parental and filial generations. The manifestation of Mendelian characters is often very different in successive generations, for which reason it is necessary to have a convenient means of designating the different generations concerned. The significant generation from which reckoning should be made is that in which *hybridization* occurs, *i. e.*, in which parents of unlike character are mated with each other. This, following Bateson, we may call the *parental* generation or P generation. Subsequent generations are called *filial* generations (abbreviated F) and their numerical order is indicated by a subscript, as first filial (F_1), second filial (F_2), etc. When pure races are crossed the first filial generation (F_1) is usually as uniform in character as the parental races. Any striking lack of uniformity in F_1 may be taken as *prima facie* evidence that one or other of the parent races is impure (heterozygous for one or more characters). It is in the F_2 generation that recombinations are formed of the characters in which the parent races differ from each other. The numbers of classes of individuals obtained in F_2 and their numerical proportions are the significant features which indicate how many Mendelizing factors distinguish the parental races and what their nature is, whether dominant or recessive.

The members of contrasted pairs of Mendelian characters are known as *allelomorphs*, *i. e.*, alternative forms. For example, colored and albino coat are allelomorphs among guinea-pigs, as also are rough and smooth, long and short. The *dominant* allelomorph is that one which is expressed in the heterozygote; the *recessive* allelomorph is that one which is not expressed in the heterozygote. It follows that *dominant* allelomorphs are regularly expressed in F_1 while *recessive* allelomorphs are as regularly suppressed in that generation, but that both of them find expression in F_2, though dominants exceed recessives in F_2 as three to one.

For the simplification of inheritance formulae, Mendelian factors are commonly designated by letters of the alphabet, members of the same allelomorphic pair being designated by the *same* letter, a capital being used for the *dominant* allelomorph, a small letter for the *recessive* allelomorph. It will assist the reader to choose letters which suggest descriptive names of the characters involved. Thus for the agouti factor we may use A, for its recessive allelomorph a; for the color factor we may use *C*, and for its recessive allelomorph (found in albinos) *c*, etc.

Though a gamete, from its simplex nature, may never contain more than a single allelomorph, and a zygote, from its duplex origin, may never contain more than two allelomorphs, the same race may contain three or more variations which belong in the same allelomorphic series; *i. e.*, which are allelomorphs of each other. In such a race, a gamete may transmit any *one* of the series, and a zygote may contain any *two*, but never more. In such cases the original terminology of Mendel, which involved the use of capitals and small letters, becomes inadequate, and it has been deemed advisable to use in its stead a numerical or descriptive subscript. Thus four allelomorphic conditions of the color factor found among guinea-pigs have been designated C, C_d, C_r, and C_a respectively.

In calculating the result to be expected from a particular cross it is obviously necessary to consider, not the number of characters which the parents *possess*, but only the number in which they *differ*, since as regards these only will heterozygotes be formed in F_1, to be followed by the production of new homozygous combinations in F_2. Our inheritance formulae therefore will contain only *differential factors* but the student must not fall into the error of supposing these to be the *only* factors concerned. A thousand factors held in common by the parents are doubtless involved to every one in which the parents are observed to differ. But factors held in common are incapable of demonstration by the method of experimental breeding. A factor reveals itself only by its disappearance or alteration in gametes produced by one of the parents crossed.

Both from Mendelian theory and from the experience of practical breeders, it is clear that individuals which *look* alike often do not *breed* alike. Hence it is useful to recognize (with Johannsen) a " phenotype " as including all individuals which look or seem alike, and in counter distinction to this to recognize a " genotype " which includes only such individuals as breed alike, *i. e.*, which produce the same kind or kinds of gametes. A single phenotype often includes two or more categories of genotypes. Thus F_2 dominants though all may *look* alike (be of one phenotype) regularly include both homozygotes and heterozygotes (wholly distinct genotypes).

CHAPTER X

CALCULATING MENDELIAN EXPECTATIONS

MENDELIAN expectations may be calculated either by the algebraic method used by Mendel himself or by the ingenious checkerboard method devised by Punnett. The first step in either process consists in ascertaining what factorial combinations are to be expected among the gametes formed by either parent. By the algebraic method, we ascertain the product of the gametic combinations of the two parents, which will give the zygotic combinations to be expected among their F_1 offspring. A repetition of this process, considering the F_1 individuals now as parents, will give the combinations to be expected among the F_2 offspring, etc.

For example, if a homozygous colored guinea-pig is crossed with an albino, the gametes formed by the parents contain C and c respectively. The F_1 zygotes will contain the two in association, Cc. The gametes formed by the F_1 individuals will contain *either* C or c, or collectively will be $C + c$. The F_1 female will produce gametes (eggs), $C + c$; the F_1 male will produce gametes (sperms), $C + c$; the F_2 zygotes will correspond with their product or $CC + 2Cc + cc$, or one homozygous colored (CC), two heterozygous colored (Cc) and one homozygous albino (cc), or altogether three colored to one albino, the observed average result.

Suppose now we wish to calculate the result to be expected from a back-cross of F_1 with the recessive (albino) parent. The F_1 gametes, we have assumed, are $C + c$; the gametes of the recessive parent are all c. Their product is $Cc + cc$ or equal numbers of heterozygous colored individuals and albinos, the observed experimental result.

The checkerboard method of calculating Mendelian expectations consists in writing the gametic contributions of one parent in a series of horizontal squares, each combination in a different horizontal row. The contributions of the other parent are then written in the same squares, but in *vertical* rows, instead of horizontal ones (since their distribution constitutes a separate contingency) each gametic combination being entered in a different vertical row. The checkerboard will then show (within its individual squares) what factorial combinations are to be expected among the zygotes (progeny of the parents in question) and with what frequencies.

For the example chosen, the cross between homozygous colored and albino guinea-pigs, all the gametes of each parent being alike, the F_1 zygotes would be all of one sort, Cc. But since the gametes formed by each F_1 parent are of two sorts, C and c, it is evident that the checkerboard must contain two horizontal and two vertical rows, or a total of four squares. (See Fig. 49.) Let us enter C in the upper horizontal row and c in the lower row as the gametic contributions of one parent, then enter C in the left vertical row of squares and c in the right vertical row as the contributions of the other parent. We then have the table as shown, one square containing CC, two containing Cc, and one cc, the same result given by the algebraic method.

Sperms \ Eggs	*C*	*c*
C	*C C*	*C c*
c	*c C*	*c c*

FIG. 49. Checkerboard method of calculating a Mendelian F_2 expectation.

Sperms \ Eggs	*C*	*c*
c	*C c*	*c c*

FIG. 50. Checkerboard method of calculating the result of a back-cross between F_1 and the recessive parent.

For the back-cross of F_1 with the recessive parent, only two squares are required. (See Fig. 50.) The recessive parent contributes always c, which we enter in the two squares placed in a horizontal row. The F_1 parent contributes C to one square, c to the other. The resulting combinations are obviously Cc and cc respectively. A checkerboard is scarcely necessary for cases as simple as these, but will be found very clarifying to thought for the beginner, particularly if he is not accustomed to thinking in algebraic terms, when he comes to deal with crosses involving simultaneously three or four independent characters.

The essential point about which one must first of all be entirely clear in his own mind is this — what kinds of gametes will each parent form. If he is clear as to this question the calculation of expectations by either method will present no difficulties. It should be borne in mind therefore that the fundamental Mendelian assumptions are (1) that homozygotes form only *one* type of gamete but (2) that heterozygotes form *two* types of gametes equally numerous, viz., dominants and recessives. Further (3) double heterozygotes (*i. e.*, individuals heterozygous for each of two independent characters) form *four* types of gametes all equally numerous, and (4) triple heterozygotes form *eight* types of gametes, all equally numerous. (5) In general every additional character in which the individual is heterozygous *doubles* the assortment of gametes which it would otherwise form. See Table 7.

TABLE 7

Zygotic Composition of Parents and the Expected Constitution of their Gametes

Parent			Gametes which it will form
Homozygote,		AA	all A
“		AABB	all AB
“		AABBCC	all ABC
Heterozygote,		Aa	A + a
“		Bb	B + b
“		Cc	C + c
Double	heterozygote,	AaBb	AB + Ab + aB + ab
“	“	AaCc	AC + Ac + aC + ac
“	“	BbCc	BC + Bc + bC + bc
Triple	“	AaBbCc	ABC + ABc + AbC + aBC + Abc + aBc + abC + abc

Inspection of a typical checkerboard calculation, that for the F_2 generation following a dihybrid cross, shows some interesting facts. All the *homozygotes* expected lie in the diagonal row of squares running from the upper left to the lower right corner of the figure. Compare Fig. 49. These are the individuals that will "breed true," *i. e.*, will form only a single type of gamete. They are four in number, each of a different sort and would result from the union of two like gametes of each of the four expected types, AB + Ab + aB + ab (or in Fig. 49, EA + Ea + eA + ea). They represent all the possibilities as regards true breeding ("fixed") forms to be expected from the cross. What the nature of the other individuals to be expected would be would depend upon the completeness of dominance. If dominance should be complete, heterozygotes would be indistinguishable except by breeding test from the four expected homozygotes; otherwise homozygotes and heterozygotes might be distinguishable by appearance as well as by breeding tests. With complete dominance, *i. e.*, with only dominant characters *showing* in the zygote, the four sorts would appear as 9 AB: 3 Ab : 3 aB : 1 ab, the typical dihybrid F_2 ratio. Let the reader make out the checkerboard and verify these statements.

In a similar way one may calculate, either by algebra or by checkerboard the F_2 expected result from a trihybrid cross. The eight kinds of gametes which the triply heterozygous F_1 individuals would produce have already been indicated, viz., ABC + ABc + AbC + aBC + Abc + aBc + abC + abc.

By the checkerboard method, each combination would be found homozygous (united with a gamete like itself) in a different square of the diagonal of the figure, and heterozygotes containing the same dominant characters would be found elsewhere in the table sufficient in number to bring the totals up to 27 ABC : 9 ABc : 9 AbC : 9 aBC : 3 Abc : 3 aBc: 3 abC : 1 abc. This is the typical trihybrid F_2 ratio, when complete dominance exists.

To repeat, *it is all essential to determine first the kinds of gametes each parent to a mating is expected to produce.* The subsequent calculation is easy and certain. One soon learns to write out F_2 ratios without going through the calculation in detail either by algebra or by checkerboard. Thus, if we take the expected completely recessive class as 1, each class containing *one* dominant factor will be 3, each class containing *two* dominant factors will be 9 (*i. e.*, 3^2) each class containing *three* dominant factors will be 27 (*i. e.*, 3^3) etc. Accordingly by mere inspection of a gametic series to ascertain *how many dominant factors* each term contains, we may at once assign to each the proportional number of F_2 zygotes in which it will be seen. See Table 8.

TABLE 8

RELATION BETWEEN THE F_1 GAMETIC SERIES AND THE EXPECTED F_2 ZYGOTES

F_1 Gametic Series	F_2 Zygotes
A + a	3A + 1a
AB + Ab + aB + ab	9 AB + 3 Ab + 3 aB + 1 ab
ABC + ABc + AbC + aBC + Abc + aBc + abC + abc	27 ABC + 9 ABc + 9 AbC + 9 aBC + 3 Abc + 3 aBc + 3 abC + 1 abc
ABCD + ABCd + etc.	81 ABCD + 27 ABCd + etc. (let the reader supply the missing terms).

Stated in general terms, as Mendel himself showed (and as follows from the binomial formula), when the number of unit-character differences between the parents is n, the visibly different classes of offspring will be 2^n, the total different *sorts* of zygotes will be 3^n, and the smallest number of individuals which may be expected to contain all of them will be 4^n.

TABLE 9

Differences Between Parents n	Visibly Different Classes 2^n	Really Different Classes 3^n	Minimum Number of F_2 Individuals Including all Classes 4^n	
1	2	3	4	Tested by Mendel for Peas and Found Correct
2	4	9	16	
3	8	27	64	
4	16	81	256	Calculated
5	32	243	1024	
6	64	729	4096	

Table 9 shows what the size of these several classes is for 1–6 independent characters.

CHAPTER XI

MODIFIED MENDELIAN RATIOS; HETEROZYGOUS CHARACTERS; ATAVISM OR REVERSION

In the last chapter Mendelian ratios have been calculated on the supposition that homozygous dominants and heterozygous dominants are not distinguishable from each other, which frequently is true; but if they are distinguishable from each other, then a larger number of F_2 classes can be recognized and their numerical proportions are different. A case of this kind was early recognized among plants by Correns. (See Fig. 51.) When a white variety of four-o'clock (*Mirabilis*) is crossed with a red variety, F_1 plants are produced which bear *pink* flowers, and F_2 consists of whites, pinks, and reds in the ratio, 1:2:1. Reds and also whites breed true, but pinks again produce the three sorts. This result indicates that both reds and whites are homozygotes (RR and rr respectively) but that pinks are regularly heterozygotes (Rr) and for this reason do not breed true but are " unfixable." Pink in this case may be called a *heterozygous* character; it is for that reason unfixable.

A similar but even better-known case among animals has been described by Bateson and Punnett, that of the blue Andalusian fowl. Birds of this race are of a slaty blue color and are known to fanciers to be unfixable as to color. When blues are mated with each other, chicks are obtained of three distinct sorts as regards color, viz., blacks, blues, and " splashed whites." The blacks breed true, as also do the whites, but the blues invariably produce in every generation the three sorts, of which blacks may be called homozygous dominants (BB), whites homozygous recessives (bb), and blues heterozygotes (Bb). But it is clear that if we so designate them, dominance must be recognized to be imperfect.

Attempts of poultrymen to "fix" the blue variety are manifestly hopeless, unless some new variation arises within the race which can be secured in homozygous form and will yet possess the desired appearance.

Another example of a heterozygous and so unfixable character is found among short-horn cattle. Here red is a true-breeding type as also is white, but the heterozygote between red and white is an unfixable roan. (See Figs. 62–64.)

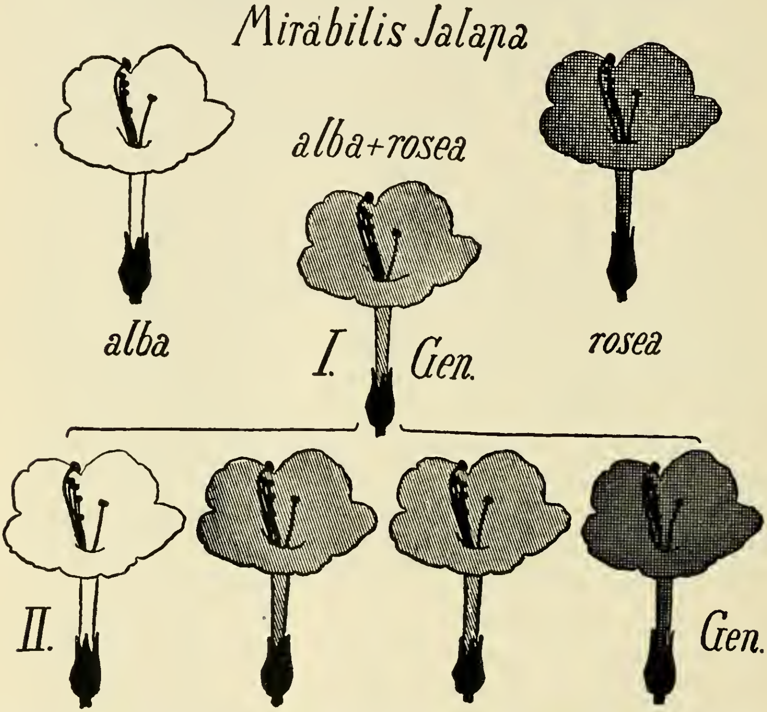

Fig. 51. A diagram to show inheritance of flower color in crosses of Mirabilis, the "four-o'clock." *Alba*, white parent; *rosea*, red parent; *alba + rosea*, the unfixable F_1 heterozygote, of intermediate color, pink. 1. Gen. = F_1. II. Gen. = F_2. (After Correns.)

The effect which the production of a recognizable heterozygous form has upon the typical F_2 monohybrid ratio (3:1) is to convert it into a 1:2:1 ratio, in which each parental type is represented by one individual while the heterozygous type is represented by two. The typical dihybrid ratio (9:3:3:1) we might expect to see modified in a similar way, if a cross were made involving simultaneously *two* Mendelian characters imperfectly dominant. The number of distinguishable classes, as shown originally by Mendel (see Appendix) would then be 9, numerically as follows: 1:1:2:2:4:2:2:1:1. For three factors all imperfectly dominant the modified trihybrid Mendelian ratio would be expressed by $(1 + 2 + 1)^3$ and for n factors by $(1+2+1)^n$. Heterozygous characters must from definition always be unfixable. In the foregoing cases comparison of their behavior in breeding experiments with that of the corresponding homozygotes has shown this to be true, but there exist cases in which only one type of homozygote has been found to occur, the other being apparently impossible of production.

The first case of this sort to be demonstrated is found among yellow mice and to Cuénot (confirmed by Little) we owe its demonstration. If certain strains of yellow mice are crossed with black ones, the offspring produced are of two sorts equally numerous, yellow and black. From this result alone it is impossible to say which is the dominant character, but breeding tests of the offspring show that yellow is the dominant character. For the black offspring bred together produce only black offspring, but the yellows bred together produce both yellow offspring and black ones. The curious feature of the case is that when yellows are bred with each other no pure yellows, that is, homozygous ones, are obtained. Hundreds of yellow individuals have been tested, but the invariable result has been that they are found to be heterozygous; that is, they transmit yellow in *half* their gametes, but some other color in the remaining gametes — it may be black or it may be brown, or gray. Non-yellows obtained by mating yellow with yellow mice never produce yellow offspring if mated with each other. This shows that they are genuine recessives and do not contain the yellow character, which is dominant.

Now ordinary heterozygous dominants, when mated with each other, produce three dominant individuals to one recessive. Accordingly we should expect yellow mice, if, as stated, they are invariably heterozygous, to produce three yellow offspring to one of a different color, but curiously enough they do not. They produce *two* yellows (instead of the expected three) to every one of a different color. About the ratio there can be no reasonable doubt. It has been determined with great accuracy by Dr. C. C. Little, who finds that in a total of over twelve hundred young produced by yellow parents almost exactly two-thirds are yellow. Instead of the regular Mendelian ratio, 3:1, we have then in this case the peculiar ratio, 2:1, and this requires explanation. The explanation of this ratio is to be found in the same circumstance as is the total absence of *pure* yellow individuals. Pure yellow zygotes are indeed formed, but they perish for some reason. A yellow individual produces gametes of two sorts with equal frequency, viz., yellow and non-yellow (let us say black). For, if yellow individuals are mated with black ones, half the offspring are black, half yellow, as already stated. Now if yellow individuals are mated with each other we expect three sorts of young to be produced, numerically as 1:2:1, viz., 1 Y Y, 2 Y B, and 1 B B. But since observation shows that only *two* combinations are formed which contain yellow to one not containing yellow, and since further all yellows which survive are found to be heterozygous (YB), it must be that the expected Y Y individual either is not produced or straightway perishes. As to which of these two contingencies happens we also have experimental evidence. Dr. Little finds (confirming Cuénot), that yellow mice when mated to black ones produce larger litters of young than when they are mated to yellow ones. The average-sized litter contains something like 5.5 young when the mate is a black animal, but only 4.7 when it is a yellow animal. It is evident, then, that about one young one out of a litter perishes when both parents are yellow, and this undoubtedly is the missing yellow-yellow zygote. The yellows which are left are heterozygous yellow-black zygotes, and they are to those that perish as 2:1. They are also to the

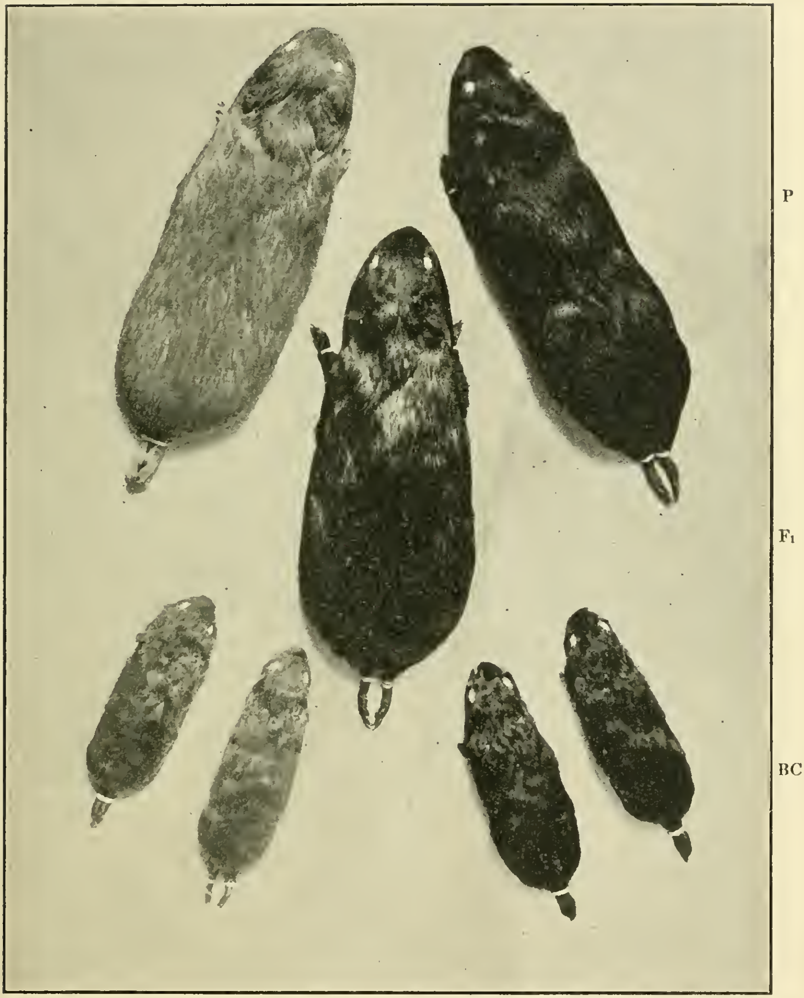

FIG. 52. Simple Mendelian inheritance in crosses of red guinea-pigs with black ones. P, parents; one red, one black. F_1, one of the young, all heterozygous blacks. BC, young produced by a back-cross of an F_1 black with the red parent. Half are red, half are black.

non-yellow zygotes as 2:1, the ratio observed also among the surviving young of yellow by yellow parents.

This interpretation of the 2:1 ratio observed in this case is strongly supported by a similar case among plants, in which the evidence is even more complete. A so-called " golden " variety of snapdragon, one in which the foliage was yellow variegated with green, was found by the German botanist, Baur, to be unfixable, producing when self-pollinated fully green plants as well as golden ones, in the ratio 2 golden: 1 green. The green plants were found to breed true, that is, to be recessives, while the golden ones were invariably found to be heterozygous. Baur found, however, by germinating seeds of golden plants very carefully, that there were produced in addition to green plants and golden ones a few feeble seedlings entirely yellow, not variegated with green, as the golden plants are. These, for lack of assimilating organs (green chlorophyl), straightway perished. Clearly they were the missing pure yellow zygotes.

Frequently one of the visible characters of an organism depends upon the combined action of two or more independent Mendelian factors, in which case it is demonstrably not a *unit*-character, as has already been pointed out, since each of the known " factors " is indispensable to the development of the visible character, as are probably also a great many other as yet unknown factors. The dependence of a visible character upon two or more *simultaneously varying* factors leads to the production of modified dihybrid or polyhybrid F_2 ratios. It also leads to a phenomenon known as *atavism* or *reversion*, by which is meant the restoration of a lost ancestral character, which frequently follows crossing of unrelated varieties.

Atavism or reversion to an ancestral condition is a phenomenon to which Darwin repeatedly called attention. He realized that it is a phenomenon for which general theories of heredity must account. He supposed that the environment was chiefly responsible for the reappearance in a species of a lost ancestral condition, but that in certain cases the mere act of crossing may reawaken slumbering ancestral traits. Thus he noticed that when rabbits of various sorts are turned loose in a warren together, they tend to revert to the gray-coated condition of wild rabbits. And when pigeons are crossed in captivity they frequently revert to the plumage condition of the wild rock pigeon, *Columba livia.* In plants, too, Darwin recognized that crossing is a frequent cause of reversion. The explanation which he gave was the best that the knowledge of his time afforded, but it leaves much to be desired. This lack, however, has been completely supplied by the Mendelian principles. An illustration or two may now be cited.

When pure-bred black guinea-pigs are mated with red ones, only black offspring are as a rule obtained. (See Fig. 52.) The hairs of the offspring do indeed contain some red pigment, but the black pigment is so much darker that it largely obscures the red. In other words, black behaves as an ordinary Mendelian dominant. In the next generation black and red segregate in ordinary Mendelian fashion, and the young produced are in the usual proportions, three black to one red, or 1:1 in back-crosses of the heterozygous black with red. All black races behave alike in crosses with the same red individual, but among red animals individual differences exist. Some, instead of behaving like Mendelian recessives, produce in crosses with a black race a third apparently new condition, but in reality a very old one, the agouti type of coat found in all wild guinea-pigs, as well as in wild rats, mice, squirrels, and other rodents. In this type of coat reddish yellow pigment alone is found in a conspicuous band near the tip of each hair, while the rest of the hair bears black pigment. The result is a brownish or grayish ticked or grizzled coat, inconspicuous, and hence protective in many natural situations. (See Fig. 53.)

Some red individuals produce the reversion in half of their young by black mates, some in all, and others, as we have seen, in none, this last condition being the commonest of the three. It is evident that the reversion is due to the intro-

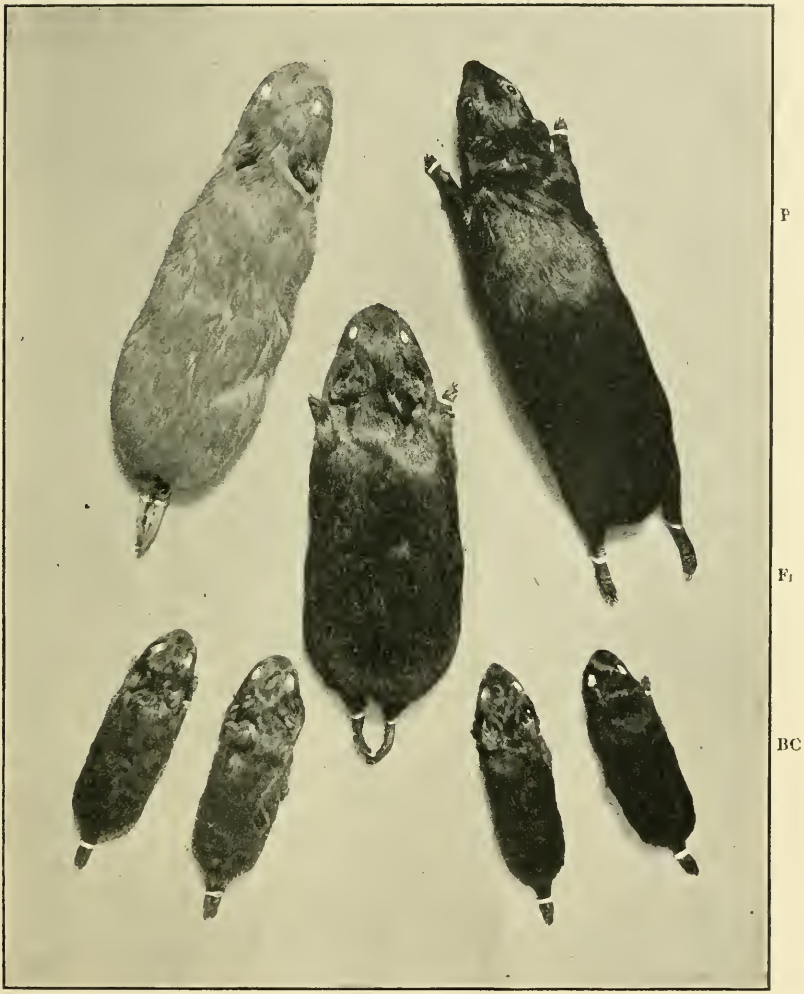

Fig. 53. Reversion in crosses of a red guinea-pig with a black one. P, parents. F_1, one of the reversionary (agouti) young. BC, young produced by a back-cross of an F_1 agouti with an ordinary red individual. Half the young are red. The other half are equally divided between agoutis and blacks.

duction of a new factor, additional to simple red or simple black. It is evident further that this new factor, which we will call A (agouti), has been introduced through the red parent, and that as regards this factor, A, some red individuals are homozygous (AA) in character, others are heterozygous (Aa), while others lack it altogether (aa). The agouti character becomes visible only in the presence of both black and red, because it is a mosaic of those two pigments. If the F_1 agouti individuals are bred together they produce in the next generation (F_2) three sorts of young, viz., agouti, black, and red, which are numerically as 9:3:4. This evidently is a modification of the dihybrid Mendelian ratio 9:3:3:1, resulting from the fact that the last two classes are superficially alike. They are red animals with and without the agouti factor respectively; but this agouti factor is invisible in the absence of black, so that both sorts of reds look alike. Together they number four in sixteen of the F_2 offspring. Figure 54 is intended to show by the checkerboard method how this modified dihybrid ratio is obtained.

Black and red varieties differ from each other by a variation in what has been called the *extension* factor (E), the reference being to the fact that black (or brown) pigment, found in the eyes of both varieties, *extends* throughout the coat in the black variety but is *restricted* to the eye in the red variety. The allelomorphic conditions of this factor are designated E (in black) and e (in red) respectively. The agouti factor (A) may exist in red animals without producing visible effects because there is no black pigment in the fur of such animals to bring out the ticking, but its existence in animals which would otherwise be black changes the coat to agouti. Hence the constitution of the parental gametes is: Black parent, Ea; red parent eA. F_1 is EeAa, a double heterozygote. Its gametes are EA + Ea + eA + ea, which with dominance complete will produce F_2 zygotes, 9 EA + 3 Ea + 3 eA + 1 ea. (See Figure 54.) But EA contains the two factors which together produce agouti; Ea contains the factors for black; eA contains the factor for agouti but without the factor (E) necessary to make it visible, and so will be red; and ea contains neither the factor for agouti nor that for black, hence will also be red. Accordingly the expected F_2 distribution is nine agouti, three black, four red, the ratio observed. This is a very common modification of the F_2 dihybrid ratio and owes its production to the fact that *two independent Mendelian factors are involved one of which produces no visible effect except in the presence of the other.*

	E A	*E a*	*e A*	*e a*
E A	*E A* *E A* **Agouti**	*E A* *E a* **Agouti**	*E A* *e A* **Agouti**	*E A* *e a* **Agouti**
E a	*E a* *E A* **Agouti**	*E a* *E a* **Black**	*E a* *e A* **Agouti**	*E a* *e a* **Black**
e A	*e A* *E A* **Agouti**	*e A* *E a* **Agouti**	*e A* *e A* **Red**	*e A* *e a* **Red**
e a	*e a* *E A* **Agouti**	*e a* *E a* **Black**	*e a* *e A* **Red**	*e a* *e a* **Red**

FIG. 54. Checkerboard to explain the modified dihybrid F_2 ratio, 9 : 3 : 4, as observed when black guinea-pigs are crossed with red ones which transmit the agouti factor (A).

Another example of this same modified dihybrid ratio (9:3:4) is obtained by crossing an albino rodent (rat, mouse, rabbit or guinea-pig) derived from a black race, with a wild (agouti) individual. F_1 consists of agoutis, like the wild parent, but F_2 contains agoutis, blacks, and albinos in the proportions, nine agouti, three black, four albino. The explanation is as follows. The albino parent differs from the wild agouti parent as regards two factors, viz., the color factor (C) and the agouti factor (A). The albino parent is

Fig. 55. Reversion to full intensity of pigmentation on crossing a pink-eyed cream-and-white rat with an albino. P, parents; cream-and-white at left, albino at right. F_1, one of the black-and-white young. F_2, cream-and-white at left, black-and-white in middle, albino at right. Their numerical relations are about as 3 : 9 : 4. A slight departure from these proportions is observed on account of linkage (in this case repulsion) between the genes for pink-eye and albinism. See chapter on Linkage.

ac; the agouti parent AC. F_1 is AaCc, a double heterozygote. Its gametes consequently should be of four types, viz., AC + Ac + aC + ac, and the F_2 zygotes, 9 AC:3 Ac: 3 aC:1 ac. But only zygotes which contain C will develop a colored coat, hence both 3 Ac and 1 ac will be albinos. The 9 AC individuals contain the factors of the wild parent and hence will be agouti; the 3 aC individuals will develop a colored coat since they contain C, but this coat will be non-agouti (a), *i. e.*, they will be like the wild type except for the lack of the agouti factor and so will be black.

Precisely the same result in F_1 and F_2 is obtained if a black rodent (rat, mouse, rabbit, or guinea-pig) is crossed with an albino which transmits the agouti factor, as for example an albino whose *parents* were homozygous for the agouti factor. In this case F_1 is agouti by reversion, C being derived from the black parent, A from the albino parent. But F_1 is doubly heterozygous, precisely as in the foregoing case, and the F_2 generation contains only *three* apparent classes of individuals instead of the usual four for the reason that *one* of the two differential factors concerned in the cross (viz., A) is unable to produce a visible effect except in the presence of the other (C).

Another somewhat similar case involving reversion in F_1 with the production of the modified dihybrid ratio, 9:3:4, in F_2 is illustrated in Fig. 55. A pale-coated " cream-and-white " rat was crossed with an albino and produced black-and-white young, a reversion to pigmentation of full intensity, though white spotting was retained, this being an independent Mendelian character transmitted by both parents. The F_2 generation consisted of black-and-white, cream-and-white, and albino individuals in numbers approximating the 9:3:4 ratio. Black-and-white is here the double dominant class, 9; cream-and-white is the single dominant class, 3; and the albinos include three which transmit the dominant character, black-and-white, but which fail to show it because they lack the color factor, and also one which transmits cream-and-white but which fails to show it for the same reason, lack of the color factor. Together the albinos number four.

A different modification of the typical dihybrid ratio is illustrated by the following case in which two varieties were crossed which possessed complementary factors *neither* of which is able to produce a visible effect apart from the other. When certain white-flowered varieties of sweet peas are crossed with each other they produce F_1 plants which bear *red-colored* flowers (Bateson and Punnett). F_2 consists of two apparent varieties only, viz., reds and whites in the ratio, nine red to seven white. This is explained as a modified dihybrid ratio (9:3:3:1) in which the last three terms are indistinguishable (all being white). The two factors involved in this case are assumed to be a *color factor* found in one white parent and a *red* factor found in the other, both together (in F_1) producing a *red color*, but either by itself producing no color whatever. One parent accordingly produces gametes all Cr, the other produces gametes all cR. F_1 is CcRr, a double heterozygote; its gametes, CR + Cr + cR + cr; and the F_2 zygotes containing the same assortments of factors are 9CR:3Cr:3cR:1cr. But if C and R, neither of them, produce color apart from each other, then only the 9 CR zygotes are colored, all the others, seven in sixteen, being white, and the observed F_2 ratio (9:7) is thus accounted for as the result of a dihybrid cross at the same time that the F_1 result is explained.

When some other white-flowered varieties of sweet peas are crossed with each other, there are produced, not red-flowered F_1 plants as in the foregoing case, but those which are purple bi-color, like the wild sweet pea, a case of reversion or atavism, like those known for pigeons, rabbits and guinea-pigs. This reversion involves a third independent factor (a factor for blue, B) which is ineffective except in the presence of both the color factor (C) and the red factor (R). When in such reversionary crosses a colored F_1 is produced which is heterozygous for all three factors, F_2 manifests a peculiar modified trihybrid ratio, less common than the modified dihybrid ratios just discussed. If, for example, one white parent contributes the color factor while the other parent contributes the red and the blue factors, then we may represent the parental gametes as Crb and cRB respectively. F_1 will then be a triple heterozygote, CcRrBb, which from the combined action of the three dominant characters will be a purple bi-color. Its gametes will then be of eight sorts and the zygotes in which corresponding groupings of the dominant factors occur will be as follows: [1]

27 CRB, purple
9 CRb, red
9 CrB, white
9 cRB, white
3 Crb, white
3 cRb, white
3 crB, white
1 crb, white

But only the first two of these eight groupings contain combinations of factors capable of producing colored flowers, viz., CRB, which will produce purples, and CRb, which will produce reds. All the other six combinations lack one or both of the two factors (C and R) which must be present together in order to produce colored flowers. Consequently all will produce uncolored (white) flowers, and the expected classes of phenotypes will be as follows: twenty-seven purple, nine red, twenty-eight white, a modified trihybrid ratio.

Summary on Modified Ratios

1. When a cross involves two factors, *one* of which produces no visible effect except in the presence of the other, the dihybrid F_2 ratio, 9:3:3:1, is modified to 9:3:4, because the last two classes of the typical ratio are indistinguishable.

2. When a cross involves two factors, *neither* of which produces a visible result in the absence of the other, the dihybrid ratio becomes 9:7, because the last three classes of the typical ratio are indistinguishable; if in addition a third factor is involved which produces no visible effect except in the presence of both the others, a modified trihybrid ratio is obtained, viz., 27:9:28.

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[1] It is suggested that the reader make out the trihybrid checkerboard calculation for this cross and color the squares with crayon in accordance with the assumption made.

Modification of the ratio, 9:3:3:1, due to linkage. When two Mendelian characters are not wholly independent of each other, but show a tendency to be inherited together, they are said to be *coupled* or *linked* to each other. Thus, in the sweet pea, purple and red are alternative color forms, and long pollen and short pollen are alternatives as to pollen shape. And if a purple plant with long pollen is crossed with a red plant having round pollen, four classes are obtained in F_2, viz., purple long, purple round, red long and red round. This being apparently a dihybrid Mendelian cross, we should expect the four classes to be respectively as 9:3:3:1, but in reality the classes *purple long* and *red round* (the parental combinations) are in excess of these proportions. When these facts were discovered by Bateson and Punnett, it was stated that coupling exists between the characters purple and long and their allelomorphs red and round. Later, however, when a cross was made between purple round and red long, it was found that *these* combinations were in excess in F_2. Purple and long which in the first case were coupled, now showed repulsion. Morgan explains both cases by supposing that the two character-pairs have determiners or genes located near to each other in the germ-cell, probably in the same chromosome, so that the parental combination has a tendency to persist in F_2. Morgan also proposes to substitute a single term, linkage, for the two terms of Bateson, coupling and repulsion.

TABLE 10

THE F_2 RATIO, 9:3:3:1, AS AFFECTED BY COUPLING OR LINKAGE, A AND B ENTERING THE F_1 ZYGOTE IN THE SAME GAMETE

Ratio, Crossover to Non-crossover Gametes	Proportion Crossover Gametes	F_2 Zygotes				
		AB	Ab	aB	ab	Total
$1:x$	$\frac{1}{x+1}$	$3x^2 + 2(2x + 1)$	$2x + 1$	$2x + 1$	x^2	$(2x + 2)^2$
1:1[1]	1/2	9	3	3	1	16
1:2	1/3	22	5	5	4	36
1:3	1/4	41	7	7	9	64
1:4	1/5	66	9	9	16	100
1:5	1/6	97	11	11	25	144
1:6	1/7	134	13	13	36	196
1:7	1/8	177	15	15	49	256
1:8	1/9	226	17	17	64	324
1:9	1/10	281	19	19	81	400
1:99	1/100	29,801	199	199	9,801	40,000
Limiting values[2]	....	3	0	0	1	4

[1] No coupling.

[2] Not distinguishable from the case in which A and B are due to a single genetic factor.

It is evident that linkage will cause modification of the typical dihybrid ratio, 9:3:3:1, since the four possible classes of gametes formed by F_1 individuals will not all be equally numerous. Accordingly the stronger the linkage, the greater will be the modification of the typical ratio. Conversely, we may estimate *the strength of the linkage* by the observed departure from the 9:3:3:1 ratio.

In so doing, tables 10 and 11 may be found useful, in which the expected modification of the 9:3:3:1 F_2 ratio is given for various integral ratios of gametes showing the *parental* combinations, to gametes not showing them. Morgan calls the gametes which show novel combinations *crossover* gametes and those which show the original combinations *non-crossover* gametes. If the latter are two, three, four, etc., times as numerous as the former, then we get the modified F_2 ratios shown in the tables, where also formulae are given for extending the tables to any desired extent. In making use of these tables, it is necessary only to reduce to the basis of a common total the observed F_2 zygotic series and any series of the table with which a comparison is desired. This will be facilitated by consulting Table 11a, in which each zygotic class of Tables 10 and 11 is expressed as a percentage of the total population.

TABLE 11

THE F_2 RATIO, 9:3:3:1, AS AFFECTED BY REPULSION (NEGATIVE LINKAGE), A AND B ENTERING THE F_1 ZYGOTE IN DIFFERENT GAMETES

Ratio, Crossover to Non-crossover Gametes	Proportion Crossover Gametes	F_2 Zygotes				
		AB	Ab	aB	ab	Total
1:x	$\frac{1}{x+1}$	$2(x^2+2x)+3$	x^2+2x	x^2+2x	1	$(2x+2)^2$
1:1[3]	1/2	9	3	3	1	16
1:2	1/3	19	8	8	1	36
1:3	1/4	33	15	15	1	64
1:4	1/5	51	24	24	1	100
1:5	1/6	73	35	35	1	144
1:6	1/7	99	48	48	1	196
1:7	1/8	129	63	63	1	256
1:8	1/9	163	80	80	1	324
1:9	1/10	201	99	99	1	400
1:99	1/100	20,001	9,999	9,999	1	40,000
Limiting values[4]	....	2	1	1	0	4

[3] No repulsion.

[4] Not distinguishable from the case in which A and B are allelomorphs.

TABLE 11*a*

A Combination of Tables 10 and 11, in which the Size of each F_2 Class is expressed as a Percentage of the F_2 Population. It is assumed that the Gametic Series is the same in both Sexes

Ratio, cross-over to non-crossover gameles	Percentage F_2 zygotes when					
	A and B enter together (Table 10)			A and B enter separately (Table 11)		
	AB	Ab (or aB)	ab	AB	Ab (or aB)	ab
1:1	56.2	18.7	6.2	56.2	18.7	6.2
1:2	61.1	13.6	11.1	52.8	22.2	2.8
1:3	64.0	10.9	14.0	51.5	23.4	1.5
1:4	66.0	9.0	16.0	51.0	24.0	1.0
1:5	67.3	7.6	17.3	50.7	24.3	0.7
1:6	68.3	6.6	18.3	50.5	24.5	0.5
1:7	69.3	5.8	19.3	50.4	24.6	0.4
1:8	69.7	5.2	19.7	50.3	24.7	0.3
1:9	70.2	4.7	20.2	50.2	24.8	0.2
1:99	74.5	0.5	24.5	50.0+	24.9	0.0+
1:∝	75.0	0.0	25.0	50.0	25.0	0.0

In using Table 11*a* to test a case of suspected linkage, the size in per cent of each observed F_2 class should first be determined and comparison made with the corresponding class in the Table. In cases of doubt, determination of the probable error of linkage may show whether the observed departures from the normal 9:3:3:1 ratio are or are not significant. The 9:3:4 ratio as affected by linkage may be obtained by combining in Tables 10 or 11, the numbers in the columns headed aB and ab.

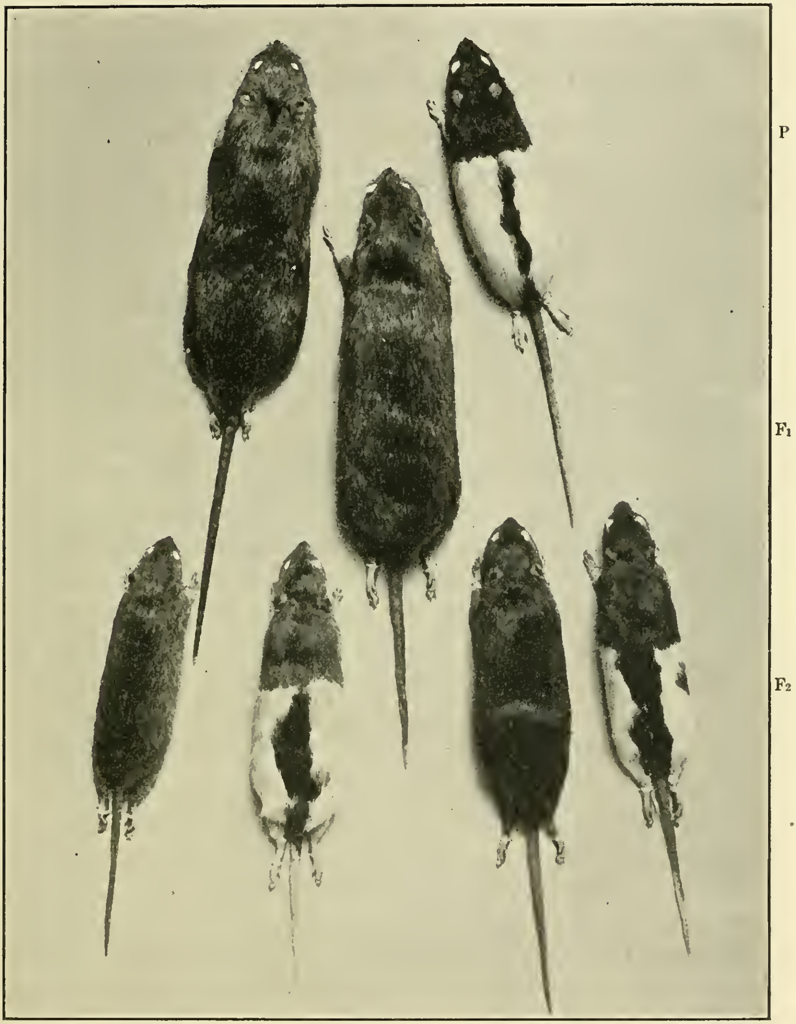

FIG. 56. A dihybrid Mendelian cross between a wild Norway rat and the tame variety known as black hooded. P, parents; wild gray at left, black hooded at right. F_1, a heterozygote, gray like the wild parent, but showing traces of the recessive white spotting. Note white left fore foot. F_2, the four second-generation classes of offspring. From left to right, gray self, gray hooded, black self, black hooded. Numerically as 9 : 3 : 3 : 1. Let the reader identify in Table 12 the unit-characters involved.

CHAPTER XII

THE UNIT-CHARACTERS OF RODENTS

No group of mammals has been studied as thoroughly, in respect to heritable characters, as have the rodents. This is particularly true as regards those striking variations of the coat which form the basis of the many recognized domestic varieties. In nearly every case the distinctive features of these several varieties are found to be Mendelian unit-characters. As an example we may take the varieties of the domestic cavy or guinea-pig, probably the first of the rodents in point of time to be domesticated. Certainly in richness of varieties it surpasses all others. It was domesticated by the ancient Peruvians before the discovery of America and formerly held an important economic place among the natives of tropical America where it was reared as an article of food in every cabin, a practice which to some extent still continues among the poorer classes. Its variation in color and other coat characters has been very extensive, unequalled in amount perhaps among mammals other than dogs. Nearly every distinct variety is characterized by the possession of one or more Mendelian unit-character variations. At least ten such unit-characters are concerned in the production of these varieties. Several of these unit-characters have already been referred to. (See Table 12.) All but one of them (" rough ") may be regarded as recessive unit-character variations from the conditions found in wild cavies generally.

Perhaps the earliest in point of time, certainly the commonest among rodents wild or domesticated, is the albino variation, in which the fur is white and the eye pink. This makes its appearance as a sport, probably originally in a single individual and later as a recurring variation among its descendants. Albino individuals are undoubtedly at a disadvantage in the struggle for existence in a wild state because of the conspicuousness of the albino to its enemies and also because of its defective vision. For the eyesight of the albino is very poor owing to the imperfect pigmentation of its eyes. Albino sports accordingly never become very common in a wild species but are probably among the earliest formed domestic or tame varieties, because of their striking character and the ease with which a distinct variety is established. For, being recessive, the albino variation is secure as a racial character as soon as a pair of albinos has been isolated.[1]

TABLE 12

SOME UNIT-CHARACTERS OF RODENTS

Name of Factor	Symbol, Dominant Phase	Appearance of Dominant Individual	Symbol, Recessive Phase	Appearance of Recessive Individual
Color	C	Colored	c	Albino
Extension	E	Black or brown	e, e′	Yellow, yellow spotted with black or brown
Agouti	A	Gray (agouti)	a	Black or brown (non-agouti)
Black	B	Black or black agouti	b	Brown or brown agouti
White spotting	S	Self colored	s	Spotted with white
Dark eye	D	Dark eyes and coat	d	Pink eyes and coat pale, where not yellow
Intensity	I	All pigments dark	i	All pigments pale
Hair length	L	Short-haired like wild cavies	l	Hair long and silky
Rough coat	R	Coat rosetted	r	Coat smooth
Rough modifier	M	Coat slightly rosetted	m	Coat rosettes fully developed

The albino variation is commonly considered to be the result of a recessive variation in a *color factor* whose dominant phase is expressed by the symbol, C, its recessive or albino phase by c. (See Table 12.)

Another color sport occasionally observed among wild rodents, and which is the basis of distinct varieties among

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[1] The contemporary origin of an albino race of field mouse (Peromyscus) has recently been recorded (Castle, 1912) in a species in which neither this nor any other of the common color sports had previously been recorded.

tame ones, is a change to yellow coat. This results from a disappearance of black pigment from the hair or its replacement by yellow. But the black pigment still persists in the eye. Hence one may speak of this change as being a *restriction* of black to the eye, whereas in wild rodents it is regularly *extended* throughout the coat. The factor which has undergone change is therefore said to be the *extension factor* for black (or brown) pigment. Its dominant phase may be expressed by E, its recessive phase (found in yellow animals) by e. (See Plate 7, Fig. 29.) An alternative recessive phase (e′) is found in yellow animals spotted or brindled with black or brown.[1]

A third sport among wild rodents is responsible for the origin of black varieties which lack the yellow tip of the fur found in most wild gray or "agouti" varieties. (See Plates 6 and 7, Figs. 22–26). This yellow tip sometimes takes the form of a subapical band of yellow on hair which is black (or brown) both at the base and at the extreme end. This is the case for example in the agouti varieties of the rabbit and the guinea-pig. The optical effect of the agouti factor in either case is to produce a protectively colored, neutral gray coat, inconspicuous against many natural backgrounds. The black sport may be regarded as a recessive variation in an *agouti* factor possessed by most wild rodents. The dominant phase of this factor may be expressed by A, its recessive phase (the non-agouti variation) by a.[2]

Another unit-character variation found in many rodents, as well as in some other mammals, is responsible for the replacement of black pigment by brown throughout the coat and even in the eye. (See Plate 7, Figs. 27 and 28.) This

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[1] The occurrence of yellow sports among wild meadow mice (Microtus) has been observed by Cole, Barrows, F. Smith and others, though no tame races of this very common rodent have yet been established. The contemporary origin in England of a yellow race of the Norway rat has been recorded by Castle (1914), and the origin of a yellow race of Mus rattus by Bonhote.

[2] Sometimes black varieties arise by a process other than a change in the agouti factor, as is the case probably in a locally common black variety of the gray squirrel of Eastern North America. This shows the agouti marking of the fur to so small an

Plates 6 and 7 are reproduced by permission from Publication No. 241 of the Carnegie Institution without change of figure numbers. They show in the natural colors how a single pure-breeding domestic type (20) crossed with a single pure-breeding wild type (23 and 24) may produce in the next generation only a single type (22), which however may, in the following generation, through the operation of Mendel's law, produce half-a-dozen very distinct pure-breeding types (25–30). Through a knowledge of Mendel's law the multiplication of color types among animals and plants has ceased to be a haphazard process and has become a simple and orderly procedure.

PLATE 6

Fig. 20, half-grown guinea-pig, race C. Figs. 23, 24, male and female Cavia cutleri, adult. Fig. 22, F_1 hybrid, race C x Cavia cutleri, adult. Fig. 21, F_1 hybrid, race B (Plate 5, Fig. 34) x Cavia cutleri, adult.

PLATE 7

F_2 hybrids, race C x Cavia cutleri. Fig. 25, agouti; 26, black; 27, chocolate; 28, cinnamon; 29, yellow; 30, albino.

change converts an ordinary gray variety into a "cinnamon" variety, and black into "chocolate," while yellow with black eyes becomes changed to yellow with brown eyes. The factor which in such cases has undergone change we may call the *black* factor, its original or dominant phase being expressed by B, the recessive (brown) phase by b. (See Table 12.)

Another unit-character color variation perhaps commoner than any of those yet mentioned is found both among wild and among domesticated mammals. It consists in spotting with white. It takes the form among wild rodents of a white spot in the forehead (common among wild rabbits) or a white spot on the belly, a white foot, or a white-tipped tail. Rarely does it go beyond these slight and inconspicuous markings, probably for the reason that it would render the possessor too conspicuous for his safety, though this appears to be a consideration of no consequence in the case of skunks, which possibly are less disturbed because of their advertisement. But under artificial selection in captivity it is possible rapidly to increase the extent of the white areas in the coat, which then takes on striking and often rather definite outlines, as in Dutch-marked rabbits, "English" rabbits (Fig. 123), hooded rats (Fig. 56), and black-eyed white mice, the latter being all white except the eyes. The production of white-spotted races from small beginnings observed in wild stocks has been accomplished in the laboratory by Castle and Phillips in the case of Peromyscus and by Little in the case of the house-mouse (unpublished data). Physiologically this variation is quite distinct from the albino variation. It appears to be due to a locally inhibited action of the color factor, which in

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extent that the prevailing color of the coat is black. The same is true in some specimens of the black rat (Mus rattus), this black character being dominant in crosses over the true agouti character found in the gray variety of the same species which is known as the "roof-rat" (*Mus Alexandrinus* of some systematists). A similar dominant black has been discovered among domestic rabbits by Punnett, who has shown that it owes its origin to a change, not in the agouti factor, but in the extension factor, *E*, which has become of such unusual strength or potency that the agouti factor is unable in its presence to produce the usual conspicuous effect.

other parts of the body retains its full force; whereas in an albino the action of the color factor is everywhere wanting or greatly weakened.

The variation, "white spotting," may be regarded as a unit-character change from a condition of *uniform* action of the color factor to a condition of locally suppressed action of the color factor. The former may be designated S, the latter s. Its inheritance is as sharply Mendelian as that of any other color variation but, the precise extent to which color development is suppressed being obviously quantitatively variable (Fig. 56), it is easier by selection to modify the modal state of a white-spotted race than of races of most other color varieties.

That this factor is genetically entirely distinct from albinism is shown by the fact that white-spotting is transmitted quite as readily through albinos as through colored individuals.

In some rodents not only the color factor, but also the extension factor is subject to locally inhibited action. Local inhibition of the extension factor produces yellow spots in an otherwise black, brown, or agouti coat. This color variation, which follows Mendel's law in crosses, may be called *yellow spotting*. It behaves as a third allelomorph (e′) alternative both to full extension (E) and to full restriction (e). When yellow spotting coexists with white spotting, a tri-color condition of the coat results, spots of yellow, white, and black (or brown) being found on the same individual. Familiar examples are found among guinea-pigs, cats and dogs.

Another unit-character variation of certain rodents greatly reduces the production of black and brown pigments without affecting at all the production of yellow pigment. As the pigmentation of the eye consists almost entirely of black or brown, it follows that in this variation the eyes become pink, while the coat pigments other than yellow are greatly reduced in amount. Pink-eyed blacks or browns are very pale coated, but pink-eyed yellows are indistinguishable from other yellows except by the eye-color. The changed eye-color is ac-

FIG. 57. A trihybrid Mendelian cross between a black hooded rat (top left) and an all-yellow sport (top right) recently captured among wild Norway rats in England. F_1, one of the first-generation progeny, gray by reversion, like wild rats. F_2, the eight classes of second-generation young, from left to right, black hooded, black self, gray hooded, gray self, yellow self, yellow hooded, cream (non-agouti yellow) self, cream hooded. Numerically these classes should be as 3 : 9 : 9 : 27 : 9 : 3 : 3 : 1. Let the reader determine which of the eight classes may be expected to breed true and to what extent the other varieties will not breed true without " fixation " (elimination of heterozygotes).

cordingly the most constant feature produced by this variation. The dominant phase of this unit-character, which is regularly found in all wild races, may be designated *dark-eye*, D; its recessive allelomorph, *pink-eye*, d. The recessive variation, pink-eye, occurs in guinea-pigs, rats, and mice. It has not been reported as yet for any other mammal. (See Fig. 55.)

Another unit-character variation, which affects the pigmentation of rodents, occurs also in other mammals. This consists in a reduced quantity of pigment and in such a clumping of the pigment granules within the air spaces of the hair as to produce a *dilution* of the pigmentation as a whole. Black under these circumstances becomes a slaty *blue*, chocolate becomes a dull muddy brown, and yellow acquires a pale washed-out appearance. The best-known examples are found in blue (Maltese) cats, blue rabbits and blue mice.[1] This condition may be regarded as a recessive variation of a factor for *intense* pigmentation normally found in wild rodents. We may designate this intensity factor by I, its recessive allelomorph by i (dilution).

In guinea-pigs and rabbits there has occurred a unit-character variation which affects, not the color, but the length and texture of the hair, which in the so-called "angora" variety is long and silky. This results from a failure of the hair follicle to end its activity when the hair has attained its normal length. In the angora variety the hair keeps on growing for an indefinitely long period. The long or angora coat of guinea-pigs and rabbits is a recessive character in relation to normal (short) coat. We may regard a normal and dominant character for short coat, L, as having undergone variation to long coat, l. (See Figs. 36, 37, and 41.)

Among guinea-pigs alone of rodents has occurred another morphological unit-character variation of the coat, which, instead of being *smooth* and sloping uniformly from the nose

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[1] This variation probably does not occur in guinea-pigs; what was at one time described as a variation of this sort having proved to be an alternative form of the color factor.

backward as in wild mammals, may become *rough* or rosetted with the hair radiating out from centers located in various parts of the body. (See Fig. 33.) Rough coat is dominant over smooth coat, for which reason we may consider a unit-character, rough coat, R, to be responsible for it, the recessive phase of which, r, is found in smooth-coated guinea-pigs.

It should be noted that both rough coat and short coat, like the uniformity factors affecting pigmentation, obviously vary quantitatively. For some rough guinea-pigs are rougher than others and some long-haired guinea-pigs have longer, silkier hair than others. Selection has undoubtedly been concerned in producing the present high standard long-haired and rough-coated guinea-pigs respectively. Dr. Sewall Wright has shown (Castle and Wright, 1916) that an independent Mendelizing factor found in many wild cavies interferes with or partially inhibits the development of the rough coat in hybrid guinea-pigs. We may designate this factor rough modifier (M), its recessive phase which permits full development of the rough coat may be expressed by m. Aside from this striking modifier of rough, it is probable that numerous other factors act as slight modifiers of rough and that the apparently continuous variation in the development of the roughness may thus be accounted for. Continuous variation in the expression of the angora character, as regards length of hair, may be accounted for on similar grounds.

Leaving out of consideration such quantitative variations, it is possible to obtain by crosses a large number of different unit-character combinations of the ten independent variations which have been mentioned as occurring in guinea-pigs. Theoretically one thousand and twenty-four are possible, or if we count separately homozygous and heterozygous combinations, fifty-nine thousand and forty-nine are possible. Needless to say there have been produced thus far only a small part of the varieties of guinea-pigs theoretically possible as unit-character combinations of the ten factorial variations known to have occurred in this species. And the variation of the guinea-pig is not different in kind or degree from that of other rodents. Its variation has probably merely been followed up more closely by selective breeding. Among domesticated rabbits, at least seven of the ten enumerated variations have occurred; all except the pink-eye and the rough-coat variations are reported for rabbits, and most of them are well known. The house mouse has undergone at least six of the ten variations listed in Table 12. Its yellow varieties have apparently not arisen in the same way as yellow varieties of guinea-pigs and rabbits, but by a peculiar change in the agouti factor, for yellow in mice is a third allelomorph of agouti and non-agouti. Mice also lack long-haired and rough-coated varieties, but in other respects the variations of mice are parallel with those of guinea-pigs. In the Norway rat four of the ten unit-character variations of guinea-pigs find exact equivalents, viz., in albinism, non-agouti, pink-eye and white spotting. A third allelomorph of the color factor (ruby-eye) has been shown by Whiting and King to occur among wild rats.

A red-eyed yellow variety of rats is due to a unit-character variation distinct from the yellow variations known in guinea-pigs and in mice respectively. In one and the same linkage system in the Norway rat are found (1) the color factor and its allelomorph, ruby-eye, (2) the factor for pink-eyed yellow and (3) the factor for red-eyed yellow.

CHAPTER XIII

UNIT-CHARACTERS IN CATTLE AND HORSES

Unit-character changes have produced new varieties among our more important domesticated mammals as well as among our pet rodents.

Cattle. Among cattle four or five Mendelizing color variations occur similar to those of rodents and in addition two variations of a morphological character have been reported, one of which has considerable economic importance. Wild cattle existed within historic times in central Europe, the hunting of the last-existing herds being held as a royal prerogative by the kings of Poland. These cattle represented probably the chief source from which domesticated cattle were derived. They were of large size but of what color we do not certainly know. It seems probable, however, that their coat, like that of most wild ruminants, contained a mixture of yellow and black pigments somewhat like the coat of Jersey cattle at the present time. In most existing domestic breeds either the black or the yellow pigments have become predominant or white has taken their place in whole or in part. Such is the general tendency of man's agency in modifying the color characters of his domesticated animals. Nature's colors are usually adapted to concealment or protection. Mixtures of pigments are common and minute color patterns abound. Man seeks to make his domestic animals as different as possible from the wild. He either gives preference to pure colors, black, white, or yellow, or seeks to outdo nature in the production of color patterns in great blotches of two or three colors. The materials for his operations consist of sports to solid black, yellow, or white, together with white spotting and yellow spotting. All of these have occurred among cattle and have been used to the fullest extent.

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FIG. 58. Wild white cattle from Chartley Park, England. (After Wallace.)

FIG. 59. Wild white cattle from Chartley Park. Note *black* individual produced by white parents. (After Wallace.)

FIG. 60. Kerry cow, a black breed, originated in Ireland. (Figs. 60 and 61 from photographs by Professor C. S. Plumb.)

FIG. 61. Dexter-Kerry cow. Its short-legged compact form is a dominant Mendelian character according to Professor James Wilson.

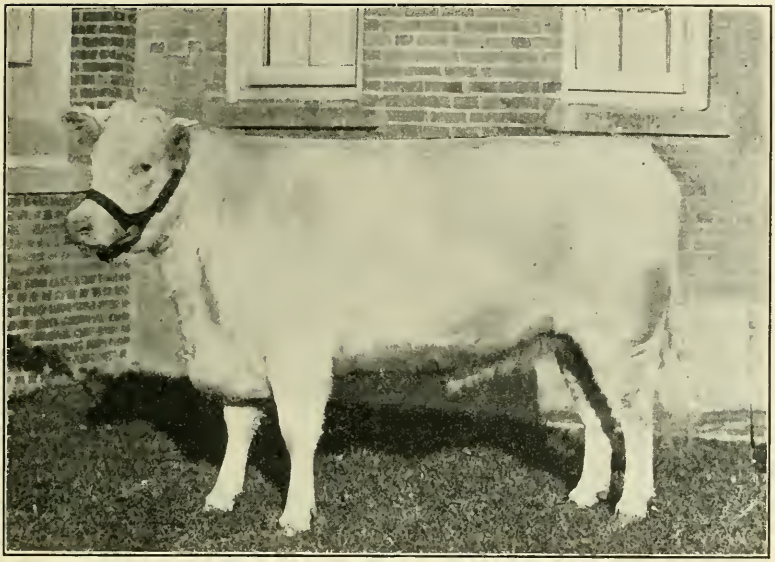

FIG. 62. White short-horn heifer.

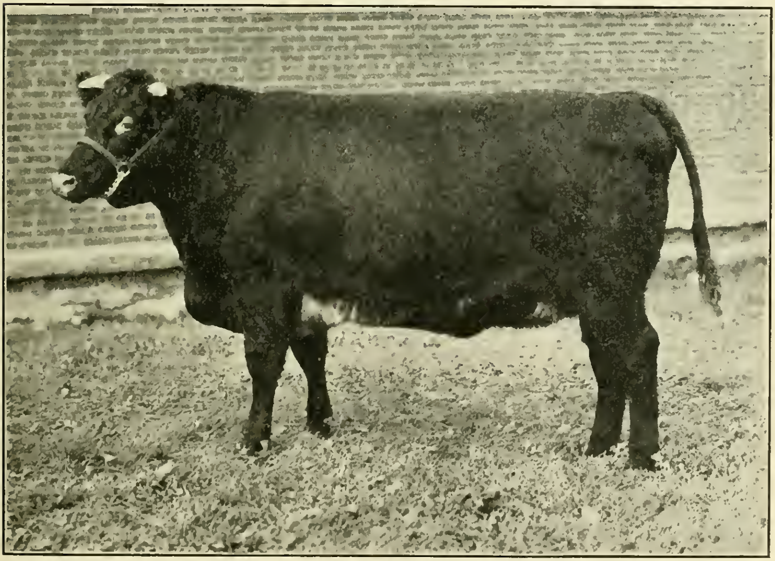

FIG. 63. Red short-horn heifer with a small amount of white spotting underneath.

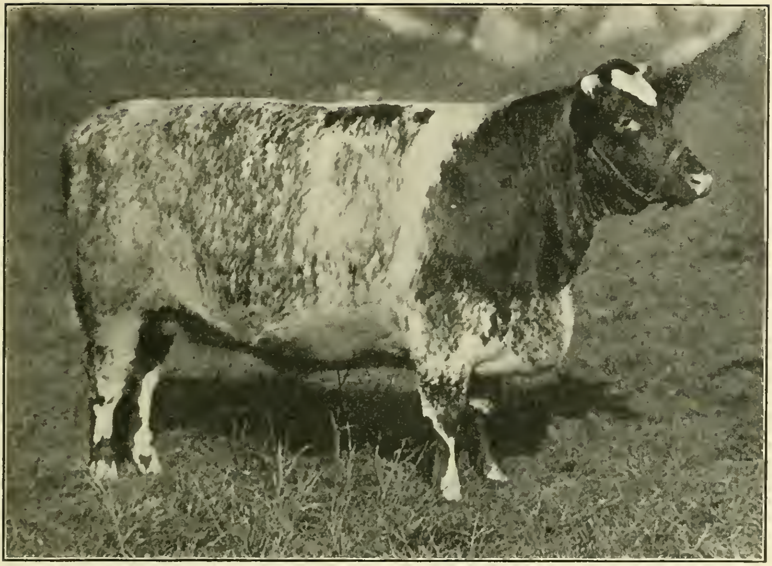

FIG. 64. Roan short-horn cow. Beef type. The fine mosaic of red and white spots indicates that this animal is a heterozygote between red and white (FIGS. 62 and 63).

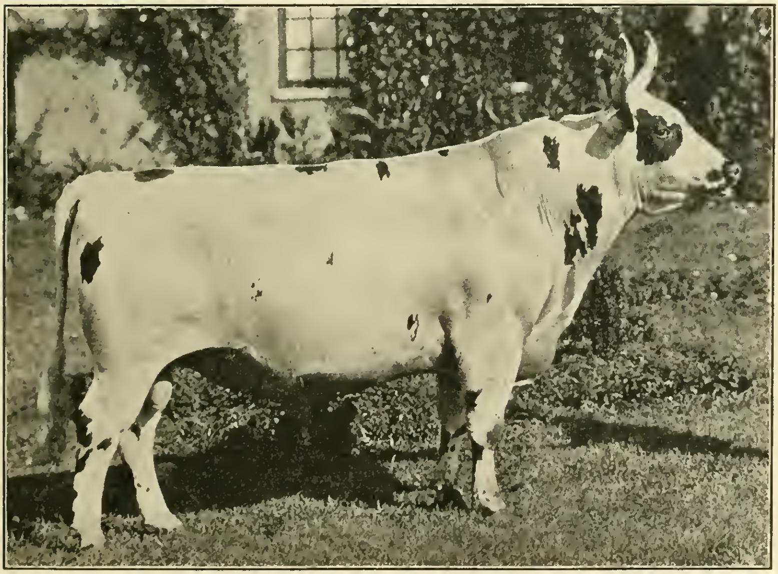

FIG. 65. Ayrshire bull. Extensive white spotting in this breed leaves only an occasional small spot pigmented. The breed is hardy, "dual purpose" but inclining more to the dairy type, yet less specialized and better adapted to a severe climate than the Jersey and Guernsey breeds. It originated in Scotland.

In English parks there have existed, since Roman days and perhaps longer, herds of all-white cattle kept in a half wild state. Some have supposed that these white cattle represent the unchanged original stock of European wild cattle, but it seems much more probable that they represent a striking sport from the original stock, which was isolated and allowed to increase in the hunting preserves of princes, a semi-sacred character perhaps attaching to it. These cattle differ from albinos among rodents in that they have pigmented eyes. They also have some sooty black or brownish pigment in the skin and hair of the extremities (feet, nose, ears, and tail). Ordinarily they breed true, but occasionally an all black calf is produced, but whether as a recessive in the Mendelian sense or as a reversion, through recombination of complementary color factors, is unknown. (See Figs. 58 and 59.) In any case it seems highly probable that the white race resulted from an ancient sport derived directly from wild cattle. In the breed of " short-horn " cattle, which originated in England, white individuals frequently occur and they breed true when mated with each other. In matings with red individuals, a sort which also breeds true, roan heterozygotes are produced (as noted on page 110). The white of this breed was probably derived from the same original source as the white cattle of the English parks, but the black character which seems to inhere in the cattle of the parks has been eliminated from the short-horn breed, which produces only reds, whites, and their heterozygotes, with or without admixture of white spotting. (See Figs. 62–64.)

TABLE 13

SOME UNIT-CHARACTERS OF CATTLE

Dominant	Recessive
Black.	Yellow.
Polled.	Horned.
Dexter form (short legs).	Kerry form (legs normal).
Dominance Uncertain or variable	
White.	Colored.
Uniformly colored.	Spotted with white.
Uniformly black.	Black spotted with yellow.

Red cattle have an intensified yellow pigmentation. They probably represent derivatives of an original all-yellow sport, comparable with the yellow sports of rodents, which originate through restriction of black pigment to the eye. Among cattle yellows vary in shade from a very deep red (Devons and short-horns) to a light cream color (some South German and Swiss breeds). The extremes in both directions were doubtless secured through repeated selection. Whether the different shades or intensities of yellow are alternative is unknown, but it seems probable that in cattle as in rodents intensity of pigmentation is independent of its specific character as black or yellow.

Black breeds of cattle are represented by the Galloway and Aberdeen Angus of Scotland. In them we have either derivatives of an all black sport, or the end result of a gradual increase of black in the coat through selection. Pure-bred Aberdeen Angus cattle sometimes produce red calves, red being obviously a Mendelian allelomorph recessive to black in cattle as it is in rodents. As red is not favored in the standard of the breed, it will doubtless be entirely eliminated in time, as seems already to be the case in the best families of the Galloway breed. (See Fig. 73.)

In most breeds of cattle white spotting occurs and this is a Mendelian alternative to uniform coloration, though neither condition is entirely dominant over the other. The self-coloration of breeds which are all black or all white has a strong tendency to prevail in the offspring. Black breeds in which white spotting occurs are represented by the Holstein-Friesian cattle originally bred in Holland and Denmark, but now extensively kept in this country, also by the belted cattle of Holland. (See Figs. 66 and 69.) Red-and-white and yellow-and-white cattle are represented by Hereford and Guernsey cattle respectively. (Figs. 68 and 67.) Black-and-white breeds may produce red-and-white offspring as recessives, but red-and-white breeds never produce black-and-white calves, which shows clearly that black is dominant over red. In the Hereford breed a definite pattern of white

Fig. 66. Holstein-Friesian cow and her triplet calves. Note the black-and-white mottling similar in all four animals, yet with individual differences. This breed of large vigorous cattle originated on the borders of the North Sea in Europe. It excels all other breeds in milk production. (Photograph by the owner, N. P. Sorensen, Bellingham, Wash.)

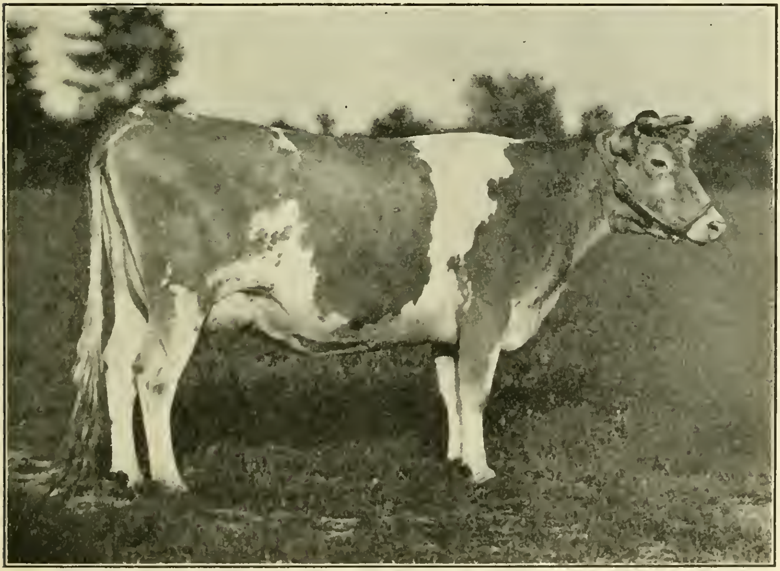

Fig. 67. Guernsey cow, "golden yellow-and-white" in color, graceful in form, gentle in disposition, producing a good quantity of milk extremely rich in butter-fat. The breed came originally from the island of Guernsey. (Photograph from Langwater farms, N. Easton, Mass., F. L. Ames, proprietor).

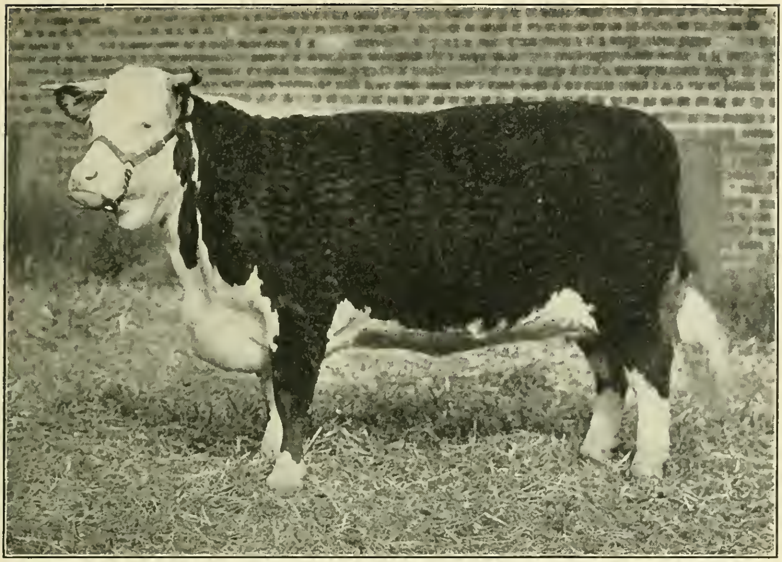

Fig. 68. Hereford heifer. One of the leading beef breeds, dark red and white in color. The white face, back stripe and underline constitute a pattern which has a tendency to dominate in crosses. (See Fig. 80*a*.) Like the short-horn, its principal rival as a beef breed, this breed arose in England.

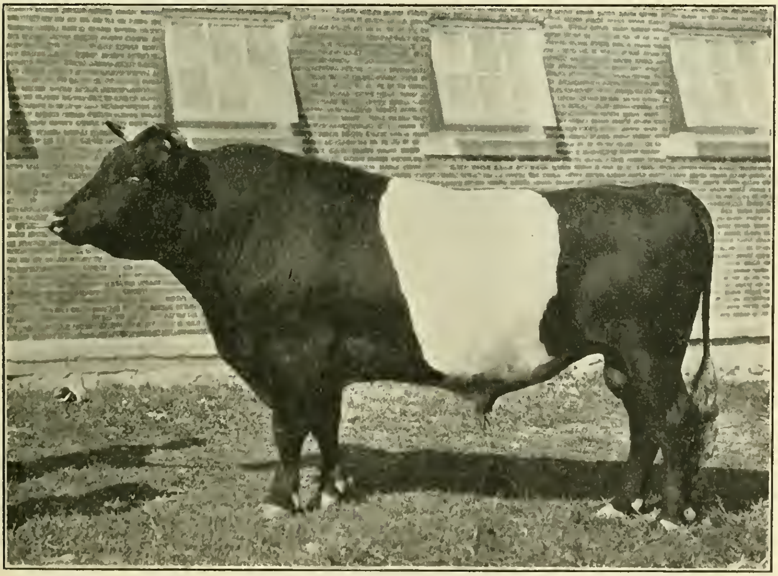

Fig. 69. Dutch belted or "Lakenfeld" bull. Bred for three centuries for this characteristic pattern by aristocratic families of Holland. Probably derived from the same original general stock as the cattle of Holstein farther east, but selected more closely for color pattern to which productiveness has been sacrificed.

Fig. 70. Polled Durham (or short-horn) cow. Produced by a hornless sport within the short-horn breed or possibly by some unrecorded cross, as with the polled red breed.

Fig. 71. Polled Hereford heifer. A breed of English origin, dehorned in America by the application of genetic principles. Hornlessness is a dominant sport or "mutation." Compare Fig. 68. A comparison of the white spotting in Figs. 70 and 71 suggests strongly that one is only a more advanced stage (quantitatively) of the other.

spotting has been so fixed by selection that it shows itself (as a white forehead) in crosses with self-colored breeds and even in hybrids with the American bison.

Yellow spotting on a black background is not very common among cattle, no standard breed with this characteristic being known, but a brindling of yellow and black spots is occasionally seen in mongrel animals and no doubt good black-and-yellow spotted animals could be produced, if it were considered sufficiently desirable, or even tri-colors with black-yellow-and-white coats. It is possible that brindling (yellow spotted with black) is a third allelomorph of black and of yellow, as in guinea-pigs.

A morphological variation of cattle of some economic importance is hornlessness. This has occurred among cattle of Scotland and England for several centuries at least and is known also to have occurred among cattle kept on the continent and still earlier to have occurred among cattle of the ancient Egyptians. Loss of horns is a completely discontinuous variation, dominant in crosses. Heterozygotes may develop mere traces of horns, known as scurs, but never a fully formed horn with bony core. Hornlessness has become an established racial character (homozygous) in the Scotch breeds of black cattle, Aberdeen Angus (Fig. 73) and Galloway, also in an English breed of red cattle called Red Polled. Within the last thirty years polled sports have appeared in pure-bred Holstein cattle in the United States and a breed of polled Holsteins is now being established in this country. A breed of polled Herefords was produced in the United States from a three-quarters Hereford, one-quarter short-horn polled calf born in 1889. (Wallace, p. 122.) See Figs 68 and 71. Polled cattle are easier to manage and less liable to injure each other than are horned cattle. There can be no doubt that hornlessness had its origin as a unit-character variation dominant in crosses.

Another morphological character, said to be a Mendelian dominant, occurs in Dexter-Kerry cattle. They have abnormally short, stumpy legs. (See Figs. 60 and 61.)

Horses. The original color of wild horses is probably seen in a wild horse still existing on the plains of central Asia (Mongolia) and known as Prevalski's [1] horse. (See Fig. 81.) It has somewhat the appearance of an ordinary bay horse, except that the yellow pigment is paler and the black pigment more diffuse dorsally. The mane, tail and legs are black, the back reddish or yellowish brown shading off into pale sooty yellow below. In tame horses of the bay color variety as compared with this, the yellow pigmentation is of a brighter and more intense sort, called red, and more free from black dorsally, while the black markings of mane, tail, and feet are probably more distinct, changes that seem to have come in with careful selective breeding. For in mongrel horses of no particular breeding the fine points of the bay are often wanting, the yellow being of a dull shade and mixed dorsally with black and approaching a "dun" in general appearance. Unit-character variations are less in evidence in domestic horses than in cattle. The bay appears to be an improved type of wild-horse coloration not produced by abrupt changes in any particular characters but by gradual changes in several characters. Black is a color variety recessive to bay in crosses. It seems to have arisen in the same way that black varieties of rodents usually arise, by loss of a pattern factor. In rodents it is the agouti factor which having disappeared produces a black (non-agouti) variety.

TABLE 14

SOME UNIT-CHARACTERS OF HORSES

Dominant	Recessive
1. Bay.	Not bay (i. e., black or chestnut).
2. Black.	Chestnut.
3. Gray.	Not gray (any color but gray).
4. Trotting.	Pacing.
Dominance Uncertain or Wanting	
5. Uniformly colored.	Spotted with white.

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[1] The common spelling of this name is Prejvalski, but as this makes in English an unpronounceable combination, I take the liberty of dropping the *j* in the interest of my readers, without intentional disrespect to Mr. Prejvalski or his horse.

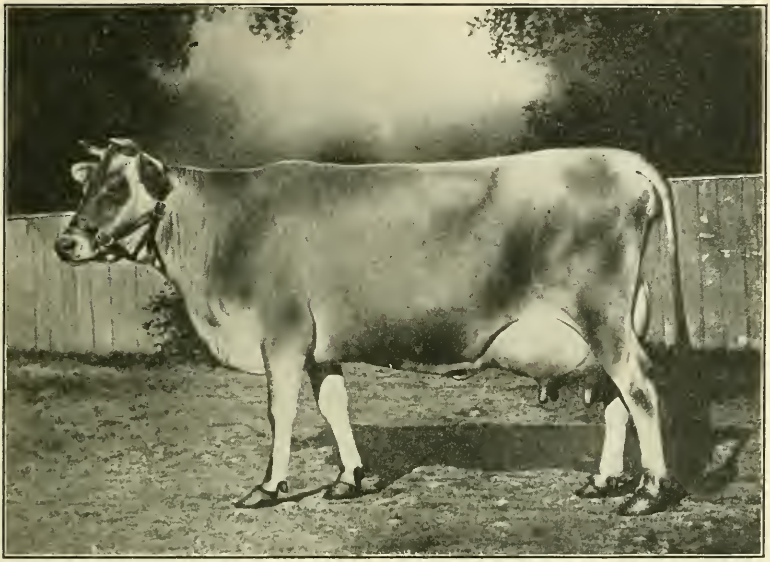

Fig. 72. Jersey cow. One of the best strictly dairy breeds. Color light yellow ("fawn") shaded with diffuse black pigment, possibly a primitive type of coloration in cattle. Similar to the Guernsey in character and source. Home the island of Jersey. A little delicate in constitution and nervous in temperament.

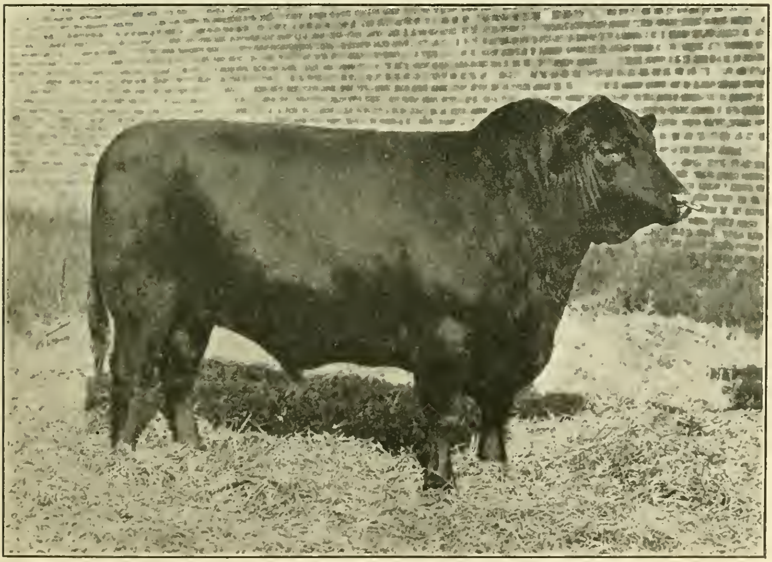

Fig. 73. Polled Aberdeen Angus bull. A Scotch breed, self black in color, of beef type and hardy.

Fig. 74. F_1 cow, black, polled.

Fig. 75. Choice F_2 heifer.

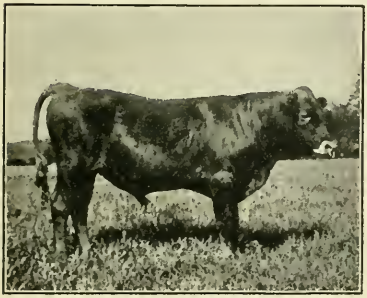

Fig. 76. Selected F_2 bull.

Fig. 77. Selected F_2 cow.

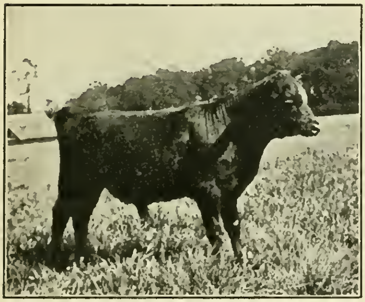

Fig. 78. Rejected F_2 bull.

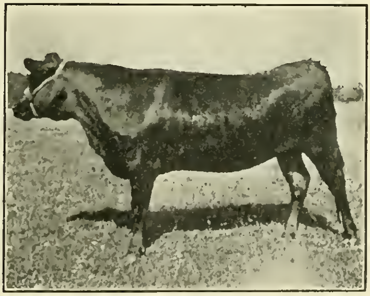

Fig. 79. Rejected F_2 heifer.

Results of crossing Jersey cows (Fig. 72) with an Angus bull (Fig. 73) in an effort to combine in one race the dairy excellence of the former with the size, hardiness and good feeding qualities of the latter. Figs. 74, 78 and 79 show the dominant black of the Angus, Figs. 75–77 show the recessive fawn of the Jersey somewhat darkened. All show dominant hornlessness. (After Kuhlman.)

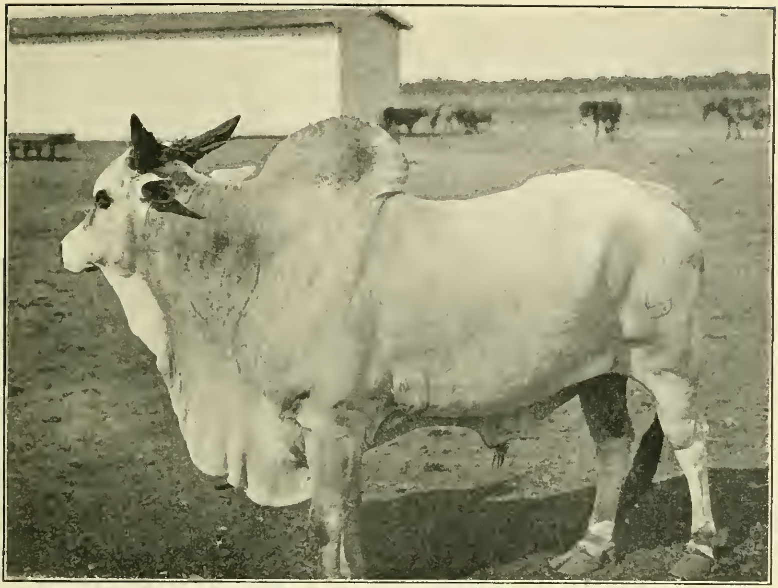

FIG. 80. A zebu bull, typical example of one of the humped cattle of India. (Photograph from Professor Nabours, Kansas Agr. College.)

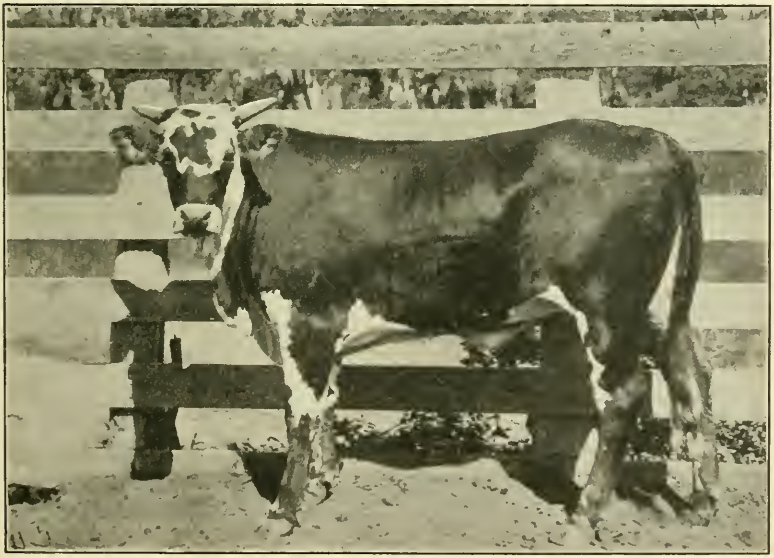

FIG. 80*a*. F_1 calf from cross of zebu bull with Hereford cow. Notice imperfect dominance of Hereford pattern (Fig. 68). Indian cattle being more tolerant of heat and more resistant to Texas fever, the cross is made to combine these qualities with the beef excellence of the Hereford. (Photograph from Nabours.)

In horses it is a *bay* factor which the black variety has lost. This factor appears to inhibit the development of black in regions where the bay variety shows red, just as an agouti factor inhibits the development of black pigment in certain regions of the coat of rodents which then are yellow. When the bay factor is lacking, black pigment develops throughout the entire coat. Whether this loss occurred originally as a single sudden change (a sport) or whether it occurred gradually is uncertain, but it seems clear that at present in crosses black is a unit-character recessive to bay, and this makes it seem probable that it arose as a discontinuous variation originally.

A unit-character difference has also been shown to exist between black and chestnut horses, a difference comparable to that which exists between black and brown varieties of rodents. Chestnut is recessive to black, corresponding with the " chocolate " varieties of rodents. " Suffolk " or " Suffolk Punch " horses are invariably chestnut in color. But the term " chestnut " as here used probably includes both brown animals which, like black, lack the bay factor and those which possess this factor. For the latter it would probably be better to use a term in common use, *sorrel.* We should then have parallel black and brown series with and without the bay factor. Black pigmented horses with the bay factor are " bays," without it they are " blacks." Brown pigmented horses with the bay factor should be called " sorrel "; those without it, chestnut. Records compiled by Wentworth and others indicate that such a factorial difference does exist among horses called " chestnut " in the records. For blacks mated *inter se* produce some chestnut colts (which should be possible if the black parents are heterozygous for chestnut) with a doubtful record of a few bays, but black mated with " chestnut " produces more bays than anything else, which shows clearly that some at least of the chestnut parents do transmit the bay factor.

The gray (or white) color variation of horses corresponds roughly with the white variation in cattle. It is a dominant unit-character in crosses, but shows itself only in the second and later coats. For the colts are born with colored coats, but at the first shedding of the hair, white hairs begin to come in mingled with the colored ones. (See Fig. 84.) Later white hair may almost completely replace the colored ones. The eyes of gray horses are always colored. The term gray as applied to horses has the same significance as when applied to human beings. It means the occurrence of white hairs among colored ones, more or less completely replacing them. When among horses the original coat partially replaced by white was a black one, an ordinary or " iron " gray coat results; but when the original coat was bay or sorrel, then a roan coat is produced.

White spotting is of frequent occurrence among horses, though it is usually less extensive than among cattle. In this variation the loss of pigment from the body area affected is complete and is present from birth on, so that its nature is evidently very different from the gray variation already described. (Figs. 81–85.) It corresponds physiologically with white spotting in cattle and in rodents. The commonest form of white spotting is the occurrence of a white spot in the forehead sometimes extending down over the nose, or the possession of one or more white feet, or both. These are regular features of the coloration of Clydesdale and Shire horses. More extensive spotting takes the form of irregular white areas extending across the neck or body. (Fig. 81a.) It is less common than the former and unlike it behaves as a dominant character in crosses. Often seen in children's ponies, it is probably genetically distinct from the spotting of horses with white stockings and blaze. The pacing gait in American race horses is a character recessive to the trotting gait, according to Bateson. In pacing the two legs of the same side of the body move in unison or nearly so, while in trotting the foreleg of one side moves almost simultaneously with the hind leg of the other side. Some trotters may be made to acquire the pacing gait and these, of course, may produce trotters, but natural pacers produce only natural pacing colts when bred with each other, whereas in crosses trotting dominates.

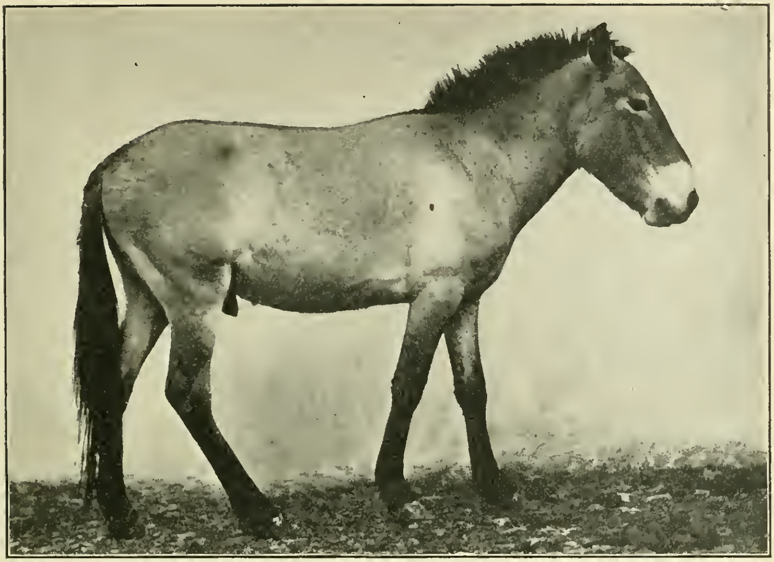

Fig. 81. Prevalski horse in the New York Zoölogical Garden. (Photograph by courtesy of Director W. T. Hornaday.) Notice large head, erect mane, absence of forelock and taillock, faint zebra-like striping on front leg, and general pattern of " bay," with light muzzle and darker mane, tail, and legs.

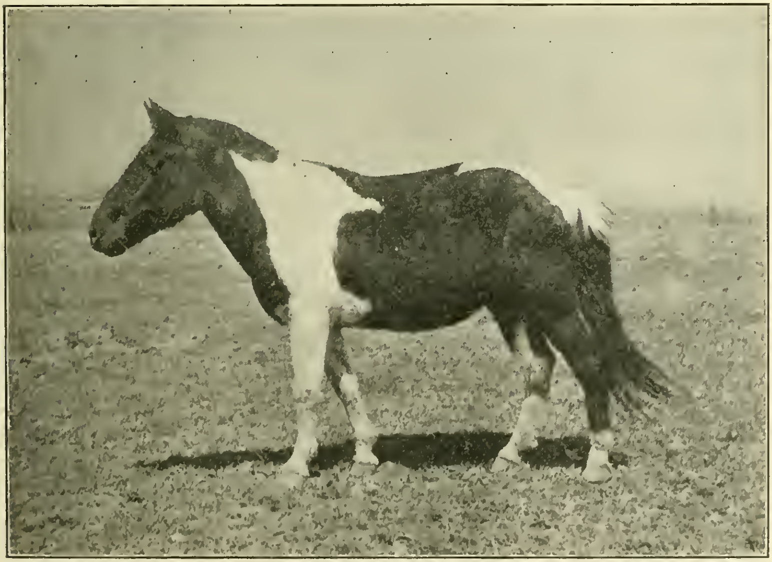

Fig. 81*a*. Pony of uncertain pedigree on farm of Simpson Bros., Palmer, Ill. (Photograph by courtesy of Professor J. A. Detlefsen.) Notice general form like that of Prevalski horse, but with white spotting extending up over front legs and entirely around body. Spotting of hind feet also extends up over body on right side.

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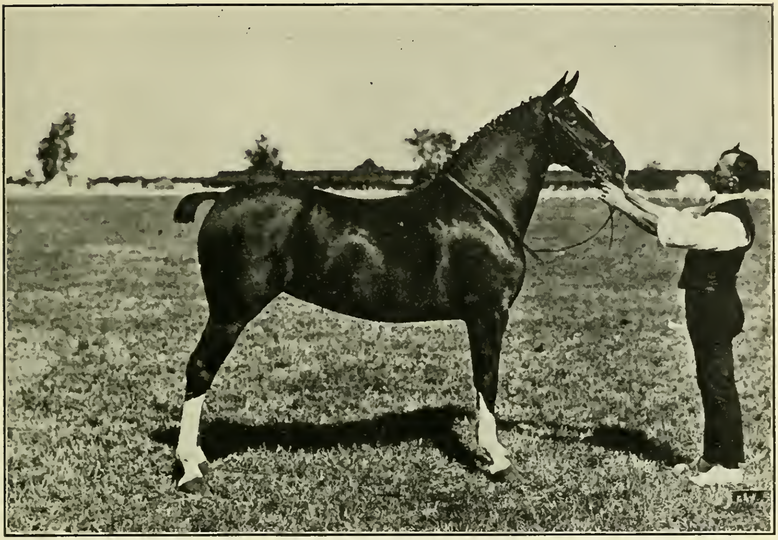

FIG. 82. A saddle horse ("hunter") showing typical white markings, "white stockings" and "blaze" (face stripe). These are manifestations of white spotting fully developed at birth and not changed subsequently.

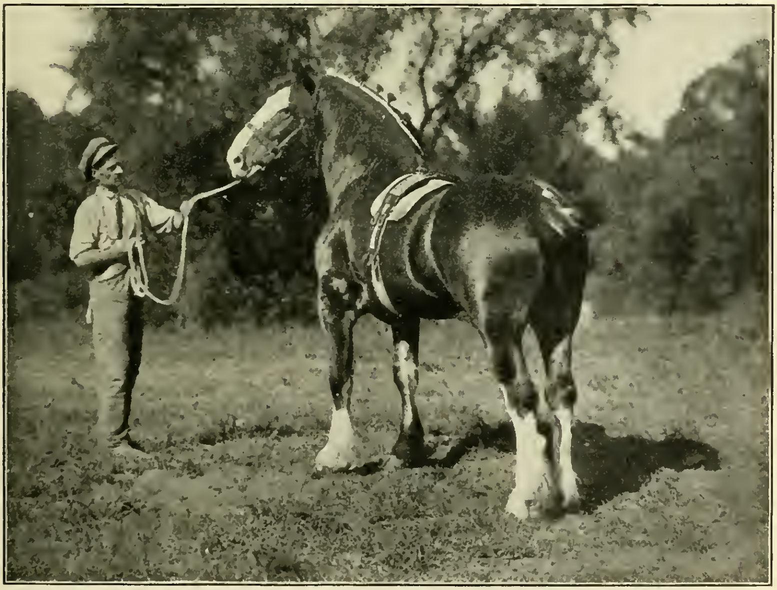

FIG. 83. Clydesdale, typical example of one of the breeds of heavy draft horses. White stockings and blaze of white are regularly present in this breed.

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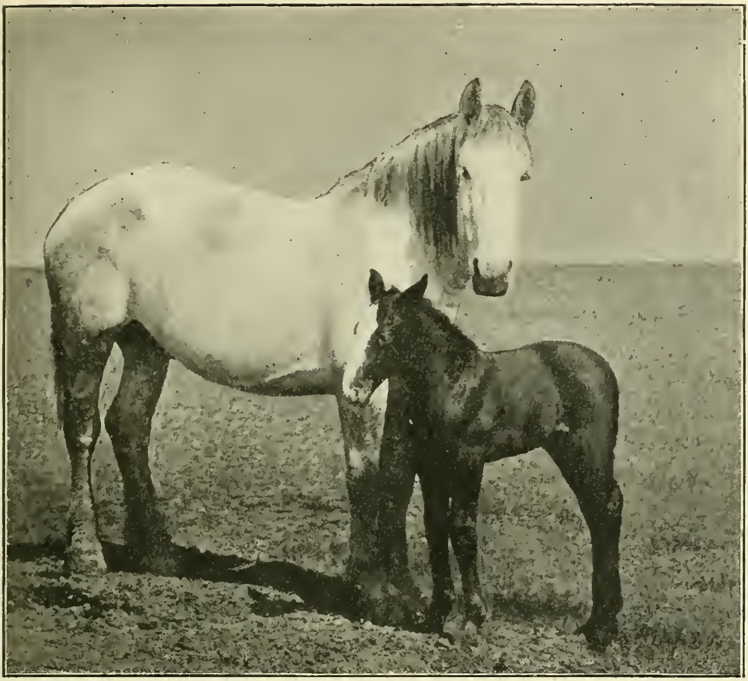


FIG. 84. Gray Percheron mare and colt. Such colts, black at birth, become gray later in life. Notice, however, that the colt's face is already white. This is due to white spotting, as in the hunter and Clydesdale, not to the gray factor. The two forms of white are genetically quite distinct.

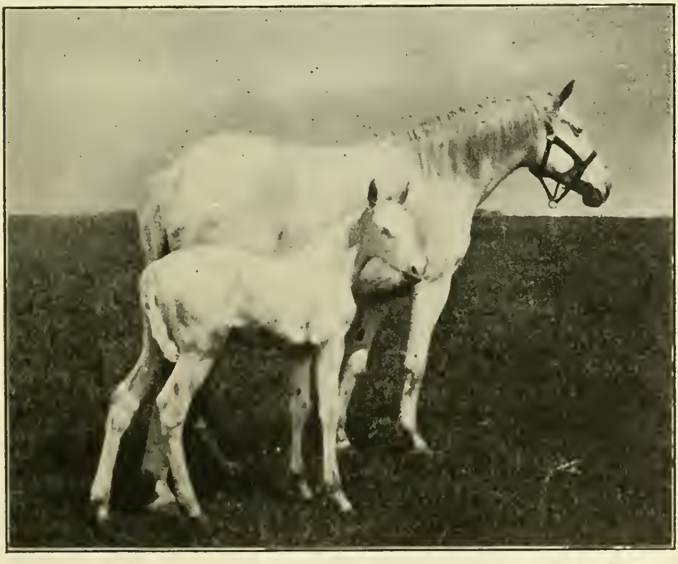


FIG. 85. White mare and colt. (Photograph by courtesy of W. P. Newell, Washburn, Ill.) An extreme condition of white spotting is here shown, in which the entire coat is white from birth on.

CHAPTER XIV

UNIT-CHARACTERS IN SWINE, SHEEP, DOGS, AND CATS

Swine. In the wild boar of Europe, from which in part domestic swine are descended, the coat is slaty black, the individual bristles bearing a band of pale yellow like the agouti marking of rodents. The young of the wild boar are also marked with longitudinal body stripes, a character perhaps correlated with the agouti-like banding of the bristles. This banded character of both young and adult has apparently been lost in all domestic breeds, which are either self black, red, or white, or else black or red spotted with white, yet it occasionally reappears in crosses, showing a probable dependence upon complementary factors still found separately in certain breeds (Severson). In the white variety the entire coat is colorless but the eye is colored. This is a dominant variation. White spotting is possibly a distinct variation from the foregoing, and uncertain as to dominance. But it may be that the two differ only in degree and are really allelomorphs.

TABLE 15

Unit-Characters of Swine

Dominant	Recessive
1. Wild color.	Not wild color (black or red).
2. Black.	Red.
3. Self white.	Colored.
4. Mule-footed (syndactyl).	Normal foot.
Dominance Uncertain or Wanting	
5. Uniformly colored.	Spotted with white.

Two forms of white spotting (which occur naturally and are comparable with the two types of white spotting among horses) are sought after by breeders and have become breed characters, viz., (1) a condition in which a broad white belt encircles the body (as in Hampshire hogs) and (2) a condition in which white appears at the extremities, on the feet and snout (as in Berkshires). It is probable that they are similar in genetic character. Black among swine is dominant over red, as in cattle, horses and rodents. But the dominance of black is commonly imperfect or complicated by the presence of a spotting factor in the red breeds known as Tamworth and Duroc-Jersey. (See Figs. 86–93.)

A curious morphological variation, syndactylism, is a dominant unit-character. In this variation the normal two hoofs of each foot have completely fused together and the foot has a single hoof like a "mule." Hence the variety is called "mule-footed." A breed having this characteristic has been established in the United States. Although the hoofs are fused the bones proximal to the toe retain their original paired character. (See Figs. 94 and 95.)

Sheep. In sheep ordinary white fleece is dominant over black fleece, the latter occasionally cropping out in flocks as a recessive, as indicated in the old saying "every flock has its black sheep." Black sheep breed true *inter se.* Black is probably not a reversionary variation but a loss variation of a pattern factor found in wild sheep and similar to the bay pattern of horses. Wild sheep are white or whitish except at the extremities where the pigmentation is heavier. In some breeds of sheep the skin and wool of the extremities is dark, similar to the coat of Himalayan rabbits, and white spotting may affect these pigmented regions just as it does the coat of Himalayan rabbits. (See Figs. 96–100.) Hornlessness is a variation from the original horned condition of wild sheep which is dominant in females but recessive in males, a matter deserving further consideration in connection with the subject of heredity as affected by sex. (See Figs. 96–104.)

Dogs. By Darwin and most other students of the origin of dogs, the conclusion has been reached that dogs are descended from several different wild species of wolves independently domesticated in different parts of the world. These, it was thought, having been subsequently intercrossed have produced a highly variable stock from which selection has isolated the genetically diverse modern breeds.

Fig. 86. Berkshire boar. Black with white points.

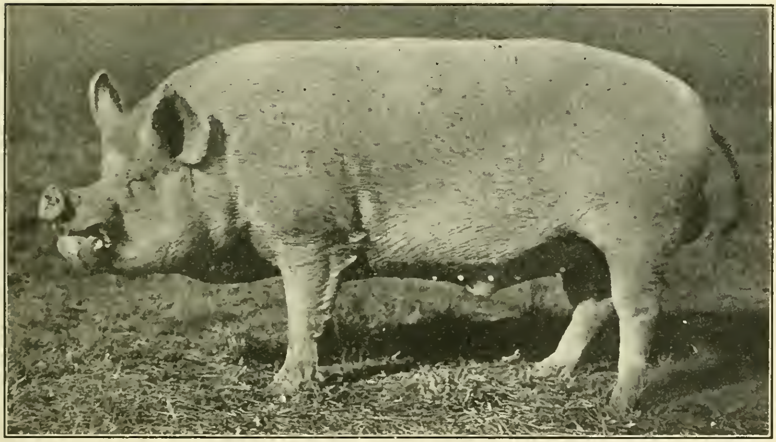


Fig. 87. Yorkshire boar. A self white breed.

Fig. 88. F_1 sow from cross, Berkshire × Yorkshire, and F_2 pigs. Note reappearance of recessive blacks but with white spotting increased in amount. (After W. W. Smith.)

Fig. 89. F_1 sow from cross, Berkshire × Yorkshire, and pigs produced by a back-cross with Berkshire boar. Note 1 : 1 ratio and modified spotting. (After W. W. Smith.)

Fig. 90. Hampshire sow, typical example of a belted black-and-white breed.

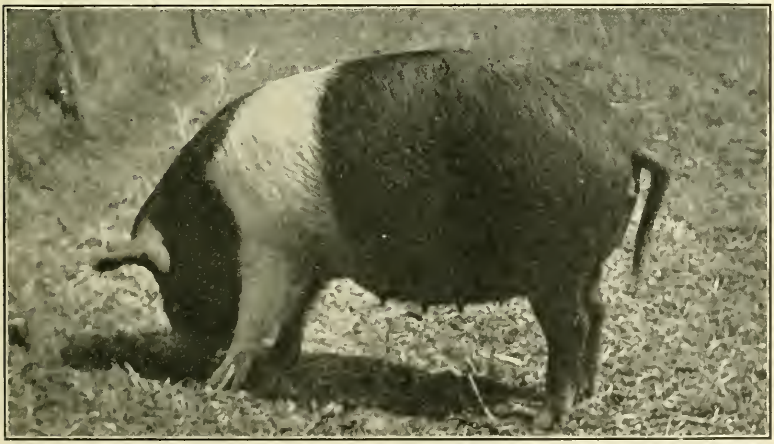


Fig. 91. Belted red sow. This breed produced by Q. I. Simpson by crossing black belted (Hampshire) with self red (Tamworth and Duroc) swine.

FIG. 92. A litter of pigs by two belted red parents. Evidently this form of white spotting is not fully recessive, since part of the pigs are not belted. (By courtesy of Simpson and Detlefsen.)

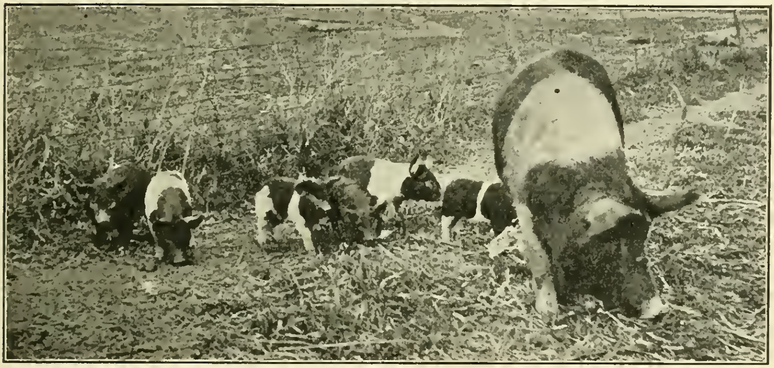
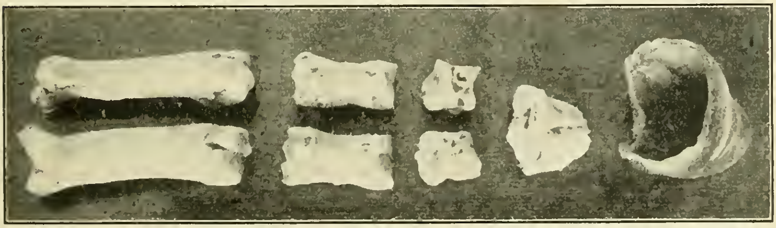


FIG. 93. A belted red sow and her litter by a belted red boar. Note variation in belt or its total absence. (By courtesy of Simpson and Detlefsen.)



FIGS. 94 and 95. Foot bones of mule-footed (syndactyl) swine. Only the hoof and nearest pair of bones show complete fusion. (After Spillman.)

A different opinion as to the ancestry of dogs has recently been expressed by G. S. Miller and particularly by G. M. Allèn, who has made a careful study of the cranial characters of dogs kept by the aborigines of the American continent. Allen finds strong evidence that the native dogs of America are not descended from American wolves but came with man in his migration from north-eastern Asia to north-western America. Previous to that migration there existed in Europe and Asia both a large and a small type of dog, and both types were introduced into America when it was peopled from Asia. A third type, the Eskimo dog with heavy coat and tail curled forward over the hip, occurs in the northernmost parts of both Asia and America and doubtless came with the Eskimos in their comparatively recent migration from Asia.

What part, if any, species hybridization has played in the genesis of dogs can not at present be stated, but a survey of existing breeds of dogs shows the occurrence among them of several unit-characters and accordingly unit-character variation (mutation) may be regarded as having been an important element in their production. A case which well illustrates the point is the color variation of Great Danes as worked out by Little and Jones. (See Fig. 104*a*.) Starting with the self black variety (3, Fig. 104*a*), we have as its recessive allelomorphs either brindle (4) or fawn (5). A recessive dilution factor, if present in a homozygous condition, gives us dilute black (6), dilute brindle (7) and dilute fawn (8). A dominant factor for white spotting produces the harlequin variety (2). A recessive factor for white spotting produces white feet or breast spot (1). These types of white spotting remind us respectively of the English and Dutch patterns of white spotting among rabbits. Presumably either pattern might occur in association with dilute black, brindled, dilute brindled, fawn, or dilute fawn coat (4–8, Fig. 104*a*). What are probably more developed forms of the recessive type of white spotting are represented in Figs. 106–109. In the breeds there shown white spotting has been selected for, whereas in the Great Dane it is rigidly selected against. A more specialized form of the dominant spotting (harlequin) is found in the coach-dog (Fig. 110). Besides the five unit-character variations of Great Danes, several other unit-character variations can be recognized in other breeds. (See Table 16.) The cranial characters of dogs show their ancestors to have been wolf-like.

Most wolves have a protectively colored gray coat, in which black and yellow pigments are intermingled on the same hair somewhat as in the agouti pattern of rodents. This pattern is wanting in most dogs, but has been retained in some examples of the Eskimo-dog or "husky." It is probably due to a dominant factor.

A more conspicuous pattern is seen in black-and-tan dogs. In a black-and-tan the general body-color is yellow (tan) but with a blanket of black extending down from the back over the sides of the body and the outer surfaces of the legs. A yellow spot is found also above each eye. Fox hounds and beagles have this pattern regularly. Airedale terriers are distinguished chiefly by this pattern from Irish terriers. Some setters and pointers have it while others do not. Although the white spotting in these breeds often obscures it, the black-and-tan pattern can readily be recognized in the light spot above the eye. It is apparently a recessive pattern factor in various breeds of dogs. Since the pattern seen in black-and-tan dogs may be transferred in crosses as a unit-character to dogs which are brown or red pigmented, it is probably better to adopt for it a term appropriate in different combinations. *Bi-color* has been suggested by Barrows and Phillips as such a term. Bi-color black dogs are "black-and-tan," bi-color brown dogs are "liver-and-tan," and bi-color red dogs are "red-and-lemon." Self black breeds of dogs have probably originated by a loss of an original pattern factor such as the bi-color factor; and self yellow (or red) breeds by independent loss (sudden or gradual) of black from the coat. Brown ("liver") varieties have originated by a unit-character variation from black to brown, comparable with that of various rodents. Self white occurs in dogs

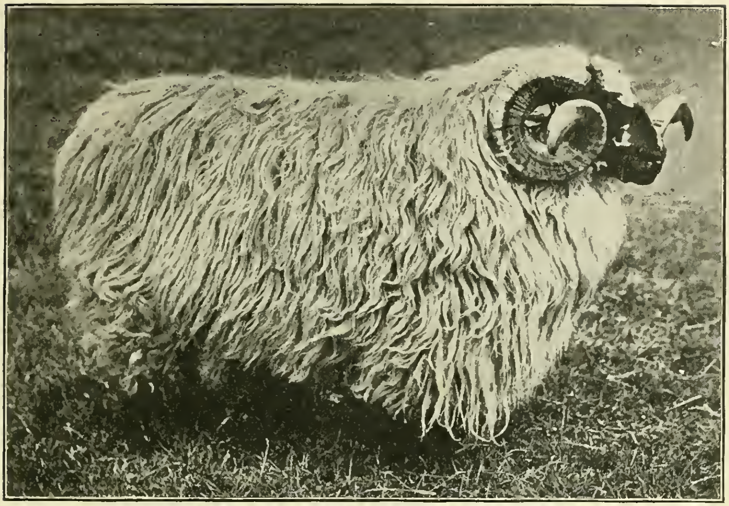


Fig. 96. "Black faced" Highland ram. (After Plumb.)

Fig. 97. Black faced Highland ram and ewes. Note white spotting of pigmented face and legs, also sexual difference in size of horns. (After Plumb.)

Fig. 98. Malitch sheep. An Asiatic flock containing self-black, spotted black-and-white and grayish white sheep, the last probably the primitive condition. (After C. C. Young.)

Fig. 99. Cheviot ram. This Scotch breed has long and coarse wool with face and legs bare and white. Both sexes are hornless.

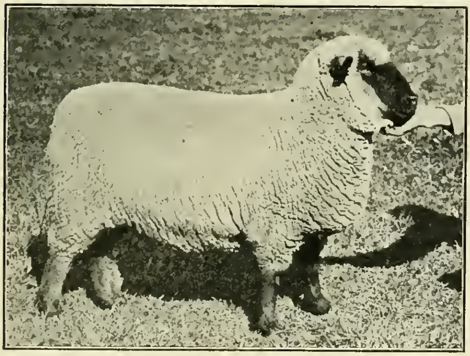


Fig. 100. Hampshire Down ewe. Extremities pigmented. Hornless in both sexes.

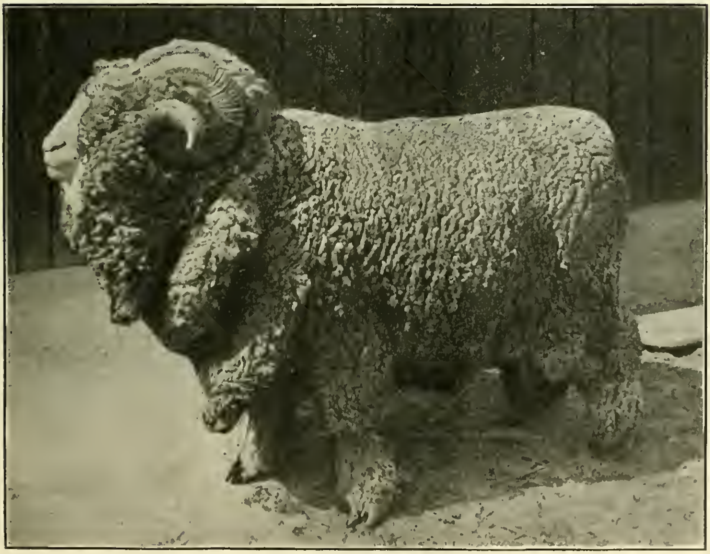


Fig. 101. Delaine merino ram. This breed produces abundant, fine wool. Males have well-developed horns, females are hornless. (Figs. 99–101 after Plumb.)

FIG. 102. Lincoln ram. A large coarse-wooled breed.

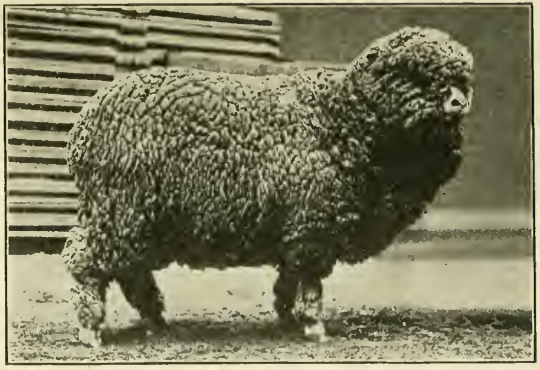


FIG. 103. Merino ewe. Compare Fig. 101.

FIG. 104. Corriedale ewes. A breed recently produced in New Zealand by crossing merino ewes with Lincoln rams and then inbreeding the progeny until a permanent blend or intermediate race was secured. (Figs. 102–104 after Marshall.)

either as a sport from the colored condition, or more probably as an extreme form of white spotting. In this variety the eye pigmentation is never entirely lost as in albino rodents; it is largely retained, as is the case also in white cattle, horses and swine. In crosses between the different colored breeds, black-and-tan (*i. e.*, bi-color black) is dominated by self black and bi-color brown by self brown; black is dominant over yellow (or red) and also over brown. As yellow and brown are independent unit-character variations they may be combined, a result seen in brown-eyed yellow dogs. Thus among pointers (Little, 1914) or cocker spaniels (Barrows and Phillips, 1915) a cross of black-eyed yellow with brown produces in F_1 black dogs and in F_2 blacks, browns, black-eyed yellows and brown-eyed yellows. The same result in both F_1 and F_2 may be obtained by crossing black with brown-eyed yellow. What appears to be self white, but is more probably a very pale yellow, according to Barrows and Phillips, has appeared in spaniels as a sport and is recessive in heredity. Whether in other breeds self white is recessive or dominant is not known at present. It is probable that in some cases, as in bull terriers, it is only an extreme form of white spotting, in which case we should expect the dominance to be imperfect. A short stumpy tail is probably a dominant unit-character variation in dogs, as it is in cats.

TABLE 16

UNIT-CHARACTERS OF DOGS

1. Gray.	Black.
2. Self-color.	Bi-color (black-and-tan, brown-and-tan, red-and-tan).
3. Black.	Brindle, yellow, or red[1]
4. Black.	Brown (liver).
5. Harlequin type of white spotting.	Self color.
6. Color intense.	Color dilute.
7. Colored all over.	Spotted with white (Dutch type).
8. Stumpy tail.	Normal tail.

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[1] In Dachshunds red is not uniformly recessive; it apparently may be dominant.

Cats. Domestic cats are descended from a wild species (*Felis maniculata*) still found in northern Africa. The domestication was accomplished in ancient Egypt and the domestic cat was introduced into Europe in the middle ages, since Roman times. The wild species is similar in size and color to the common tabby or tiger cat. This has a coat consisting of agouti-like hairs, which contain both black and yellow pigments, but the body is marked with stripes in which black pigment predominates, and it is these black stripes that produce the tiger pattern, which is a dominant unit-character. Different forms of the tiger pattern, distinguished as lined, striped, blotched, etc., are probably multiple allelomorphs. In the self-black variety the tiger pattern and agouti marking of the hairs have been covered up by a greatly increased amount of black. The black variety probably originated as a sport and it behaves as a recessive to tabby. An all yellow variety represents another unit-character variation imperfectly dominant over black. Homozygous individuals are all yellow but heterozygous females usually show both yellow and black (tortoise shell) though occasionally they may be all yellow. The inheritance of yellow is sex-linked and of the Drosophila type. (See Chapter XVIII.) Yellow cats usually, if not always, show the tiger pattern, which leads to the question whether this pattern is ever lost even in the black variety. It may be only covered up with black pigment. Darwin notes the fact that black kittens often show the tiger pattern which is not visible in them later in life. All-white varieties of cats exist having colored eyes (either "yellow" or blue). The relation of this variation to colored forms, as regards dominance, is uncertain, but it probably represents an extreme form of white spotting. Blue (or Maltese) is a dilute form of black, recessive to the latter. The dilution factor probably affects the appearance of tabby and yellow also, but definite information on the point is not available. White spotting is a character the behavior of which as regards dominance is unknown. Yellow spotting occurs only as a heterozygous character in the cross between

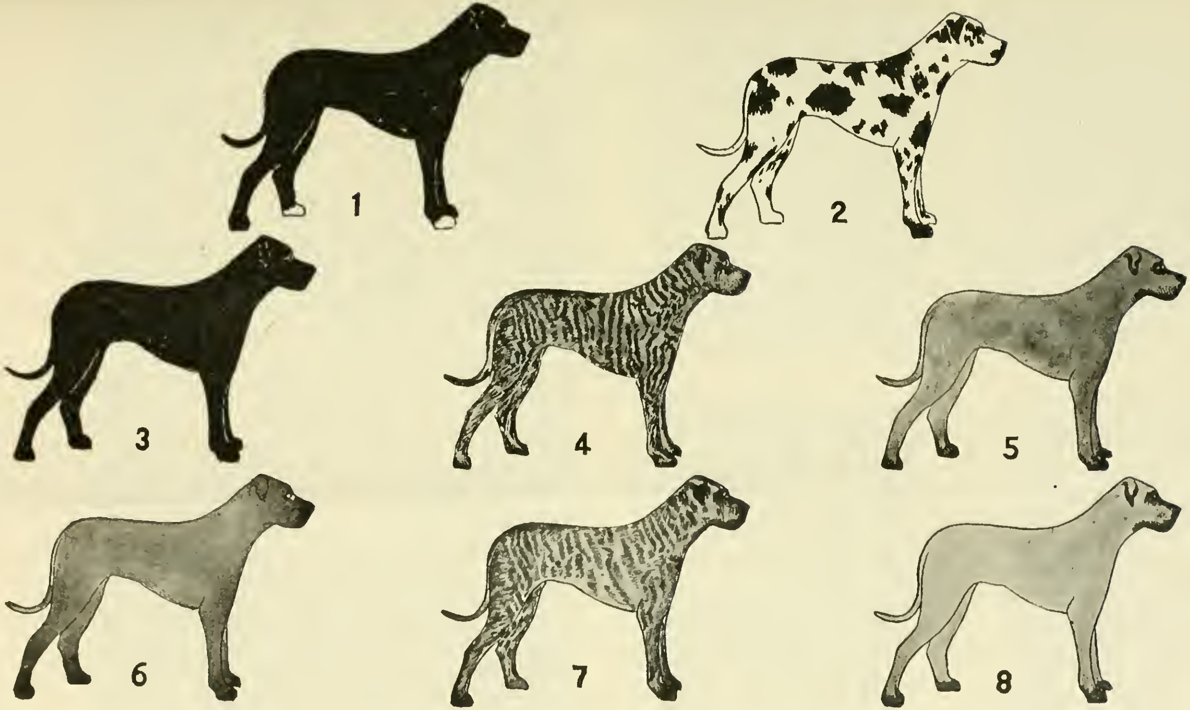

FIG. 104*a*. Color varieties of the Great Dane. 1, black with recessive white spotting; 2, black with dominant (harlequin) white spotting; 3, black self; 4, brindle (black and yellow); 5 fawn (yellow); 6, dilute black; 7, dilute brindle; 8, dilute fawn. (After Little.)

Fig. 105. Pomeranian, self-colored, and having long silky hair. Toy variety.

Fig. 106. Boston bull terrier. Pattern in white spotting like the Dutch marking of rabbits.

Fig. 107. Saint Bernard.

Fig. 108. Beagle. Tri-color, black-and-tan with white.

Fig. 109. Collie. Figs. 106–109 show white spotting of the same general character.

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FIG. 110. Dalmatian or coach dog. A peculiar form of white spotting, resembling that of the English rabbit, is found in this breed.

FIG. 111. Great Dane. Brindled type, with yellow spotting on a black background.

FIG. 112. Irish setter. Color, dark red.

FIG. 113. Dachshund. Black-and-tan.

FIG. 114. Bull terrier. All white except nose and eyes.

(Figs. 105–114, by courtesy of F. G. Carnochan, from *Field and Fancy.*)

yellow and black and then chiefly in the female sex. Long (angora) hair is a recessive variation from normal coat in cats as in rabbits and guinea-pigs. A short stumpy tail, seen in the "Manx" cat, represents an imperfectly dominant unit-character variation. Homozygous dominants are tailless; heterozygotes are *short-tailed*; normal (long) tail is recessive. Polydactylism (the possession of extra toes) is an imperfectly dominant variation.

TABLE 17

UNIT-CHARACTERS OF CATS

	Dominant	Recessive
1.	Tabby.	Not tabby (black or blue).
2.	Black.	Blue.
2a.	Normal (intense) pigmentation.	Siamese dilution.
3.	Short hair.	Long hair (angora).
	Dominance Imperfect or Uncertain	
4.	Colored all over.	Spotted with white.
5.	White (eyes only colored).	Colored all over.
6.	Yellow.	Not yellow (tabby or black).
7.	Tailless (Manx).	Long-tailed.
8.	Polydactyl.	Toes normal.

CHAPTER XV

UNIT-CHARACTERS IN POULTRY AND IN PLANTS

Poultry. The production of varieties by unit-character variation is nowhere more clearly seen than among domestic fowls. The wild ancestor is supposed to be represented at present in the jungle fowl of India (*Gallus bankiva*) a small bird of bantam size having the color character of the breed known as brown Leghorn, and producing fully fertile offspring in crosses with domestic breeds.

Under long centuries of domestication size in many breeds has been increased, though certain breeds of bantams are no larger than the jungle fowl. Punnett and Bailey (1914) have maintained that several unit factors are concerned in size differences between bantam and ordinary breeds, but there is some doubt as to the correctness of their interpretation. We have no information at present as to whether the bantam represents the persistent small size of the wild ancestor or has resulted from secondary variation in races of normal size. The size changes from the wild jungle fowl to our large breeds of poultry have undoubtedly been numerous and probably gradual, involving long-continued selection.

Color variations are in fowls, as among mammals, the most conspicuous unit-character changes. The plumage of the jungle fowl contains both black and yellow pigments combined in a pattern of some complexity. This pattern may possibly be lost or suppressed as a unit-character variation, but in most cases it is changes in the relative amounts of black and yellow which give rise to self black or self yellow (red or buff) breeds. White spotting may come in to produce colorless patches in the plumage and if these become sufficiently extensive an all-white breed results such as the white Leghorn. The white of Leghorns is a dominant character but even pure bred birds may develop an occasional colored feather, and in crosses with brown Leghorns, which have the ancestral color, the heterozygotes produced may show traces of color, as for example a reddish breast. A form of white plumage genetically distinct from the foregoing is found in white silky fowls and in some other breeds. In this the down plumage is colored and the adult plumage is not as clear and pure a white as that of white Leghorns. When such recessive whites are crossed with white Leghorns, fully colored offspring result in F_2 though not in F_1. It is probable that recessive white is not an extreme form of white spotting, as perhaps the white of Leghorns is, but that it is due rather to some change which produces fainter pigmentation; to a loss variation, rather than to an inhibition. It is accordingly comparable with the albino or the pink-eye variation of rodents, whereas the white of Leghorns is comparable with the black-eyed white variation of rodents, an extreme form of white spotting. Bateson has shown that there are two or possibly three distinct classes of recessive white varieties, probably of independent origin, for when two of these (one being the white silky) were crossed, fully colored F_1 offspring were obtained similar in appearance to the wild *Gallus bankiva*. This is a result comparable with that obtained when pink-eyed rodents are crossed with albinos producing fully colored young. It shows that white plumage in fowls, like pink eyes and pale coats in rodents, may result from different genetic changes. Pigment formation is a complex chemical process in which several factors are concerned. Change in any one of these may interfere with the normal pigmentation.

It seems doubtful whether the *Gallus bankiva* pattern is lost in the ordinary black breeds of fowls; more probably it is simply covered up by an excessive development of black pigment. Indeed in some cases the pattern is faintly visible in the black breed and can readily be brought out in crosses. Such varieties are comparable with the blackened agouti varieties of some rodents (black squirrels for example). In self yellow (red or buff) breeds, the pattern fails to develop merely for lack of black pigment. Yellow varieties are imperfectly recessive to black in crosses, the ancestral pattern usually resulting in F_1. Blue is a heterozygote between black and splashed white (an impure sooty strain of white). It is unfixable.

A color pattern of fowls, not ancestral in origin, but dominant in crosses is found in breeds with barred plumage, such as the Dominique and the barred Plymouth Rock. Its inheritance is sex-linked. It may be transmitted through white breeds, as for example the white Leghorn.

A black pigmented skin associated with black bones is found in certain strains of fowls, *e. g.*, silkies. This is dominant over normal (white or yellow) skin.

Several morphological variations of the plumage are inherited as unit-characters. Thus, the possession of a topknot or crest (usually associated with cranial hernia) is an imperfectly dominant character; frizzled (twisted) feathers are dominant over normal feathers; silky feathers (devoid of barbules) are recessive to normal feathers (with barbules). An extra or fifth toe (due to a divided hind toe) is an imperfectly dominant character found in Houdans and Dorkings. The comb is also a highly variable character. Single comb is the form found in *Gallus bankiva* and in the commoner breeds of poultry. It consists of a high serrated ridge. Pea comb is a dominant variation from this ancestral form in which the comb is lower and broader, without distinct serrations but with two low lateral ridges in addition to a chief central ridge. It is found in Indian Games and the Brahma breeds. Rose is another form of comb, likewise dominant over single. It consists of a broad flat comb with numerous papillae not arranged in distinct rows. A cross of rose with pea produces a peculiar type of comb known as walnut, which is found in the Malay breeds. When produced by crossing, it does not breed true without fixation, but in F_2 gives rise to walnut, rose, pea, and single comb in the ratio, 9:3:3:1. Evidently walnut in such cases is due to the joint action of two dominant factors (R and P) which act separately in pea-combed and rose-combed varieties respectively, and when both P and R are lacking the original type of single comb is formed.

TABLE 18

UNIT-CHARACTERS OF DOMESTIC FOWLS

A. Sex-linked

	Dominant	Recessive
1.	Black skin (silkies).	Normal skin (dominant in females, imperfectly recessive in males).
2.	Silver (lacing, spangling, penciling).	Gold (lacing, spangling, penciling).
3.	Striped down of chicks, black breast of adult male (game bantams).	Plain down, brown breast of male.
4.	Barred feathers.	Unbarred feathers.
4.*a*	Spangling (Hamburgs)	Non-spangled feathers.

B. Not Sex-linked

	Dominant	Recessive
5.	Black plumage.	Yellow (or buff or red) plumage. (Heterozygote often like jungle fowl.)
6.	White of white Leghorns.	Colored.
7.	Colored.	White (of silkies).
8.	Colored.	White (of rose-comb bantams).
9.	Colored.	White (of white rocks).
10.	Normal feathers.	Silky feathers.
11.	Frizzled feathers.	Plain feathers.
12.	Crest.	No crest.
13.	Extra toe.	No extra toe.
14.	Yellow skin.	White skin.
15.	Rumpless.	Normal tail.
16.	Walnut comb.	Rose, pea, or single comb.
17.	Pea comb.	Single comb.
18.	Rose comb.	Single comb.
19.	Single comb.	Combless (Breda).

Plants. No attempt will be made at a detailed survey of unit-character variations in plants but certain general categories of variations may be indicated and examples cited. These will serve to show that the same sorts of changes are at work among plants as among animals to produce striking varieties.

1. *Colors of flowers.* Some of the clearest cases relate to the colors of flowers. Wild species often exhibit in their flowers a mixture of pigments associated in a definite pattern. Loss or suppression of the pattern, or of one or more of its component colors, leads to the formation of self-colored flowers,

or those which are white. Thus in the sweet pea the wild plant has flowers of a purple bi-color, resulting from the association of red and blue pigments in a definite pattern. Red flowers may arise by a suppression of a factor for blue. This change alone produces a red flower with wings lighter than the standard (a red bi-color). Another recessive factorial change does away with the lightness of the wings, producing a flower with both wings and standard full red. A corresponding change in pattern in purple (the original color), not attended by suppression of blue, produces purple with both wings and standard of full color. A quantitative change in the color factor (a *partial* loss of color) produces faintly colored varieties known as picotee, either purple or red. In the flowers of many cultivated plants striping, mottling or spotting with white or red comes in as a unit-character variation, as in petunias, snapdragons, etc.

TABLE 19

UNIT-CHARACTERS OF PLANTS

1. *Colors of Flowers*

(Example, unit-characters of the sweet pea flower.)

Dominant	Recessive
(1) Colored.	White.
(2) Colored.	Slightly colored (picotee).
(3) Purple.	Red.
(4) Bi-color.	Self.
2. *Forms of Flowers*	
(1) Normal.	Peloric.
(2) Single.	Double.
3. *Colors of Leaves and Stem*	
(1) Variegated with yellow.	Normal green (dominance imperfect).
(2) Containing much red.	With little red (Oenothera, Coleus, maize).
4. *Colors of Fruits and Seeds*	
(Example, maize)	
(1) Yellow endosperm.	White endosperm.
(2) Aleurone black.	Aleurone red or uncolored.
(3) Aleurone red.	Aleurone uncolored.
(4) Endosperm starchy.	Endosperm sugary.
(5) Endosperm starchy.	Endosperm waxy.
(6) Seed-coat red.	Seed-coat colorless.
(7) Seed-coat variegated.	Seed-coat not variegated.

5. Forms of Leaves

(1) Serrate.	Entire (Urtica, Fig. 115).
(2) Normal.	Laciniate (Chelidonium).
(3) Palmate.	Pinnatifid or fern-leaf (Primula).
(4) Hairy.	Glabrous (dominance often imperfect).

2. *Forms of flowers.* The forms of flowers, no less than their colors, are subject to unit-character variation. In sweet peas the ordinary form of flower with erect standard is dominant over a variation in which the standard lops down at either corner forming what is called a "hood." Symmetrical forms of flowers which appear as sports in species having normally asymmetrical flowers are a unit-character variation. Thus a peloric (symmetrical) variation in the snapdragon is recessive to normal (asymmetrical) shape of flower (Baur). Double flowers, those which have an increased number of parts (commonly petals), are in general recessive to singles. This is the case for example in primulas, poppies and larkspurs. But some cases occur in which the heterozygote is intermediate, as for example in carnations. Here a good commercial double type is found to be regularly heterozygous, producing when selfed both singles and extremely double types ("busters"), each of which sorts breeds true, and in addition the unstable but more valuable heterozygous type of the parent (Norton).

3. *Colors of leaves and stems.* The colors of leaf and stem often vary abruptly in cultivated plants by unit-character changes. Thus strains variegated with yellow arise from local loss or inhibition of chlorophyl, a change which impairs the assimilative power of the plant but adds to its ornamental value in horticulture. Of course plants largely or completely yellow because of deficiency of chlorophyl would be unable to maintain themselves other than as parasites, such as dodder; hence the yellow of variegated plants is usually limited in amount. Some varieties of cultivated plants possess as a distinguishing character an unusual amount of red coloring matter (*anthocyan*) in leaf or stem. Examples of this are seen in purple beeches and maples, variations known

to have originated as sports and doubtless Mendelizing in crosses. The cultivated celosias are good examples of plants in which an excessive amount of anthocyan pigment produces brilliant red or yellow plants, the latter a probably recessive sport from the former, just as the yellow fruit of the tomato is known to be recessive to red fruit. In Coleus the red has a mosaic and highly variable distribution on the green leaves, like that of yellow spotting in mammals.

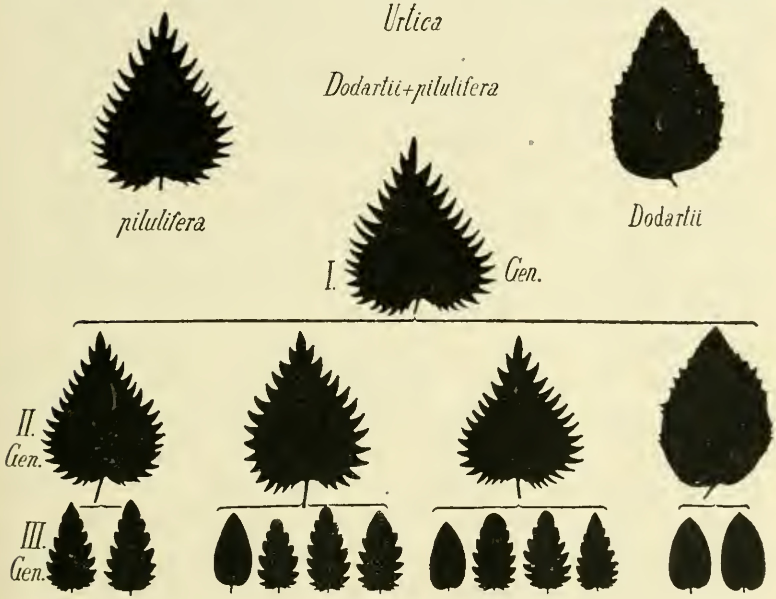

FIG. 115. A Mendelian cross between two varieties of nettle differing in shape of leaf. I. Gen. = F_1. II. Gen. = F_2. III. Gen. = F_3. The diagram indicates that the serrated form is dominant, the recessive form reappearing in F_2 and breeding true in F_3. (After Correns.)

4. *Colors of fruits and seeds.* The colors of fruits and seeds vary discontinuously in the same way that the colors of flowers, leaves and stems vary. As an example we may consider some variations in the color and composition of the seed of maize. The common varieties of corn are either yellow or white seeded, the yellow grain containing a yellow colored endosperm, a character dominant to white. A black pigment which is present in the aleurone layer just under the seed-coat is responsible for a dominant variation in some

varieties. Red aleurone color is a recessive allelomorph of black. Both are dominant over colorless aleurone. Red seed-coat is a character dominant over colorless seed-coat, and a seed-coat striped with red is allelomorphic to unstriped seed-coat. A highly starchy condition of the endosperm is found in ordinary varieties of field corn, which have relatively plump seeds. A recessive allelomorphic condition is found in sweet corn cultivated for table use, in which sugar predominates in the seeds so that on drying it takes on a shriveled, wrinkled appearance. A different recessive variation is found in a variety of corn recently imported from China, in which the endosperm is waxy rather than sweet or starchy. If the variety with waxy endosperm is crossed with sweet corn, starchy corn is obtained by reversion in F_1, and in F_2 all three sorts are obtained in the ratio, nine starchy to three waxy, and four sweet.

5. *Forms of leaves.* Leaf form in many cultivated plants is known to vary by Mendelizing units. In the nettle (*Urtica*) Correns has shown that the much-serrated leaves of one natural variety possess a character dominant over the nearly entire leaves of another variety (Fig. 115). In *Chelidonium majus*, a laciniate leaf form is known to be recessive to the normal form of leaf. In *Primula sinensis*, normal palmate leaves are dominant over fern-like pinnatifid leaves. In a great number of plants hairy or spinous leaves, stems, or fruits, are known to be dominant (more or less completely) over smooth ones.

6. *Form of stem.* One of the seven discontinuous variations with which Mendel dealt in his original paper is involved in the difference between tall and dwarf races of peas and beans. The original and the dominant form of stem is the tall form. Dwarf form, in which the internodes of the plant are relatively short, segregates in regular recessive fashion. Semi-dwarf races also exist, which indicate either imperfect segregation or alternative forms of dwarfness. Dwarfness occurs as a variation alternative to normal tall form in snapdragons, nasturtiums, and many other cultivated plants.

The original much-branched condition of the annual sunflower and of stocks and of many other cultivated plants is dominant over the unbranched condition found in certain cultivated races.

These illustrations serve to show that practically all parts and structures of plants, as well as of animals, are likely to be affected by unit-character variations and that combining of such variations by means of crossing is a ready means of producing new varieties.

CHAPTER XVI

UNIT-CHARACTERS OF INSECTS

The so-called " silkworm " is the larva of an Asiatic moth which feeds principally on the leaves of the mulberry tree. The " worms " when full grown spin a silken cocoon (which furnishes the silk of commerce) within which they complete their metamorphosis into the moth stage. As moths they mate and the females lay eggs. In some races there is only one generation a year, the eggs laid one summer hatching the next spring. These are said to be *univoltine*, having one flight or mating period annually. In other races there are two or more broods a year depending on temperature conditions. These are said to be *bivoltine* or *multivoltine*. In crosses between *univoltine* and *bivoltine* races the eggs laid have the character of the mother's race, being purely maternal structures. Thus, eggs laid by a univoltine mother refuse to hatch before the following season, whatever the racial character of the male that fertilized the eggs. And eggs laid by a bivoltine mother are regularly bivoltine regardless of the father's racial character. But the females which hatch from cross-bred eggs are really heterozygous as regards voltinism. Their *eggs* show the dominant (*univoltine*) character but their daughters, the F_2 females, are some univoltine, others bivoltine, in the ratio, 3:1.

Races of silkmoths differ by numerous characters, many of which are Mendelian. Toyama has enumerated more than a dozen such Mendelizing characters found in the larva alone. Some races differ in the number of larval moults, which may be either three or four. Tri-moulting is dominant over tetra-moulting in crosses. The blood of the larva may or may not be yellow colored, yellow blood being dominant. Yellow-blooded larvae spin yellow cocoons so that there is a correlation between blood-color of the larva and the cocoon-color. Presence of pigments in the larval skin is dominant over uncolored skin. Various patterns of the larval pigmentation (spotting, striping, etc.) are dominant over their absence. Reddish-brown color of the larva is recessive to black. The possession of knob-like outgrowths of the larval skin is dominant over smooth skin.

TABLE 20

UNIT-CHARACTERS OF SILKWORMS

1. *Egg Characters, all Maternal in Origin*

	Dominant	Recessive
(1)	Univoltine.	Bivoltine.
(2)	Eggs oval.	Eggs spindle-shape.
(3)	Eggs normal slate color.	Eggs light brown or gray.

2. *Characters of the Larva or the Cocoon, of Biparental Origin*

	Dominant	Recessive
(1)	Tri-moulting.	Tetra-moulting.
(2)	Blood (and silk) yellow.[1]	Blood (and silk) white.
(3)	Silk white (European races).	Silk yellow.
(4)	Larval skin pigmented.	Larval skin unpigmented.
(5)	Larva spotted or striped.	Larva not spotted or striped.
(6)	Larva black.	Larva reddish brown.
(7)	Larval skin with knob-like outgrowths.	Larva not knobby.

White cocoon-color (silk) has been found in some races to be a recessive character and in others to be dominant. The two kinds of white have been shown to be genetically distinct. One is probably a loss variation like albinism in rodents, the other a white variation due to inhibition of color, like some forms of white spotting in mammals. Certain variations in the color and shape of the egg have been found to Mendelize, but with the same complication as in the variation from univoltinism to bivoltinism. Egg characters being determined entirely by the mother, the influence of the father does not show in the F_I generation. Which of the contrasted characters is dominant does not become evident until eggs

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[1] Uda has recently shown that yellow color of the blood is due to a single dominant factor but that the silk will also be yellow only when a second and independent factor is also present. When this second factor is lacking, white silk will appear to be dominant over yellow silk, even though the blood is yellow.

are laid by the F_1 females and segregation is seen first in the eggs laid by F_2 females. Spindle-shape of egg is a recessive variant from normal, oval shape, and light brown egg-color and gray egg-color are recessive variations from normal slate-color.

Bateson (1913) has brought together records for numerous cases of unit-character color variation in moths and beetles occurring in the wild state. These cases present nothing in principle different from the variations of silkworms, but show that Mendelian sports occur among insects "in nature" as well as under artificial conditions.

The most complete and in many respects the most instructive series of unit-character variations recorded in any insect has taken place within a very few years in a small fruit fly, Drosophila, while it was under observation in the Zoölogical Laboratory of Columbia University. For this discovery we are indebted to Professor T. H. Morgan and his pupils. *Drosophila melanogaster* is a small fly with grayish brown body and red eyes, which lays its eggs in fermenting fruits. Apples, peaches, grapes or bananas with broken skin afford good conditions for its multiplication. It is sometimes known as the vinegar or pomace fly because the alcoholic fermentation of apple juice attracts it to vinegar jugs, pickle jars, and cider mills. This fly while breeding in Professor Morgan's laboratory produced a white-eyed sport, which lacked entirely the normal red eye-color. The sport was first observed in a male individual, which bred to normal mates produced only normal offspring. But when these F_1 offspring were bred together they produced white-eyed offspring as recessives in the expected proportion, one-fourth. Curiously enough, however, all were males. Nevertheless, when these obviously recessive white-eyed males were mated with F_1 females (heterozygotes) a generation was produced consisting of white-eyed individuals and red-eyed individuals in equal numbers, and among both sorts the sexes were approximately equal. White-eyed individuals bred together breed true, but in crosses the white-eyed character seems to have a preference for male individuals, which has led to its being called a sex-linked character. White-eye has proved to be only the first of a long series of unit-character variations, which have appeared in Professor Morgan's cultures of Drosophila, which have this same curious sex-linked character. Among these may be mentioned a variation in which the entire body is *yellow*, another in which the eye-color instead of being an ordinary red, is a brilliant *vermilion*, and several variations in the form of the wing known as rudimentary, miniature, forked, etc. It is found that when a race possessing two of these recessive sex-linked characters (as white eye and yellow body) is crossed with another race which lacks them, there is a tendency for the two sex-linked characters to *go together* in heredity, so that whatever F_2 individuals possess one of them possess also the other. This suggests that the material basis or "gene" of each lies in the germ-cell near that of the other, that their genes are either connected directly with each other or with a common third structure. Since there are several of these variations which show "linkage" with each other and a peculiar relationship to sex, the pertinent suggestion was made by Morgan that they had as a common connecting element a structure concerned in the determination of sex, commonly known as the sex-chromose or X-chromosome. The "genes" of sex-linked characters, according to Morgan, lie in the X-chromosome and the peculiar features of the inheritance are due to the fact that the X-chromosome is paired in females but unpaired in males. Strong support is given to this idea by the result of crosses in which each parent introduces a different sex-linked character, as in the cross between a white-eyed race and a yellow-bodied race, each being otherwise normal. The two characters in this case keep apart as strongly as they keep together when introduced into a cross by the same parent. This is exactly what we should expect if, as Morgan supposes, sex-linked characters have their genes in a common cell structure (for example an X-chromosome). For when two genes lie in the *same* X-chromosome, they will go together (show linkage), but when they lie in different X-chromosomes, as for example, in those furnished by the father and mother respectively, then each will go with a different X, when the paired chromosomes separate from each other, as they do when gametes are formed.

But we are forced to suppose that occasionally in the eggs of Drosophila a gene may detach itself from one X-chromosome and pass over into the other, for once in a while we find that two sex-linked characters which were repelling each other have in some way got into the same gamete and are now coupled, and *vice versa* two which were coupled may later show repulsion. Morgan's hypothesis offers a simple explanation of such occurrences. The supposed changing of a gene from one X-chromosome to another, when repulsion gives place to coupling or *vice versa*, Morgan calls a "crossing-over." It occurs only in female individuals, or more properly in their eggs, for it has not been observed to occur in the sperms of Drosophila.

CHAPTER XVII

SEX-LINKED AND OTHER KINDS OF LINKED INHERITANCE IN DROSOPHILA

All the facts of sex-linked inheritance in Drosophila harmonize with Morgan's hypothesis that the genes of sex-linked characters lie in a common cell structure (X-chromosome) which is duplex in females, simplex in males. Accordingly, in a race which breeds true for a sex-linked character, that character may be transmitted by *every egg*, but by only *half* the *sperms*, namely by such as possess an X-chromosome and by virtue of that fact determine as *female* all zygotes into which they enter. To *male* zygotes the sperm will not transmit sex-linked characters. This hypothesis is supported by some curious facts already alluded to but deserving of fuller consideration in this connection, viz., facts observed in reciprocal crosses involving a sex-linked character, as for example white eye in Drosophila.

TABLE 21

Reciprocal Crosses of White-Eyed with Red-Eyed Drosophila

	Male		Female	Male		Female
P	White	×	Red	Red	×	White
F_1	Red		Red	White		Red
F_2	1 Red : 1 White		Red	1 Red : 1 White		1 Red : 1 White

It has already been stated that a white-eyed *male* Drosophila crossed with normal females has only normal children of both sexes, while the white-eyed grandchildren are all of the male sex. In the reciprocal cross, between a white-eyed female and a normal male all the daughters are normal, but *the sons are white-eyed*, and among the grandchildren white-eyed individuals occur *in both sexes*. Diagrams will best explain these facts on the basis of Morgan's hypothesis. (See Figs. 116 and 117 and Table 21.)

To state the foregoing facts in another way, it will be observed that the recessive sex-linked character in Drosophila, when introduced in a cross by the *male* parent, disappears entirely in F_1 and reappears in F_2 only in male individuals.

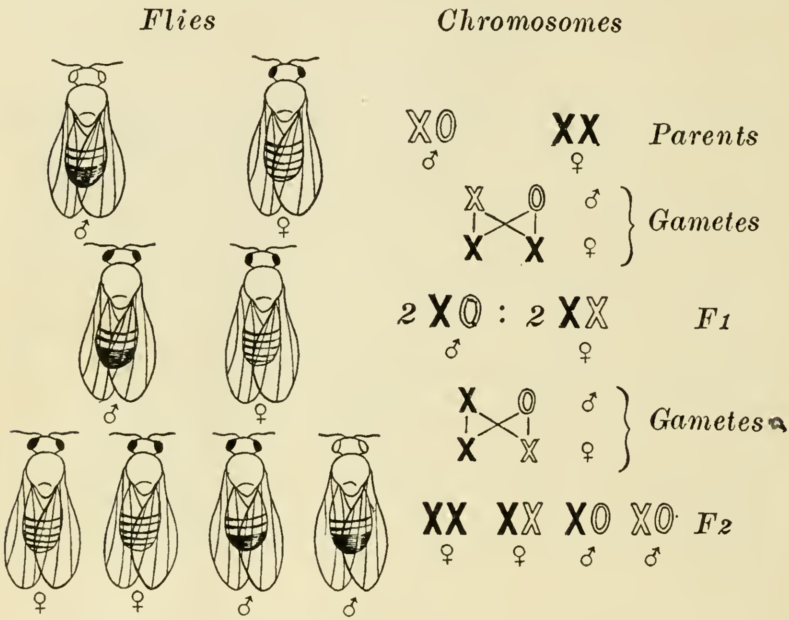


FIG. 116. Sex-linked inheritance of white and of red eyes in Drosophila. Parents, white-eyed male and red-eyed female; F_1, red-eyed males and females; F_2, red-eyed females and equal numbers of red-eyed and white-eyed males. A black X indicates an X-chromosome bearing the gene for red eye, a white X bears white eye. O indicates that an X is wanting; in recent publications Morgan replaces it by Y. (From Conklin, after Morgan.)

But if the recessive sex-linked character is introduced by the *female* parent, it appears in F_1 in *male* individuals but in F_2 in *both sexes*.

Suppose now a cross is made between two races, each of which possesses a different sex-linked recessive character, as for example white eye and yellow body. (See Table 22.) If the white-eyed parent is a female, there will be produced white-eyed males in F_1 and white-eyed flies of both sexes in F_2. But the male parent being yellow, there will be no yellow flies produced in F_1 and only yellow males in F_2. In the reciprocal cross (yellow female × white-eyed male) yellow males will be produced in F_1 and yellow flies of both sexes in F_2, while white-eyed flies will not appear until F_2 and then only in the male sex. In either of the reciprocal crosses we expect the production in F_2 both of yellow-bodied males and of white-eyed males. Usually no other sort of male is produced throughout the experiment except these two, but occasionally there is produced a male both yellow-bodied and white-eyed, or one which is gray-bodied and red-eyed, like wild flies. How do these arise? If in F_1 females the paired X's were to exchange loads in part, so that G and R came to be attached to the same X and g and r to the other X, and if each of the eggs having such a constitution were to be fertilized with a sperm which lacked X (male determining sperm), this would make possible the production of F_2 males possessing both dominant characters and others possessing both recessive characters or gray-red and yellow-white

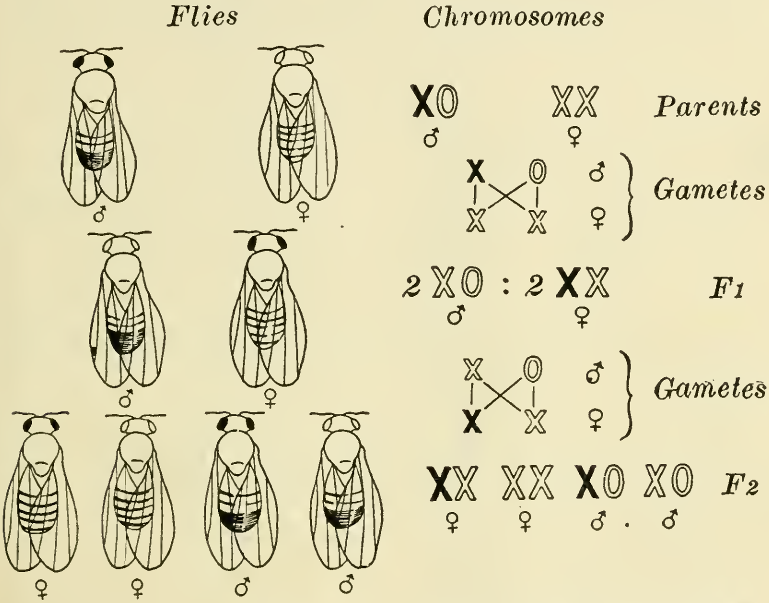


FIG. 117. Reciprocal cross to that shown in Fig. 116. Parents, red-eyed male and white-eyed female; F_1, white-eyed males and red-eyed females (" criss-cross inheritance " — Morgan); F_2, equal numbers of red-eyed and white-eyed individuals in both sexes. The distribution of the sex-chromosomes is shown at the right, as in Fig. 116. (From Conklin, after Morgan.)

respectively, as actually observed in about one case in a hundred by Morgan.

It may add interest to the case to state parenthetically that in man occur a number of sex-linked variations which are inherited in this same curious fashion. Among them may be mentioned color blindness and bleeding (*haemophilia*), which occur chiefly in males, but are never transmitted by males to their sons but only through their daughters to their grandsons.

TABLE 22

Reciprocal Crosses of White-Eyed and Yellow-Bodied Flies

	Male		Female	Male		Female
P	Yellow-red	×	Gray-white	Gray-white	×	Yellow-red
F_1	Gray-white		Gray-red	Yellow-red		Gray-red
F_2	1 Gray-white: 1 Yellow-red		1 Gray-red: 1 Gray-white	1 Gray-white: 1 Yellow-red		1 Gray-red: 1 Yellow-red

Morgan and his pupils have described between forty and fifty characters in Drosophila which are sex-linked in heredity; they also have discovered a large number of other Mendelizing characters in Drosophila which are *not* sex-linked but which nevertheless are inherited in groups, characters in the same group showing coupling when introduced in a cross from the same parent, and repulsion when introduced from different parents. The number of these groups exactly corresponds with the number of the chromosomes and Morgan believes that their genes are located in the chromosomes, an hypothesis which seems reasonable but which would be severely strained if an additional group of characters should be discovered. There are three groups of the non-sex-linked characters. (See Fig. 119.) In one of these referred to as Group II (the sex-linked group being called Group I),

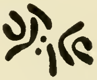


Fig. 118. Drawing showing the four pairs of chromosomes seen in the dividing egg-cell of Drosophila. (After Dr. C. W. Metz.)

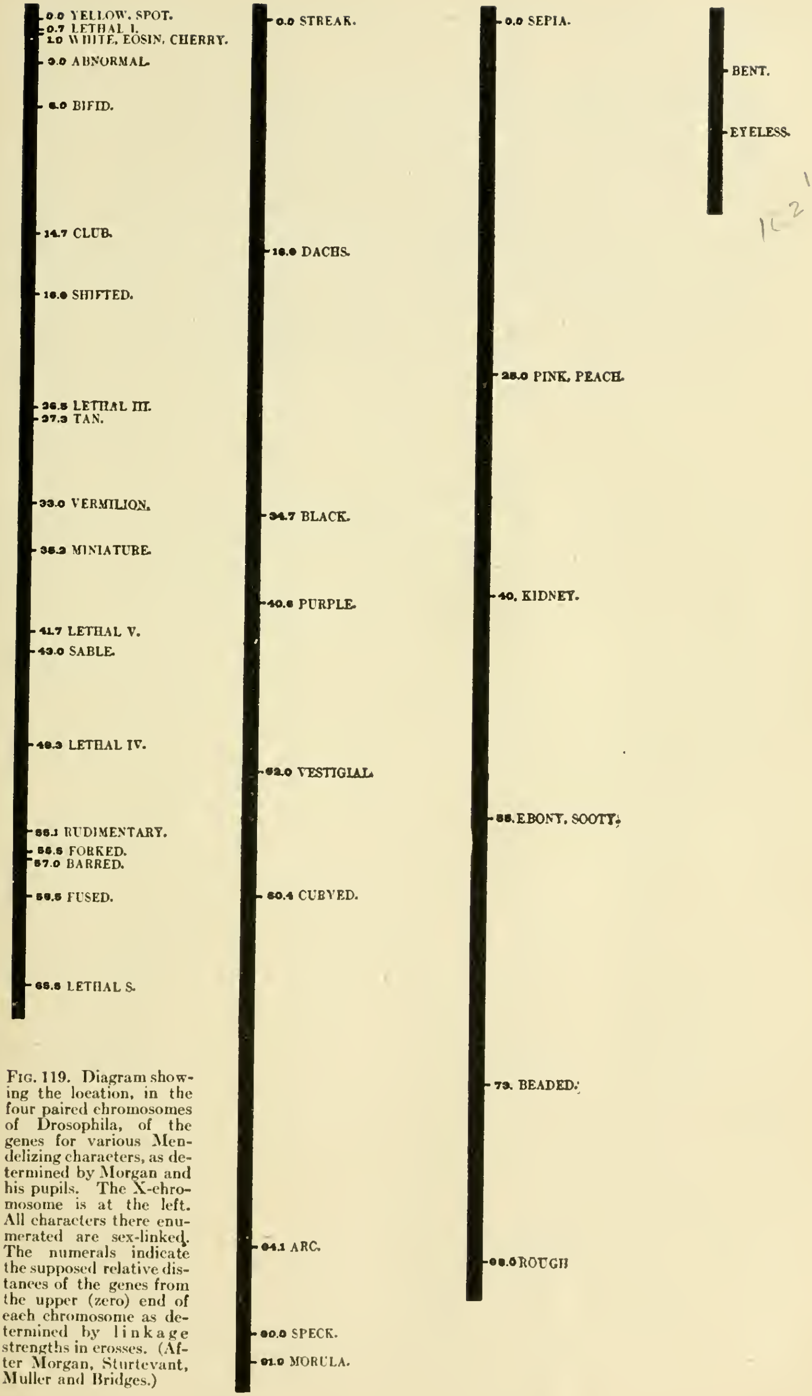


FIG. 119. Diagram showing the location, in the four paired chromosomes of Drosophila, of the genes for various Mendelizing characters, as determined by Morgan and his pupils. The X-chromosome is at the left. All characters there enumerated are sex-linked. The numerals indicate the supposed relative distances of the genes from the upper (zero) end of each chromosome as determined by linkage strengths in crosses. (After Morgan, Sturtevant, Muller and Bridges.)

are found variations known as *black body* and *vestigial wings* respectively, together with some thirty-five other variations. In Group III are found the variations known as *pink eye*, *spread wings*, and *ebony body*, together with some twenty other variations. In Group IV are included as yet only two characters, *bent wings* and *eyeless*, which however show linkage with each other. No inherited characters have been discovered in Drosophila which are not inherited in one or another of the four linkage groups.

CHAPTER XVIII

DROSOPHILA TYPE AND POULTRY TYPE OF SEX-LINKED INHERITANCE

1. *Drosophila type.* The same type of sex-linked inheritance which is found in Drosophila is found also in man, in cats (inheritance of yellow color), and in the plants, *Lychnis* and *Bryonia*. The essential feature of this "Drosophila type" of inheritance is this. In a race breeding true for a sex-linked character, the female is homozygous for the character in question while the male is heterozygous and in-

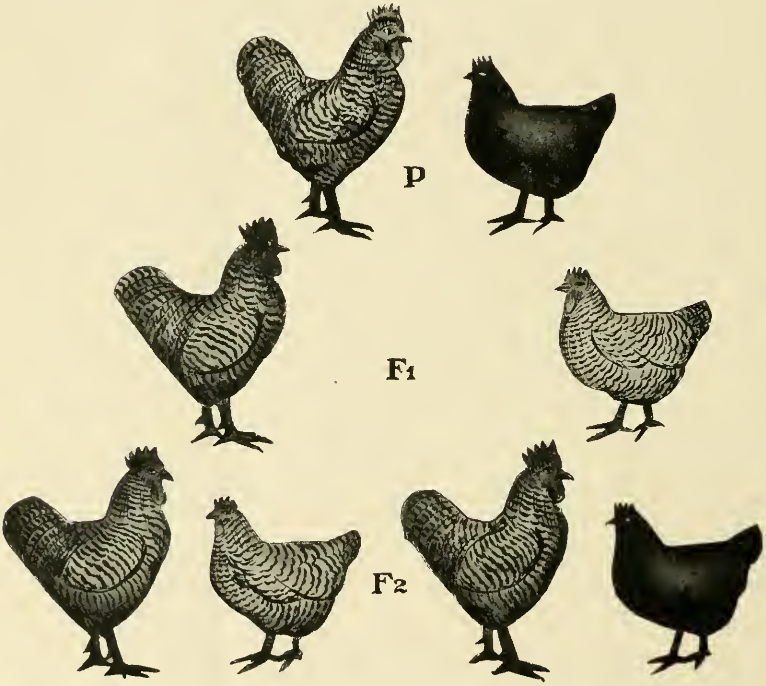


FIG. 120. Sex-linked inheritance of barred and of unbarred (black) plumage in poultry. P, parents, barred male, unbarred female; F_1, barred males and females; F_2, males all barred, females in equal numbers barred and unbarred. (After Morgan.)

capable of becoming homozygous. Reciprocal crosses with such a race give unlike results, because the female transmits the character to all her offspring, but the male transmits it to only half his offspring, viz., the females.

2. *Poultry type.* Another type of sex-linked inheritance exists in which the sex relations are exactly reversed. This was first observed in the moth, *Abraxas*, but more familiar cases occur in poultry, for which reason it may be called the poultry type of sex-linked inheritance. Here the male is the homozygous sex, the female being heterozygous. This condition is found in moths and in certain birds, viz., in domestic fowls, pigeons, ducks and canaries. As an example we may take the inheritance of the color pattern, barring, in crosses of

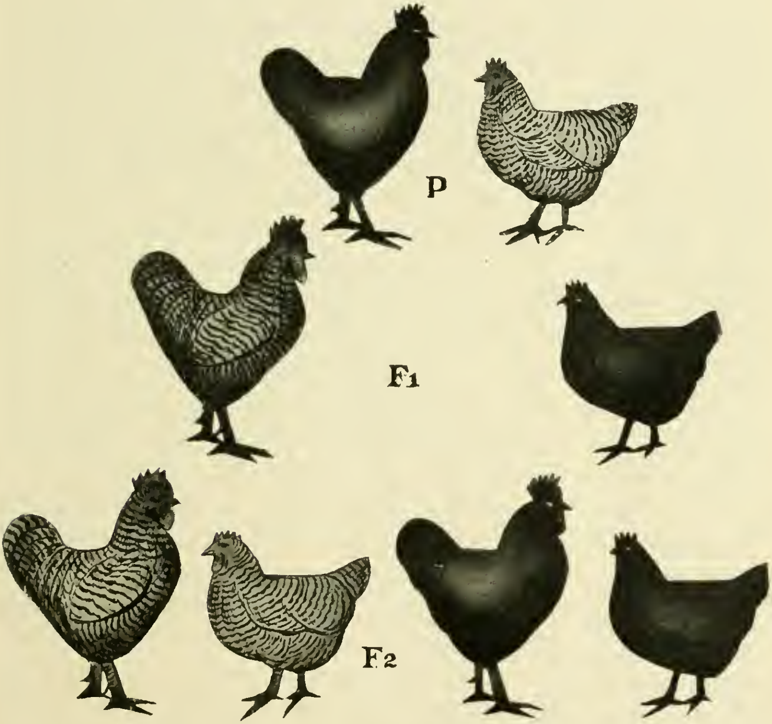


Fig. 121. Reciprocal cross to that shown in Fig. 120. P, parents, unbarred male, barred female; F_1, barred males, unbarred females (criss-cross inheritance); F_2, barred and unbarred birds equally numerous in both sexes.

barred Plymouth Rock fowls. In reciprocal crosses between pure-bred barred Plymouth Rocks and black Langshans (or any other unbarred breed), the results are not identical. If the barred parent is the male (Fig. 120 and Table 23), all F_1, offspring are barred and in F_2 all males are barred, but half the females are black and half are barred. If, however, the barred parent is the female (Fig. 121 and Table 23), all F_1 males are barred, but all F_1 females are black. In F_2 barred birds and black birds occur in both sexes. These curious facts, which have been repeatedly verified, suggest the occurrence of a vehicle of inheritance which is duplex in males but simplex in females. What this is we do not know. No chromosome has been found which has a distribution of this sort in fowls, but it is possible that some chromosome component, or other cell constituent, has such a distribution and may be the actual vehicle of inheritance in such cases. The most important character economically, which appears to be affected by some sex-linked factor in poultry, is fecundity. Pearl has observed that when reciprocal crosses are made between Cornish Indian games, a poor breed for winter egg production, and barred Plymouth Rocks, a fairly good breed for winter egg production, the F_1 females in each case resemble the father's race more strongly than the mother's race as regards egg production. Pearl did not maintain, however, nor do his experiments suggest, that the inheritance of fecundity depends exclusively upon a sex-linked factor. Goodale, however, has not been able to confirm Pearl's observations, in the case of Rhode Island Red fowls. He finds no evidence of superior influence of the sire in the transmission of racial fecundity.

TABLE 23

RECIPROCAL CROSSES OF BARRED AND BLACK BREEDS OF FOWLS

	Male		Female	Male		Female
P	Barred	×	Black	Black	×	Barred
F_1	Barred		Barred	Barred		Black
F_2	Barred		1 Barred: 1 black	1 Barred: 1 black		1 Barred: 1 black
		See Fig. 120.			See Fig. 121.	

CHAPTER XIX

LINKAGE

In ordinary Mendelian inheritance, if two characters, A and B, enter a cross in the same gamete (either egg or sperm), it will be wholly a matter of chance whether they continue together or are found apart in the following generation. If in the formation of gametes by the cross-bred, A and B separate from each other and pass into different gametes, it is evident that one of them has *crossed-over* from the gametic group in which both originally lay to enter the alternative group. This event may be called simply a *crossover.* Crossovers and non-crossovers will be equally numerous (50 per cent each) where no linkage occurs. Also, if A and B enter a cross in different gametes, one in the egg, the other in the sperm, it will in ordinary Mendelian inheritance be a matter of chance whether they emerge from the cross together or apart. If together, it is evident that a crossover has occurred; if apart, a non-crossover, that is a persistence of their previous relations. Again, crossovers and non-crossovers will be equally numerous (50 per cent each) if no linkage occurs.

Linkage may be defined as the tendency sometimes shown by genes to maintain in hereditary transmission their previous relations to each other. Thus if two linked genes, A and B, enter a cross together in the same gamete, they will oftener than not be found together in the gametes formed by the cross-bred individual. Crossovers in that case will be less than 50 per cent, and non-crossovers more. And if the same two genes enter the cross separately, one in the egg, the other in the sperm, then oftener than not they will be found apart, in different gametes formed by the cross-bred individual. Again crossovers will be less than 50 per cent.

The number of genes in a linkage group varies in known cases from 2 to 50 or more. However many genes there are in a linkage group, each gene shows linkage with every other gene belonging to the same group, but the apparent strength of the linkage varies greatly. Under uniform environmental conditions, A and B show a fairly constant linkage with each other, A and C show a different and likewise fairly constant linkage strength, and so on through the entire group. This leads to the conclusion that the genes of a linkage system are bound together, gene with gene, with bonds of definite strength in each case. In order to visualize the matter and get a more objective view of linkage relations, Morgan and his associates have developed the chromosome theory of linkage. Its essential parts are:

(1) Genes which show linkage with each other are located in the same pair of chromosomes. It is the substance of the chromosome which binds the genes to each other and causes A to be inherited when B is.

(2) Genes close together in the same chromosome show strong linkage, genes farther apart show less linkage.

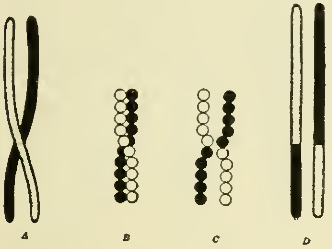
(3) Homologous chromosomes, those containing corresponding sets of genes, one set derived from the father, one from the mother, lie side by side (in synapsis) previous to the formation of gametes. At this time breaks are likely to occur in the chromosomes and parts of one are likely to replace corresponding parts of the other.

(4) Such replacement is called crossing-over.

(5) Breaks are commoner in long chromosomes than in short ones, and between distant points than between near points on the same chromosome.

(6) The genes occur in a chromosome, like beads on a string, in a single row and in definite order.

The supposed order of the genes in the four linkage groups of Drosophila and their relative distances apart are shown in Fig. 119. In these diagrams, or "maps," when the probable order of the genes in a system has once been determined, the supposed end gene of the system is placed at position 0 and the gene next to it is placed at a distance (in centimeters or other units) corresponding to the average cross-over percentage between the two, this process being repeated from gene to gene until the whole chain is plotted. The "map" is thus based on a summation of the distances (measured in cross-over percentages) from gene to gene. But if we compare the "map distances" between genes not adjacent to each other in the chain with the observed cross-over percentages between the same genes, we find that the map distance is regularly greater than the cross-over percentage, except for very short distances (5 or less). Thus if three genes occur in the order A, B, C, it is usually found that AB + BC is greater than AC. In other words, the cross-over percentage between A and B plus the cross-over percentage between B and C is commonly greater than the cross-over percentage between A and C, and the discrepancy increases with the magnitude of the values involved. This fact has been accounted for in two different ways. First, it may be supposed that the arrangement of the genes is really not linear, that B lies out of line with A and C, so that AC will be less than the sum of AB and BC, and that the more distant genes are no farther apart than indicated by the cross-over percentages between them. This explanation has met with



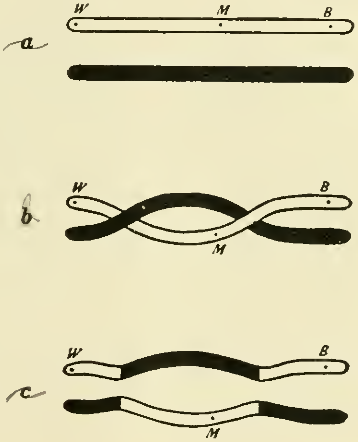


FIG. 121*a*. B and C illustrate Morgan's idea of the linear arrangement of the genes in the chromosomes. A and D show how the composition of chromosomes is supposed to change as a result of a crossover. FIG. 122. A pair of homologous chromosomes *a*, before; *b*, during; *c*, after a double crossover. (After Morgan.)

more difficulties than it has cleared away. The second explanation is that the map-distances indicate proportionate numbers of *breaks* in the linkage chain between points, not proportionate numbers of changes of relation between genes at particular points. Thus, suppose genes A B C D E of a linkage system meet their allelomorphs, a b c d e, in a cross and gametes are later formed by the cross-bred as follows, (1) A B c d e, (2) A B c d E, and (3) A b c D e. Assuming that the arrangement is linear, we must suppose that *one* break in the linkage chain has occurred in (1), *two* breaks in (2), and *three* breaks in (3). But if we did not have genes B C D under observation, and merely noted the relation of A to E, we should infer that in case (1) and in case (3) a single crossover had occurred, but that in case (2) no crossover had occurred. We should on that basis underestimate the amount of breaking in the linkage chain. Accordingly the construction of maps on the basis of *short* distances summated is justifiable, provided the arrangement is linear, as it seems to be. But it must be borne in mind that the map distances do not correspond with cross-over percentages (although they are based on them) except in the case of very short distances. Map distances often exceed 50, but cross-over percentages can not do so, as already pointed out. To get a distinctive name for the map units, Haldane has called them units of Morgan or simply "morgans." Haldane has computed a formula for converting cross-over percentages into "morgans" and *vice versa*. He finds that the two correspond only for very low values (5 or less) and diverge more and more as the observed cross-over percentages approach 50. Haldane's formula may be stated thus. If three genes, A, B, and C, occur in a common linkage group, and the cross-over percentages are known between A and B and between B and C, we may predict with a probable error of not over two per cent, what cross-over percentage will be found to occur between A and C. Calling the cross-over percentage between A and B, *m*, and that between B and C, *n*, the cross-over percentage between A and C will lie between $(m + n)$ and $(m + n - 2mn)$. It will approach the former for amounts of 5 or less, and the latter for amounts of 45 or over. In a useful table Haldane shows the calculated map distances (morgans) for all cross-over percentages between 5 and 50. This table is based on the relations of the genes observed in the sex-linked group of Drosophila, but it applies equally well to the second linkage group of Drosophila and to a group of three genes in the plant, Primula. Provisionally it may be considered to be applicable generally to linkage systems in animals and in plants.

TABLE 24

A Table for Converting Cross-Over Percentages into Map Distances ("Morgans") and Vice Versa. After Haldane

Cross-over percentage		0.0	5.0	8.0	10.0	11.0	12.0	13.0
Map distance		0.0	5.1	8.2	10.3	11.4	12.5	13.6
14.0	15.0	16.0	17.0	18.0	19.0	20.0	21.0	22.0
14.7	15.9	17.0	18.1	19.3	20.5	21.7	22.9	24.1
23.0	24.0	25.0	26.0	27.0	28.0	29.0	30.0	31.0
25.3	26.6	27.9	29.2	30.5	31.9	33.3	34.7	36.2
32.0	33.0	34.0	35.0	36.0	37.0	38.0	39.0	40.0
37.7	39.3	40.9	42.6	44.3	46.1	48.0	50.0	52.2
41.0	42.0	43.0	44.0	45.0	46.0	47.0	48.0	49.0
54.4	56.8	59.6	62.6	66.0	70.1	75.1	81.9	93.0
49.5	49.7	49.8	49.9	50.0				
99.2	109.4	117.7	128.1	∝				

As an example of how the table may be used in predicting undetermined linkage values, suppose that A is linked with B, and B with C and that between A and B there are 10 per cent of crossovers, and between B and C, 15 per cent of crossovers. What will be the cross-over percentage between A and C? Converting the observed cross-over percentages into map distances with the aid of the table, we find the distance AB to be 10.3 and the distance BC to be 15.9. On the linear theory the distance AC will equal either the sum or the difference of AB and BC, that is will be either 26.2 or 5.4. Converting these distances into cross-over percentages by interpolation in the table, we find that the cross-over percentage between A and C should be either 23.7 or 5.1, according as the linear arrangement is ABC or ACB.

Measurement of linkage. It will be observed that as the strength of linkage increases, the cross-over percentage decreases. With a cross-over percentage of 50, there is no linkage. With a cross-over percentage of 0, the linkage is complete, two characters so related behaving as allelomorphs. Accordingly we depend upon the observed cross-over percentage both for the detection of linkage and for the measurement of its strength. But unfortunately the linkage strength varies inversely as the cross-over percentage. This makes the cross-over percentage directly considered, a rather poor measure of linkage strength. It is really the amount by which the cross-over percentage falls below 50 that measures directly the strength of linkage. Thus with cross-over percentages of 50, 40, 30, 20, 10, and 0, we should have linkage strengths of 0, 10, 20, 30, 40, and 50. We should then have a standard for measuring linkage strength directly, on a scale of 50. But as we are more accustomed to grading on a scale of 100, it seems preferable to double the values indicated above. We then have grades of linkage strength on a scale of 100, as follows:

Cross-over Percentage	Linkage Strength
50	0
40	20
30	40
20	60
10	80
0	100

Accordingly, to estimate the strength of linkage in a particular case, we multiply by 2 the difference between the observed cross-over percentage and 50.

But suppose the observed cross-over percentage were *greater* than 50, what then? Such an occurrence would not indicate linkage, a tendency of characters to remain grouped as they were, but an opposite tendency, to assume new groupings. No such tendency has been observed. If it should be, it would need a different name and method of measurement.

We may now consider some further examples of linkage.

In the plant, *Primula sinensis*, Gregory observed the occurrence of linkage in a group of five characters, viz.

	Dominant	Recessive
1.	Short style	*vs.* long style (l).
2.	Magenta corolla	*vs.* red corolla (r).
3.	Tinged corolla	*vs.* full-colored corolla.
4.	Green stigma	*vs.* red stigma (s).
5.	Pale stem	*vs.* full red stem.

Altenburg later determined the strength of the linkage existing between three of these five pairs of characters, viz., 1, 2, and 4 of the above list. His results may be expressed in a linkage map as follows:

l - - - - - - - - - - - - - - r - - s
0 34.0 45.6

The cross-over percentage between l and r was found to be 34.02, between r and s, 11.62. The sum of these two, 45.64, is the total (uncorrected) map distance. The observed cross over percentage between l and s was 40.6, which falls short of the map distance by almost exactly the amount indicated by Haldane's table.

In the sweet pea the earliest discovered examples of linkage are found. Here are known two linkage groups containing each three pairs of characters as follows:

		Dominant	Recessive
	1.	Blue	*vs.* red flower color.
Group I.	2.	Long	*vs.* round pollen.
	3.	Erect	*vs.* hooded standard.
	1.	Dark	*vs.* light leaf-axil.
Group II.	2.	Fertile	*vs.* sterile anthers.
	3.	Normal	*vs.* cretin flowers.

Results described by Bateson and by Punnett indicate that in Group I the map relations of the three genes are:

E - B - - - - - - - - - - - - - L
0 .78 12.5

The group is a compact one, with E and B very closely linked, cross-over percentage less than one, with B and L showing between 11 and 12 per cent crossovers, and with E and L showing about 12.5 per cent of crossovers.

In Group II, the cross-over percentage between D and F is about 6.2, between F and N about 25.0. Until the cross-over percentage between D and N has been experimentally determined, it cannot be stated whether the "map" order is F D N or F N D. In the former case, the total map distance will be 25, or about double the length of Group I; in the latter case, it will be still longer, or about 31.2.

In garden peas two independent pairs of linked characters are known and two more are suspected (White). In one of the established cases close linkage is found between round starchy seeds and tendrils on the leaves, with about 1.5 per cent of crossing-over. In the other case a gene for late flowering is linked with red flower color with an estimated cross-over percentage of between 12 and 16.

In the snapdragon, Antirrhinum, two factors for flower color were found by Baur to be linked, with about 20 per cent of crossovers occurring.

In maize three linkage groups are known, one of four factors and two of two factors each. Group 1 includes a factor for waxy endosperm and the factor C for aleurone color. These show a cross-over percentage of 26.7. Group 2 includes four linked factors, aleurone factor R, chlorophyl factor G, chlorophyl factor L, and aleurone spotting factor, S. No crossovers have been observed between R and L which behave as if they were allelomorphs, or "completely linked." The cross-over percentage between L and G has been determined as 23, that between R and G has been determined less accurately as 19, and that between R and S as 12.5. The order of the genes is accordingly

RL – – – – S– – – – G.

Group 3 includes the two characters, starchy endosperm and tunicate ("podded") seeds. The cross-over percentage in this case is 8.3 (Jones and Gallastegui).

In the cultivated tomato two cases of linkage have been reported. A gene for "standard" vine habit and a gene for

TABLE 25

Cases of Linkage in Plants or in Animals other than Drosophila

Species	Group	Linked Characters	Cross-over Percentage	Linkage Strength	Authority
Sweet pea	1	Purple flowers, long pollen	11 or 12	76–78	Bateson and Punnett
	1	Purple flowers, erect standard	0.78	98.4	
	1	Long pollen, erect standard	12.5	75	
	2	Dark axil, fertile anthers	6.2	87.6	
	2	Dark axil, normal (not cretin) flower	?	. . .	
	2	Fertile anthers, normal (not cretin) flowers	25.0	50	
Primula sinensis	1	Short style, magenta corolla	34.0	32	Altenburg
	1	Short style, green stigma	40.6	18.8	“
	1	Magenta corolla, green stigma	11.6	76.8	“
	1	Tinged corolla, green stigma	?	. . .	Gregory
	1	Pale stem, green stigma	?	. . .	“
Garden pea	1	Round seeds, tendrils on leaves	1.5	97	Bateson and Vilmorin
	2	Late flowering, colored flowers	12–16	68–76	Hoshino
Antirrhinum	1	Red flower color, “picturatum” pattern	20.0	60	Baur
Maize	1	Waxy endosperm, Aleurone C	26.7	46.6	Breggar
	2	Aleurone R, Chlorophyl G	19.0	62?	Lindstrom
	2	Aleurone R, Chlorophyl L	0.0	100	“
	2	Chlorophyl G, Chlorophyl L	23.0	54	“
	3	Starchy endosperm, tunicate seed	8.3	83.4	Jones
Tomato	1	Vine habit, fruit shape	20.0	60	Jones
	2	Green foliage, 2-celled fruit	0?	100?	“
Beans	1	Seed pattern, Vine habit	0?	100?	Surface
Silkworm	1	Pattern Q of larva, yellow silk	26.1	47.8	Tanaka
Apotettix	1	Patterns G and M	4 (in ♀)	92	Nabours
	1	“ M “ K	1 “	98	“
	1	“ K “ Y	6 “	88	“
	1	“ Y “ R	10 “	80	“
	1	“ Y “ T	12 “	76	“
	1	“ R “ T	0 “	100	“
	1	“ M “ R	10 “	80	“
	1	“ Y “ Z	10 “	80	“
Pigeon	1	Sex-linked factors I and A	40(in ♂)	20	Cole and Kelley
Rat	1	Albinism, red-eye	1.0?	98?	Castle and Dunn
	1	Albinism, pink-eye	21.0	58	
	1	Red-eye, pink-eye	18.3	63.4	
Mouse	1	Albinism, pink-eye,	14.3	71.4	Castle and Dunn

"constricted" fruit shape show about 20 per cent of crossing-over. In another linkage group, no crossovers have been observed between green foliage color and two-celled fruit, as opposed to yellow foliage color and many-celled fruit, in a total of 24 F_2 plants. It seems probable that the linkage in this latter case is close, though the number of observations is too small to do more than establish a probability.

In rats a group of three linked characters has been found, albinism (c), red-eye (r) and pink-eye (p), which may be mapped, thus

c - r - - - - - - - - - - - - - - - - p
0 1 20

In mice albinism (c) and pink-eye (p) are linked, as they are in rats, but the cross-over percentage is less, viz., 14.3.

In the silkworm, linkage occurs between a factor, Q, which gives to the larva characteristic pattern markings, and a factor, Y, which gives to the blood of the larva and the silk of the cocoon a yellow color. Crossing-over occurs only in males, and in a percentage of 26.1 (in a large series of back-crosses of F_1 hybrid male with double recessive female, producing 24,918 individuals). In Drosophila crossing-over occurs only in the female parent, that is in the maturation of the eggs. This is true of all linkage groups, whether they involve sex-linkage or not. In the grouse-locust, Apotettix, a linkage group of seven or more characters has been discovered by Nabours, which have this curious feature, that crossing-over seems to occur much more frequently in females than in males. In all other known cases of linkage, crossing-over occurs with about the same frequency in the gametes formed by both sexes. This accordingly is to be regarded as the normal condition. Failure of crossing-over to occur in the oögenesis of Drosophila and in the spermatogenesis of the silkworm would seem to imply unusual cytological conditions in those cases.

CHAPTER XX

THE NATURE OF GENES

WHEN a pair of alternative characters, such as pigmentation and albinism, is involved in a cross, we assume that the gamete which transmits one of the alternative conditions differs structurally from that which transmits the other and that this structural difference is the cause of their different powers of transmission. By the study of linkage relations we find that the structural difference is confined to a particular linkage group, in mice and rats to the group which also includes the factor for pink-eyed dilution. If we adopt the chromosome hypothesis, we locate the structural difference in a particular chromosome and suppose that it exists in a definite region (or locus) of that chromosome. Each structurally different state of a locus is called a gene. The color gene shows the alternative forms which we call C and c. With all the residual heredity unchanged, C will cause the development of full pigmentation, while c will leave the skin unpigmented. For information as to what C and c are, we may consult the biochemists, who have devoted considerable attention to the chemical processes involved in pigment formation. Wright (1917) after an exhaustive review of the chemical evidence concludes (1) "that melanin (pigment) is produced by the oxidation of certain products of protein metabolism by the action of specific enzymes, (2) that the reaction takes place in the cytoplasm of cells probably by enzymes secreted by the nucleus, (3) that various chromogens are used, the particular ones oxidized depending on the character of the enzymes present, and finally that hereditary differences in color are due to hereditary differences in the enzyme element of the reaction." The final conclusion is of particular interest. It indicates that the gene C is concerned in enzyme production. Wright offers a provisional hypothesis to explain variations in the character or amount of pigment found in the coats of mammals, which involves two enzymes acting in succession in the oxidation of chromogens. Enzyme I performs the initial action, and acting by itself produces yellow pigment (known also as red or cream, according to the amount of pigment formed). Enzyme II cannot act on chromogens except in connection with Enzyme I in which relation it carries forward the oxidation to a brown or black stage. Without the presence of Enzyme I, no pigment at all will be produced, that is the albino state will result, even though Enzyme II is present. According to this hypothesis the gene C is concerned in the production of Enzyme I. But we are acquainted with several allelomorphic forms of this gene, which in guinea-pigs are effective respectively in full pigmentation, dilute pigmentation, red-eyed dilution, and Himalayan albinism. We must suppose that in this series of mutations, Enzyme I is produced more and more feebly, until in complete albinism (as seen in rabbits, rats and mice) no effective production of Enzyme I occurs. On the chromosome theory we must accordingly suppose that the production of Enzyme I depends upon a structure of some sort (gene C, c, etc.) having a definite position (locus) in a particular chromosome. At definite positions in this same chromosome, we must, on this theory, locate one or more genes which influence the production of Enzyme II in the rat and in the mouse. In both the rat and the mouse, a gene for pink-eye (or its allelomorph, dark eye) is linked with the color gene. This gene (in the form pink-eye) diminishes greatly the amount of black pigment produced in eye and coat, but does not diminish at all the amount of yellow pigment formed. Hence it affects the hypothetical Enzyme II but not Enzyme I. In the rat, another gene, that for red-eyed yellow, linked still more closely with the color gene, likewise reduces the amount of black pigment formed in the coat and the eye, but without diminishing at all the production of yellow pigment. But it allows of more pigment development in the eye than does the gene for pink-eye, and this is indicated in the name "red-eye." That the genes for red-eye and pink-eye are different in chemical nature is shown by their complementary action. When pink-eyed and red-eyed rats are crossed, black pigmented young result.

A gene which in mice influences the action of Enzyme II has the allelomorphic forms black (B) and brown (b). It is not linked with the color gene and so cannot lie in the same chromosome with it (Little and Phillips, Detlefsen). Gene b interrupts the action of Enzyme II when the pigment has been oxidized to a chocolate brown color, B allows the oxidation to continue until the black stage is reached.

Another gene which limits the action of Enzyme II is the agouti factor. In mice it is not linked either with C or with B. Hence it must lie in a third chromosome. It restricts the action of Enzyme II to particular parts of the hair, the base and tip of the hair in most body regions, and on the belly the base alone, or it may exclude the action of Enzyme II from the entire hair in the belly region. As the dominant allelomorph of the agouti factor, the gene yellow inhibits the action of Enzyme II more or less completely throughout the coat of mice.

In rabbits and guinea-pigs a gene called the extension factor (E, e) influences the production or action of Enzyme II. As E it permits black (or brown) pigment to be produced throughout the coat, except where its production is interfered with by the agouti factor. As e, it does not permit Enzyme II to function in the coat, but only in the eyes and skin. Consequently the coat is yellow through the unassisted action of Enzyme I. A third allelomorph, e′, in guinea-pigs allows Enzyme II to act in part of the coat only, thus producing a yellow-and-black spotted coat. The extension factor is apparently not linked with any of the other factors for color production, and so must be located in a fourth chromosome.

How many other genes there are which influence the action of Enzyme II, we do not know, nor do we know what their nature is, but it would seem improbable that any one of them is itself Enzyme II, but only that it is in some way concerned in the production of Enzyme II, either locally or generally.

As regards Enzyme I, which is produced in several grades (qualitative or quantitative) through mutations in the color gene resulting in multiple allelomorphs, we know that its action may be localized by other independently inherited genes, those not in the same linkage-group or chromosome. Such are the factors for white spotting which in no case have been shown to be linked with albinism. Some factors of this sort seem to interfere with the production of Enzyme I in particular parts of the body, others allow Enzyme I to be produced but inhibit its action in particular body regions. Again we have no present knowledge as to what the nature of these modifying genes is. In Drosophila there occur in a single linkage system (chromosome), genes affecting various parts of the body and affecting them in various ways. Thus in the sex-linked group of genes are found those which influence the shape of the eye, the color of the eye, the length of the wings, the shape of the wings, the venation of the wings, the form of the legs, the color of the body, the shape of the bristles on head and thorax, the form of the abdomen, and many others less easy of description.

Again, in the "second-chromosome" linkage group of Drosophila, are found other genes which also affect practically all regions of the body, as for example, shape, size, and venation of wings, length of legs, color and structure of the compound eyes, patterns of thorax, shape of abdomen, and general body-color. No linkage system specializes in genes of any particular sort, or affecting any particular region of the body. Often a single gene is known to affect various parts of the body. Thus the gene, "dachs," affects both the length of the legs and the venation of the wing.

If any part of any chromosome of an egg of Drosophila were removed or changed in composition, it seems probable that some departure from normality would follow in the fly which developed from the egg. In that case the chromosome change might be regarded as a *gene* responsible for the observed departure from normality. As such it would behave in crosses with normal individuals. If this is true, it seems probable that the entire chromatin, or at least so much of it as is concerned in determining the activities of the cell, may be regarded as composed of genes. A gene will be the smallest part of the chromatin capable of varying by itself. And if the gamete contains any structures not chromatin which are concerned in heredity, that is which are reproduced when the cell divides, these too will constitute genes. Further investigation alone can show whether or not genes are found exclusively in the chromatin. At present it is assumed that such is the case.

CHAPTER XXI

ARE UNIT-CHARACTERS (GENES) CONSTANT OR VARIABLE?

In some of the preceding chapters we have considered facts which show to what a large extent the varieties of animals and plants formed under domestication owe their origin to discontinuous variations or sports, which, by reason of their Mendelian behavior in heredity, may be combined in various ways through the agency of hybridization. It is a question of much interest, both theoretical and practical, whether these sports or unit-character variations, are entirely stable or whether they themselves are subject to variation. For if a unit-character is not variable, we can only vary the combinations into which it enters, the character itself being unaffected. But if a unit-character is variable, it is important to know whether its variation is continuous or discontinuous. For if it varies by distinct steps only, that is discontinuously, it would be a waste of time to try by selection to establish any other conditions than those which arise spontaneously, by " mutation " as De Vries would say.

The mutation idea has greatly weakened the faith of biologists in selection. Darwin had great confidence in the power of selection gradually to modify the characteristics of races. Practical breeders of animals and plants have always worked by this means, and Darwin based his views concerning the efficacy of selection largely on the results of their experience. But breeders do not confine their attention to the propagation of variations which they have seen arise spontaneously. They often form ideals of uncreated varieties and then work zealously for the production of these. Some of these ideals may be unattainable, but too many of them have been realized to make us think that all work of this sort is fruitless. Today animal breeders hold among their unrealized ideals, a tri-color variety of mouse; a blue variety of fowl which will

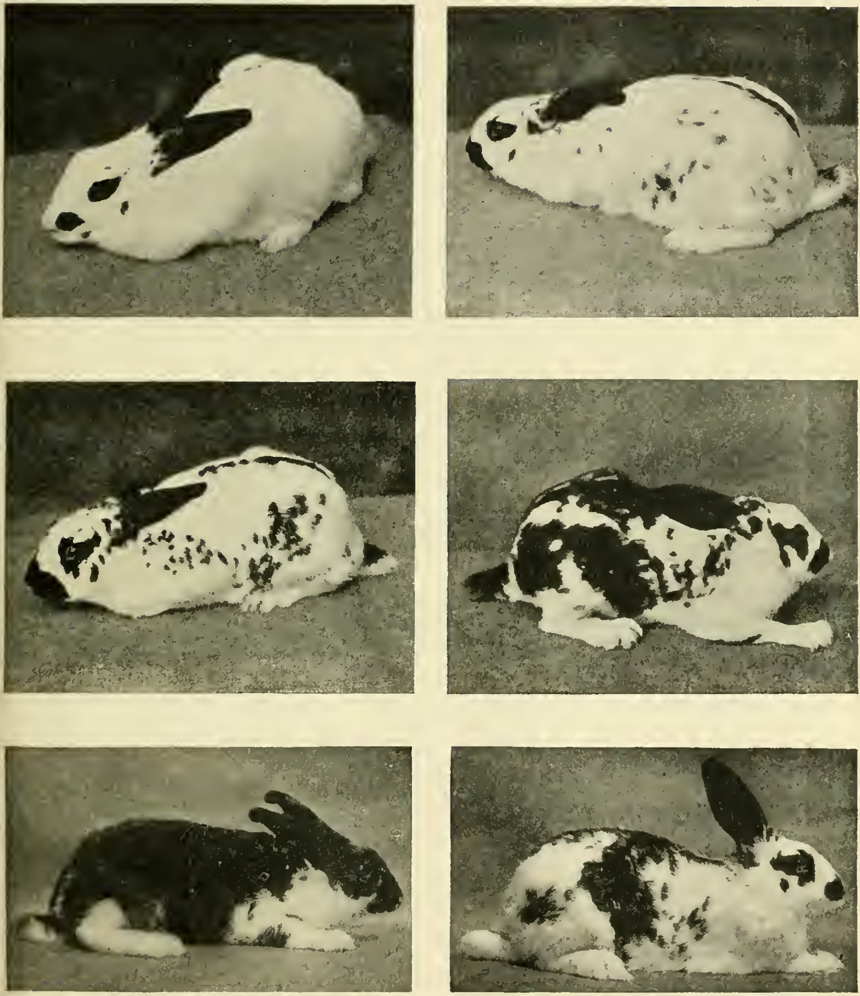


Fig. 123. English rabbits showing a dominant form of white spotting which fluctuates both somatically and genetically. The first five figures were employed as grades 1–5 in classifying observed fluctuations. The third figure (middle row, left) is close to the fancier's ideal English marking. The two rabbits shown at the top and the one at the right, bottom, were homozygous for the English pattern; the other three were heterozygous. English pattern is allelomorphic to Dutch, Fig. 138.

breed true, as blue pigeons do; a race of barred Plymouth Rock fowls of the same color in both sexes. These ideals the student of genetics says are unattainable and he can give good reasons for so regarding them. Nevertheless breeders will doubtless continue to try for them and it is hardly safe to say that success is impossible. Most advances in practical affairs are made by those who have the courage to attempt what others *with good reason think unattainable.* When such attempts have succeeded, the world simply revises its classification of things attainable and unattainable, and makes a fresh start.

Many students of genetics at present regard unit-characters as unchangeable. They consider them as impossible of modification as are the atoms. To recall Bateson's comparison, the carbon and oxygen of carbon monoxide, CO, are each unchangeable. Adding another atom of oxygen does not alter them, though it changes radically the compound formed which becomes carbon dioxide, CO_2, possessed of very different properties. But the carbon and the oxygen are still there, unaltered and recoverable. This question is one of great practical importance, — are unit-characters as constant as atoms, so that we can merely recombine them, or are they different in nature from atoms so that we can modify as well as recombine them. Much careful work has been devoted to the solution of this question. It was at first assumed from chemical analogy that characters which behave as units in heredity must, like C and O in the case of carbon dioxide, emerge from combinations unmodified. But presently case after case came to light in which this was not true. Albinism emerged from crosses tainted with color; clear yellows emerged from crosses intensified to red, or diluted to cream, or sooty with minute quantities of black; patterns such as are seen in Dutch or in English rabbits, or in hooded rats, emerged considerably altered in appearance. Facts such as these were interpreted in two different ways. It was assumed by some that the actual unit-character, factor, or gene involved was subject to quantitative and possibly to qualitative change. By others it was assumed that the observed character changes were not due to changes in single genes but to the supplemental or modifying action of the other genes. For example, the hooded pattern of rats (Figs. 124 and 125) clearly behaves as a simple unit-character allelomorphic to Irish pattern or to self in crosses. But the hooded pattern as seen either in pure-bred or in cross-bred litters of young (Fig. 124) varies slightly, and such variations have a genetic basis since by selecting either the whitest or the blackest individuals, one can either whiten or blacken the average racial condition. (See Tables 24*a* and 25*a*.) Races corresponding with the extremes of the series shown in Fig. 125 were thus produced. The question now arose whether the observed changes had occurred as a result of change in the single unit-character or gene clearly concerned in the case, or whether this was due to other agencies. To test the matter the selected races, now modified genetically in opposite directions, were crossed repeatedly with a non-hooded (wild) race. The recessive hooded character disappeared in F_1 but was recovered again in F_2 in the expected 25 per cent of this generation. Compare Fig. 56. These extracted hooded individuals, following each cross, were less divergent than their hooded grandparents from the ordinary hooded pattern. After three successive crosses (six genera-

FIG. 124. Inheritance of a recessive pattern of white spotting seen in "hooded" rats. The parents (at the left) are a homozygous hooded mother and a heterozygous "Irish" father (black with white belly). An entire litter of their young is shown at the right. Four are homozygous hooded like the mother, five are heterozygotes like the father. Note fluctuation in both classes. Such fluctuations are found to be in part heritable.

tions) the whitest individuals extracted from the dark hooded race were no darker than the darkest individuals extracted from the white hooded race. In other words repeated crossing with the non-hooded (wild) race had caused the changes in the hooded character, which had been secured by selection, altogether to disappear. This result shows conclusively that the changes in question had not occurred in the gene for the hooded pattern, but in the residual heredity. Other cases of apparent gradual change in unit-characters under the action of selection may be explained in a similar way. Accordingly we are led to conclude that unit-characters or genes are remarkably constant and that when they seem to change as a result of hybridization or of selection unattended by hybridization, the changes are rather in the total complex of factors concerned in heredity than in single genes.

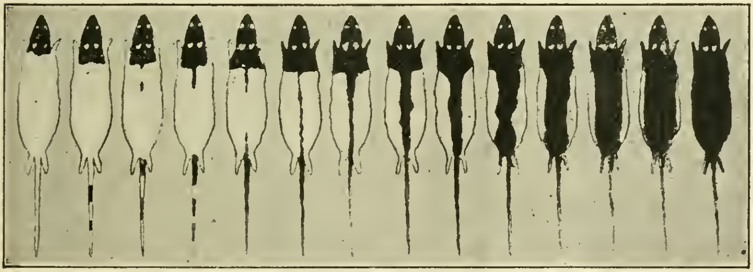


Fig. 125. A series of grades for classifying the plus and minus variations of the white spotting pattern of hooded rats.

Nevertheless changes do sometimes occur in single genes. Such, we assume, are the several unit-character variations described in previous chapters, which form the basis of the varieties of domestic animals and cultivated plants. These occur singly and sporadically as changes each in a particular locus or part of a system of genes. By hybridization these isolated changes are later combined in any desired fashion. Change in a genetic locus, that is the appearance of a new gene, is in the terminology of Morgan called a *mutation* but this use of the term differs fundamentally from that of De Vries. There is no known means by which a mutation, in this sense, can be brought about. Genes are discovered, not made in laboratories, and may be manipulated by hybridization but not changed. The suddenness of their coming and their stability are implied in the term mutation.

Sometimes a single genetic locus may undergo several different mutations, but these, so far as we know, occur independently, at different times or places, and cannot be combined for the reason that they behave as allelomorphs in crosses. For this reason not more than two of them can be brought into the same zygote, nor more than one into the same gamete. We call them multiple allelomorphs.

TABLE 24a

Results of the Plus Selection of Hooded Rats Continued through Twenty Successive Generations

Generation	Mean Grade of Parents	Mean Grade of Offspring	Lowest Grade of Offspring	Highest Grade of Offspring	Standard Deviation of Offspring	Number of Offspring
1	2.51	2.05	+1.00	+3.00	.54	150
2	2.52	1.92	−1.00	+3.75	.73	471
3	2.73	2.51	+ .75	+4.00	.53	341
4	3.09	2.73	+ .75	+3.75	.47	444
5	3.33	2.90	+ .75	+4.25	.50	610
6	3.52	3.11	+1.50	+4.50	.49	861
7	3.56	3.20	+1.50	+4.75	.55	1,077
8	3.75	3.48	+1.75	+4.50	.44	1,408
9	3.78	3.54	+1.75	+4.50	.35	1,322
10	3.88	3.73	+2.25	+5.00	.36	776
11	3.98	3.78	+2.75	+5.00	.29	697
12	4.10	3.92	+2.25	+5.25	.31	682
13	4.13	3.94	+2.75	+5.25	.34	529
14	4.14	4.01	+2.75	+5.50	.34	1,359
15	4.38	4.07	+2.50	+5.50	.29	3,690
16	4.45	4.13	+3.25	+5.87	.29	1,690
17	4.81	4.48	+3.75	+5.75	..	351
18	4.80	4.46	+3.50	+5.50	..	420
19	4.66	4.49	+3.50	+5.50	..	280
20	4.66	4.61	+3.75	+5.75	..	92
Total						17,250

A good example of multiple allelomorphism is found in the several mutations which the color factor of rodents has undergone. This is the factor which in its best known mutation assumes the form of albinism. In guinea-pigs four allelomorphic conditions of the color factor are known, (*a*) intense pigmentation, (*b*) dilute pigmentation, (*c*) red-eyed dilution, and (*d*) Himalayan albinism. In rabbits, the color factor occurs in three forms, (*a*) ordinary pigmentation, (*b*) Himalayan albinism, (*c*) pure white albinism. In rats also the color factor occurs in three forms, but not the same

TABLE 25*a*

RESULTS OF THE MINUS SELECTION OF HOODED RATS CONTINUED THROUGH TWENTY-ONE SUCCESSIVE GENERATIONS

Generation	Mean Grade of Parents	Mean Grade of Offspring	Lowest Grade of Offspring	Highest Grade of Offspring	Standard Deviation of Offspring	Number of Offspring
1	−1.46	−1.00	+ .25	−2.00	.51	55
2	−1.41	−1.07	+ .50	−2.00	.49	132
3	−1.56	−1.18	0.	−2.00	.48	195
4	−1.69	−1.28	+ .50	−2.25	.46	329
5	−1.73	−1.41	0.	−2.50	.50	701
6	−1.86	−1.56	0.	−2.50	.44	1,252
7	−2.01	−1.73	0.	−2.75	.35	1,680
8	−2.05	−1.80	0.	−2.75	.28	1,726
9	−2.11	−1.92	− .50	−2.75	.28	1,591
10	−2.18	−2.01	−1.00	−3.25	.24	1,451
11	−2.30	−2.15	−1.00	−3.50	.35	984
12	−2.44	−2.23	−1.00	−3.50	.37	1,037
13	−2.48	−2.39	−1.75	−3.50	.34	1,006
14	−2.64	−2.48	−1.00	−3.50	.30	717
15	−2.65	−2.54	−1.75	−3.50	.29	1,438
16	−2.79	−2.63	−1.00	−4.00	.27	1,980
17	−2.86	−2.70	−1.75	−4.25	.28	868
18	−3.09	−2.84	−2.25	−4.00	..	330
19	−3.10	−2.89	−2.25	−4.00	..	130
20	−2.81	−2.78	−2.00	−3.50	..	79
21	−2.58	−2.74	−2.00	−3.50	..	35
Total						17,716

three as in rabbits. They are (*a*) ordinary pigmentation, (*b*) ruby-eyed dilution (Whiting) — perhaps homologous with red-eyed dilution in guinea-pigs — and (*c*) albinism.

In Drosophila a factor for eye-color has been discovered in several allelomorphic forms, such as white, eosin, buff, cherry, blood, and red, analogous with the allelomorphs of the color factor found in guinea-pigs.

The agouti factor of rodents occurs in the rabbit in three allelomorphic forms, (*a*) ordinary gray, (*b*) black-and-tan, and (*c*) non-agouti. In mice the agouti series includes (*a*) ordinary gray, (*b*) gray with white belly, (*c*) yellow, and (*d*) non-agouti. In a cavy (*Cavia rufescens*) and its guinea-pig hybrids, it has three forms, (*a*) agouti with light belly, (*b*) agouti with ticked belly, and (*c*) non-agouti.

The extension factor has in rabbits three allelomorphic forms (*a*) ordinary extension as in gray or black rabbits, (*b*) "darkened" extension (DE, Punnett) seen in steel gray rabbits, and (*c*) non-extension (restriction) seen in yellow and in tortoise rabbits. Extension in guinea-pigs assumes three alternative forms seen in (*a*) black, (*b*) tortoise, and (*c*) yellow.

White spotting shows numerous allelomorphic forms. In rats (*a*) hooded pattern, (*b*) "Irish" pattern, and (*c*) self pattern are allelomorphs. In rabbits, all known forms of white spotting behave as allelomorphs. These include at least three different patterns of Dutch marking as well as English marking.[1]

In silkworms Tanaka discovered a series of three factors for marking of the larva, which behave as allelomorphs, although he prefers to describe them as factors completely coupled. The three are Q (quail), Qs (striped quail) and Qm (moricaud quail). He also observed several minor forms of Q, which he designated Q^1, Q^2, Q^3, and Q^4, which considerably extend the allelomorphic series, but which differ so

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[1] But in mice two forms of white spotting are known which are not allelomorphic, nor even linked. These are known as black-eyed white and piebald respectively. On the chromosome theory, they must be located in different chromosomes.

little one from another that the variation is practically continuous.

Some gametic factors show their influence chiefly, if not exclusively, in the form of changed action of other factors. Thus the ordinary extension factor in rabbits produces with the regular agouti factor an ordinary gray coat, but the darkened extension factor produces with the same agouti factor a steel gray coat. We think of the character of the gray marking as a consequence of the agouti factor but find in reality that it is changed by a change in the extension factor, no less than by changes in the agouti factor. It is assumed that there are many factors whose only discoverable function is to modify the action of other factors and when we find that some particular character, manifestly influenced mainly by a single gene, has undergone slight change, or continues to change progressively under continued selection, it is safer to assume that modifying factors are concerned in the matter than that the principal gene is gradually changing.

The substance of our present knowledge as to changes in genes may be summed up in the statement that such changes come or go suddenly and in their entirety, and cannot, so far as we know, be influenced by selection or any other controlable process. Hence we may well call changes in genes mutations.

CHAPTER XXII

INHERITANCE OF SIZE AND OTHER QUANTITATIVE CHARACTERS. THE HYPOTHESIS OF MULTIPLE FACTORS

Having observed how wide-spread unit-character variations are and what an important part they play in the formation of varieties of domesticated animals and cultivated plants, it is natural to inquire whether any other sort of heritable variations occur, whether in the last analysis all inheritance is Mendelian inheritance. This view is held by many students of genetics at the present time. The cases of doubtful interpretation relate chiefly to variations in size or shape of the organism or of its parts, cases in which the characters under observation vary continuously.

That size may be affected by ordinary Mendelian factors has never been questioned. One of the seven unit-character variations studied by Mendel himself was found in the cross between tall and short varieties of peas. Tall was found to be dominant and the alternative conditions, tall and short, were observed to segregate in true-breeding types in F_2. In man brachydactylism was early demonstrated to be a dominant unit-character, by Farabee confirmed by Drinkwater. In this peculiar condition, the skeleton is shortened throughout, and in particular the fingers are reduced from the usual three-jointed to the short, two-jointed condition. An analogous variation in Drosophila known as "dachs" is inherited in the "second chromosome" group of genes.

But the ordinary size differences between races of men, breeds of animals, or varieties of plants, are not inherited in this simple way, with dominance of one type, followed by complete segregation from an alternative type. As a rule intermediates or blends are produced in F_1 (see Fig. 130). In F_2 the commonest type is still the intermediate as in F_1, but variability is considerably increased, which may be regarded

FIG. 126. Angora male.

FIG. 127. Lop-eared female.

FIG. 128. F_1 black half-lop.

FIG. 129. F_2 albino half-lop.

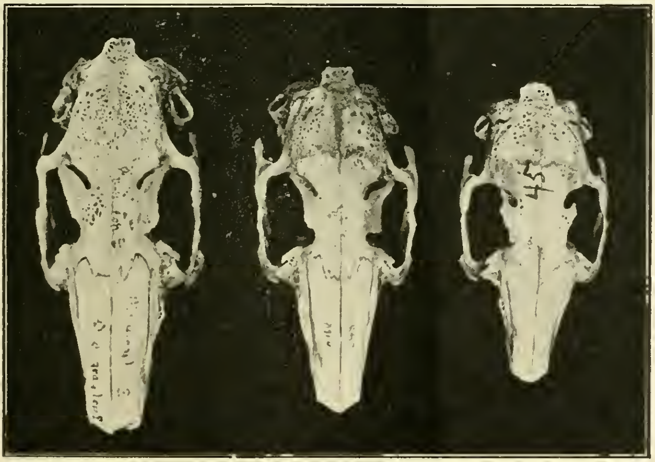

FIG. 130. Skulls of mother (at left), of father (at right) and of son (between). Compare FIGS. 126–128.

as a tendency toward segregation of the original types. These, the well established facts, were at one time regarded as showing the occurrence of a distinct type of inheritance known as blending, but at present we are inclined to give them a different explanation, the same in fact as for ordinary Mendelian inheritance except that several factors, instead of one, are supposed to be concerned in the case, and that dominance is not in evidence.

If a large rabbit is crossed with a small one, the young are of intermediate size and the F_2 offspring show no such segregation into large, small, and intermediate-sized individuals as a simple Mendelian system would demand. For if the size difference between a large and a small rabbit depended upon one unit-character, then the F_2 animals should be as regards size in the proportions, one large, two intermediate, one small. But in the cases thus far studied all F_2 individuals are intermediate in size. A specific case illustrating the point is the following: A cross was made between a large lop-eared rabbit and a small short-eared one. The former was also a sooty yellow animal and short-haired (Fig. 127); the latter an albino and long-haired (angora). See Fig. 126. The character of F_1 is shown in Fig. 128. Notice first the simple Mendelian behavior of the color characters and the hair-length. Albinism disappeared in F_1, for all the F_1 animals were black. But it reappeared in F_2; one F_2 albino is shown in Fig. 129. Long hair also behaved as a Mendelian recessive (as in guinea-pigs), disappearing in F_1 but reappearing in F_2 as expected, sometimes in colored individuals, sometimes in albinos, thus showing its independent inheritance. The black character seen in the F_1 individuals was received from the albino (angora) parent, which had black ears. The black character (dominant in F_1) was found in a majority of the F_2 colored individuals also, as we should expect, but the yellow character of the other grandparent reappeared as a recessive in F_2 in certain of the individuals. Three independent coat characters were thus Mendelizing in the cross, viz.,

Color dominant over albinism.
Black dominant over yellow.
Short hair dominant over long hair.

As regards ear-length, neither dominance nor segregation of the difference between the parents is observable. All the F_1 as well as the F_2 individuals have ears of intermediate length. The inheritance is what has been called *blending.* The same is true as regards size of the body.

In Fig. 130 the skulls of the parents are shown with the skull of the F_1 individual between them. In absolute dimensions, as well as in the proportions of its parts the F_1 skull is strictly intermediate. The same blending effect was observed in all other parts of the skeleton.

The multiple factor hypothesis. It is clear that in blending inheritance there is no *dominance,* but the suggestion has been made that nevertheless segregation may occur, and so the inheritance may have a Mendelian basis. This suggestion was first made by a Swedish plant breeder, Nilsson-Ehle (1909) who obtained some very peculiar inheritance ratios in crosses of wheat differing in color of seed or of chaff.

When a variety having brown chaff is crossed with one which has white chaff, the hybrid plants are regularly brown in F_1 and three brown to one white in F_2, but a particular variety of brown-chaffed wheat gave a different result. In fifteen different crosses it gave uniformly a close approximation to the ratio 15:1 instead of 3:1. The totals are sufficiently large to leave no doubt of this. They are one thousand four hundred and ten brown to ninety-four white, exactly 15:1. This is clearly a dihybrid Mendelian ratio, and Nilsson-Ehle interprets it to mean that there exist in this case two independent factors, each of which is able by itself to produce the brown coloration, though no qualitative difference can be detected between them.

A still more remarkable case was observed in crosses between varieties of wheat of different grain-color. Red crossed with white gave ordinarily all red in F_1 and three red to one white in F_2, but a certain native Swedish sort gave only red (several hundred seeds) in F_2. This result was so surprising that one cross which had yielded seventy-eight grains of wheat in F_2 was followed into F_3, with the following result:

					Expected
50	plants	gave	only red seed (being homozygous)		37
5	“	“	approximately	63 R : 1 W (being trihybrid)	8
15	“	“	“	15 R : 1 W (being dihybrid)	12
8	“	“	“	3 R : 1 W (being monohybrid)	6
0	“	“		*all* white	1

The interpretation given by Nilsson-Ehle is this. The red variety used in this cross bears three independent factors, each of which by itself is able to produce the red character. Their joint action is not different in kind from their action separately, though possibly quantitatively greater. The F_2 generation should contain one white seed in sixty-four. It happens that none was obtained in this generation. The next generation should contain, in a total of sixty-four individuals, the sorts actually observed as well as a sort which would produce only white seed, the progeny namely of the expected white seed of F_2, but as that was not obtained, the all-white plant of F_3 could not be obtained either. The expected proportions of the several classes in F_3 are given for comparison with those actually obtained. The agreement between expected and observed is so good as to make it seem highly probable that Nilsson-Ehle's explanation is correct. Corroborative evidence in the case of maize has been obtained by East, and in shepherd's-purse by Shull.

This work introduces us to a new principle which has important theoretical consequences. If a character ordinarily represented by a single unit in the germ-plasm may become represented by two or more such units identical in character, then we may expect it to dominate more persistently in crosses, fewer recessives being formed in F_2 and subsequent generations. Further, if duplication of a unit tends to increase its intensity, as seems probable, then we have in this process a possible explanation of quantitative variation in characters which are non-Mendelian, or at any rate do not conform with a simple Mendelian system. Consider, for example, the matter of size and skeletal proportions in rabbits. It is perfectly clear from the experiments described that in such cases no dominance occurs, and also that no segregation of a simple Mendelian character takes place, but it is possible to explain the observed facts by the combined action of several similar but independent factors, the new principle which Nilsson-Ehle has brought forward. This is known as the principle of *multiple factors.* Let us apply such an hypothesis to the case in hand.

Suppose a cross be made involving ear-lengths of approximately four and eight inches respectively, as in one of the crosses made. The F_1 young are found to have ears about six inches long, the mean of the parental conditions, and the F_2 young vary about the same mean condition. If a single Mendelian unit-character made the difference between a four-inch and an eight-inch ear, the F_2 young should be of three classes as follows:

Classes	4 in.	6 in.	8 in.
Frequencies	1	2	1

(Compare Fig. 131, bottom left, and Table 28.) The grandparental conditions should in this case reappear in half the young. This clearly does not occur in the rabbit experiment. But if two unit-characters were involved, F_1 would be unchanged, all six inches, yet the F_2 classes would be more numerous, viz., four, five, six, seven, and eight inches, and their relative frequencies as shown by the height of the columns in Fig. 131, middle left, one, four, six, four, one. The grandparental states would now reappear in one-eighth of the F_2 young, while three-eights would be intermediate. It is certain, however, that in rabbits the grandparental conditions, if they reappear at all, do not reappear with any such frequency as this.

If three independent size-factors were involved in the cross, the F_1 individuals should all fall in the same middle group, as before, viz., six inches, but the F_2 classes should number *seven*, and their relative frequencies would be as shown in

Fig. 131, top left. For four independent size-factors, the F_2 classes would be more numerous still, viz., nine (Fig. 131, right), and the extreme ear-size of either grandparent would be expected to reappear in only one out of two hundred and fifty-six offspring, while considerably more than half of them would fall within the closely intermediate classes included between five and one-half and six and one-half inches, the three middle classes of the diagram. With six size-characters, the extreme size of a grandparent would reappear no oftener than once in four thousand times, while with a dozen such independent characters it would recur only once in some seventeen million times. It would be remarkable if under such conditions the extreme size were ever recovered from an ordinary cross.

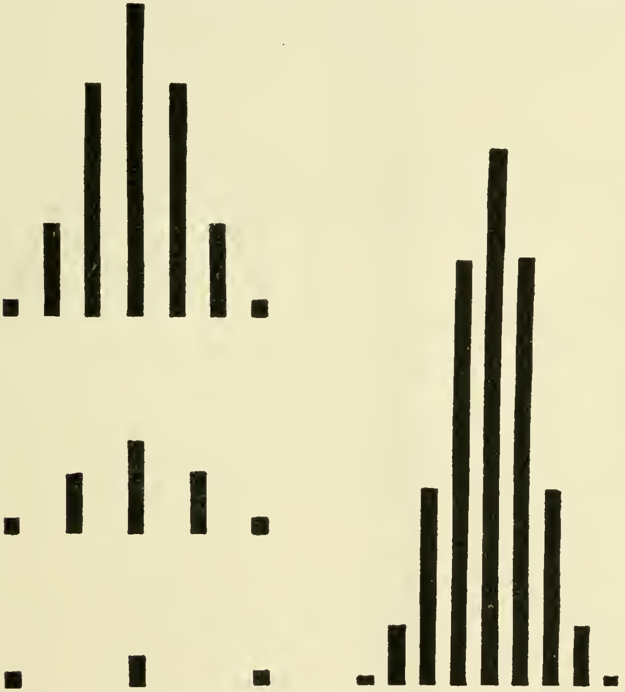

Fig. 131. — Diagrams to show the number and size of the classes of individuals to be expected from a cross involving Mendelian segregation without dominance. One Mendelian unit involved, bottom left; two units, middle left; three units, top left; four units, right.

From Table 28 it will be seen that when three like factors are concerned, fifty to one hundred individuals must be produced to insure the recovery of the parental condition in F_2;

with 4 like factors, 200–300 individuals must be produced;
“ 5 “ “ over 1000 “ “ “ “ ; and
“ 6 “ “ “ 4000 “ “ “ “ .

The foregoing calculations are based on the assumption that each of the several hypothetical factors involved has an equal influence in determining the general result and that all are mutually independent (not linked). If, however, one or more of the factors had greater influence than the others, the apparent blending would be less perfect and a “tendency toward segregation” or “imperfect segregation” would result. It is probable that this is the correct explanation of what at one time was called “a type of inheritance intermediate between Mendelian and blending.” Also if certain of the multiple factors were linked (borne in the same chromosome), this would result in a tendency of the factors to segregate in groups as originally introduced into the cross, although crossing-over might lead to the production of transitional types, any of which would “breed true” as soon as all factors involved became homozygous.

TABLE 28

Theoretical Factorial Composition of a Population Produced by a Cross Involving more than a Single Mendelian Factor, Dominance being wanting

Factors	Frequencies of F_2 Classes													Total (= 4^n)	Number of Homozygotes (= 2^n)	Per Cent of Homozygotes
1	.	..	..	..	..	1	2	1	..	..	..	..	.	4	2	50.0
2	.	..	..	..	1	4	6	4	1	..	..	..	.	16	4	25.0
3	.	..	..	1	6	15	20	15	6	1	..	..	.	64	8	12.5
4	.	..	1	8	28	56	70	56	28	8	1	..	.	256	16	6.2
5	.	1	10	45	120	210	252	210	120	45	10	1	.	1024	32	3.1
6	1	12	66	220	495	792	924	792	495	220	66	12	1	4096	64	1.5

A considerable number of cases of size inheritance has now been studied in both animals and plants. Their results may be summarized thus: (1) When animals or plants are crossed which have racial differences in size or other characters, in respect to which each race shows continuous variation about a different mean, the F_1 progeny are of intermediate size.[1] They may or may not be more variable than the races crossed, but quite commonly are not. (2) The F_2 generation as a whole commonly varies about the same intermediate mean as the F_1 generation, but its variability as measured by the standard deviation or the coefficient of variation is usually greater than that of the F_1 generation. The increased variability of F_2 as compared with F_1 may in extreme cases include forms larger than the larger parental race or smaller than the smaller race, and which show a tendency to vary in F_3 about the same size as characterized the F_2 parent.

Some illustrative cases may be cited. Phillips (1912, 1914) crossed two breeds of ducks which differed markedly in size, namely Rouens and Mallards. The average adult weight of the Rouen race used was, for males, two thousand three hundred grams, and for females two thousand two hundred and thirty-seven grams. Corresponding weights for the Mallard race were one thousand sixty-eight and nine hundred and twenty-eight grams respectively. The Rouens accordingly were more than twice as large as the Mallards. The two races did not overlap in weight, as appears from Table 29, where the animals are classified by weight. In this table the mean weight of the Mallards is taken as the center of class 2 and the mean weight of the Rouens as the center of class 10. Each sex was classified separately but the two are combined in classes bearing the same class number in Table 29. The seventy F_1 offspring have their mode in the intermediate

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[1] I leave out of consideration here such differences as exist between tall and dwarf peas, and between brachydactylous and normal men. In such cases a simple Mendelizing difference exists, which shows both dominance and segregation in typical fashion. Aside from this simple difference, however, ordinary size differences exist in such cases, which I doubt not follow the ordinary rules of size inheritance.

class 6, though they range all the way from class 2 to class 9. The sixty-three F_2 offspring likewise have their mode in class 6, and are slightly more variable than F_1, though only one aberrant individual falls beyond the range of F_1. This is a case in which apparently many independent factors of approximately equal influence on weight are concerned and which do not segregate in linked groups. The result is that both F_1 and F_2 vary symmetrically about the same strictly intermediate mode (class 6).

A case in which fewer factors are involved or in which the factors are either not all of equal influence or occur in linked groups is the following. Punnett and Bailey crossed two breeds of fowls differing widely in weight, the larger breed being represented in a gold-penciled Hamburg cock, the smaller in silver Sebright bantam hens. The relative size of the breeds is shown in Table 29*a*. As male fowls are larger than females, the weight of each sex is tabulated separately in absolute weight units (grams). The weight of the F_1 birds was much nearer that of the larger than that of the smaller parent breed, an indication that one or more of the factors for large size show dominance. An alternative interpretation would ascribe the large size of F_1 to hybrid vigor. (See Chapter XXVII.) Possibly each explanation is in part correct. The F_2 generation showed very great variability in weight, covering the ranges of both parent breeds, so far as those ranges had been ascertained for the material studied. But the variation curve for F_2 was not symmetrical about an intermediate mode,as in the case of ducks studied by Phillips. The mode was close to the F_1 mode, but the variation was very "skew," ending abruptly above, but sloping gradually downward to bantam size. When the more extreme F_2 individuals were mated, large with large and small with small, broods were obtained which averaged larger than pure Hamburgs and smaller than pure Sebrights respectively.

Punnett interprets the case as involving four independent factors having among themselves unequal influence on the total weight. He supposes that three of the four factors are

TABLE 29*a*

Weight Inheritance in Fowls

After Punnett and Bailey (1914)

Weight classes in grams	500–	600–	700–	800–	900–	1000–	1100–	1200–	1300–	1400–	1500–	1600–
Females, Hamburg....	. .	. .	. .	. .	. .	3	1	. .	. .	. .	. .	. .
Sebright............	1	1	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .
F_1................	. .	. .	. .	. .	6	1	. .	. .	. .	. .	. .	. .
F_2................	3	17	25	27	36	8	4	1	. .	. .	. .	. .
F_3 (from largest F_2s)...	. .	. .	. .	. .	1	3	5	2	2	. .	. .	. .
F_3 (from smallest F_2s)..	3	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .
Males, Hamburg......	. .	. .	. .	. .	. .	. .	. .	. .	1	. .	. .	. .
F_1................	. .	. .	. .	. .	. .	. .	5	2	1	. .	. .	. .
F_2................	. .	1	4	7	15	26	19	29	9	2	. .	. .
F_3 (from largest F_2s) ...	. .	. .	. .	. .	. .	1	2	4	2	1	2	1
F_3 (from smallest F_2s) ..	2	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .

borne by the Hamburg race, and one by the Sebright race. Recombinations which include all four factors produce a race larger than Hamburg, seen in the F_3s from largest F_2s. Recombinations which include the four allelomorphs of these factors produce a race smaller than Sebright, seen in the F_3s from smallest F_2s, Table 29*a*. He supposes further that two of the four hypothetical factors exert a greater influence than the other two on the total size, the influence of the first being to the second as 66 to 30. The figures are purely provisional and are intended to indicate a form of explanation which may cover such cases satisfactorily. But it must be confessed that the number of individuals studied by Punnett and Bailey is small and their assumptions as to the number and potency of the hypothetical factors is quite arbitrary.

The extensive and carefully executed studies of Emerson and East (1913) upon crosses of maize involving differences in size and other quantitative characters afford excellent illustrations of the usual consequences of size crosses. The simplest and clearest cut cases relate to the size of the ear or of the seeds borne upon it. The behavior of ear-diameter in crosses is shown in Table 30.

Both F_1 and F_2 are intermediate in character in comparison with the parent races, but F_2 is slightly more variable. Different lots of F_1 progeny (combined in Table 30) give coefficients of variability of 8.29 and 6.88 respectively, whereas F_2 progeny have coefficients ranging from 9.66 to 11.77. The extreme ranges of the parent races are not attained in F_2. This case is similar to that of weight inheritance in ducks, except that F_2 is on the average less than F_1, being more nearly intermediate between the parental races than was F_1. The case is probably complicated by hybrid vigor in F_1, which is not retained in F_2. (See Chapter XXVII.) It is evident that so many independent factors are involved that no complete segregation occurs in F_2.

Table 31 shows the result of crossing two races of corn (A and B) differing in seed width. In this cross also, F_1, and F_2 were alike intermediate, but the latter was slightly more variable. It was found that the F_2 plants differed in genetic character as to seed width. An F_2 with low seed width (143 mm.) produced an F_3 likewise low (mean 141.3 mm.); and F_2 with seed width above the average (178 mm.) produced an F_3 of like character (mean 172.9 mm.). The range of the low selected F_3 extended even lower than the range of the uncrossed low race (B), which is similar to the result obtained by Punnett and Bailey in the weight inheritance of fowls and suggests a similar explanation, recombination of factors.

Some instructive cases involving multiple factors affecting the size and shape of fruits have been studied by Gross. See Fig. 132. It is evident that in these cases length and width of the fruit are affected by numerous independent factors which recombine so as to form a complete series of intergrading forms.

In garden peas the time between germination of the seed and flowering varies greatly in different varieties. In early varieties the time is short, in late varieties it is relatively long.

Hoshino crossed two varieties of garden peas which had been found to breed very true as to flowering time and flower color. One variety was early and white flowered, the other was late and red flowered. F_1 was very uniform also, being red in flower color and nearly as late in flowering as the late parent. F_2 showed regular Mendelian segregation as to flower color into three reds to one white. As regards time of flower-

TABLE 29

Weight Distribution of Ducks

After Phillips (1912 and 1914)

Class Number	1	2	3	4	5	6	7	8	9	10	11	12	13
Rouen........	..	..	..	..	..	..	..	3	3	9	5	1	1
Mallard......	23	54	23	2	..	..	..	..	..	..	..	..	..
F_1...........	..	1	1	4	21	35	6	1	1	..	..	..	..
F_2...........	..	1	..	6	10	22	13	9	1	..	1	..	..

TABLE 30

Ear-Diameter in Crosses of Maize

After Emerson and East (1913, p. 56)

Class means in mm.	22.5	24.5	26.5	28.5	30.5	32.5	34.5	36.5	38.5	40.5	42.5	44.5	46.5	48.5	50.5	52.5	54.5	56.5
Race A..	..	..	..	..	..	..	..	..	..	..	2	2	2	4	2	4	5	2
Race B..	15	32	14	3	1	..	..	..	..	..	..	..	..	..	..	..	..	..
F_1......	..	..	..	..	..	1	2	4	8	11	21	12	6	1	..	..	..	..
F_2......	..	..	2	6	23	35	38	69	50	43	30	17	8	..	..	..	..	..

TABLE 31

Width of Seed in Crosses of Maize

After Emerson and East (1913, p. 63).

Class means in mm. (25 seeds)	113	118	123	128	133	138	143	148	153	158	163	168	173	178	183	188	193	198	203	208	213	218	223	228	233	238
Race A	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	2	2	2	3	1	1	..	1
Race B	..	1	2	3	3	4	4	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
F_1.........	..	..	..	..	..	..	..	..	1	1	2	3	2	4	3	6	1	1	..	1	..	..	..	..	..	..
F_2.........	..	..	..	..	..	5	7	12	10	31	23	24	15	26	12	12	6	5	..	..	..	..	..	..	..	..
F_3 (from F_2, class 143)	1	6	1	6	10	13	15	9	8	6	4	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
F_3 (from F_2, class 178)	..	..	..	..	..	..	..	1	1	5	7	5	9	10	13	2	..	..	..	..	..	..	..	..	..	..

ing, F_2 was intermediate but highly variable, covering practically the entire range from the flowering time of the early to that of the late parent. F_3 was also highly variable but a few families were found to be as "constant" in flowering time as the parent varieties, and in F_4 the proportion of constant families had increased further. Two hundred and thirty of the four hundred and twenty-one F_4 families studied by Hoshino were found to be as "constant" in flowering time as the parent varieties. The mean flowering time in days from sprouting as observed by Hoshino is given in Table 32. It will be observed that the white-flowered F_4 constant families were all early or intermediate in flowering time whereas the red-flowered families were chiefly late. This clearly indicates linkage, or coupling, between flower color and time of flowering. But flower color clearly Mendelizes, hence flowering time must also depend upon a Mendelizing gene, which is linked with the gene for red flower color.

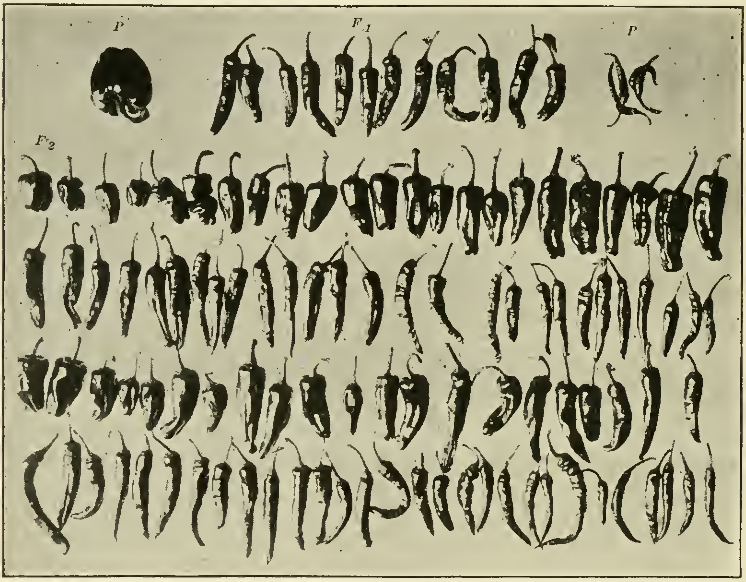

Fig. 132. A cross of two varieties of peppers differing greatly in size and shape of fruits. Fruits of the parent varieties are shown at P and P, of F_1 between them, and of F_2 in the four lower rows. Each fruit is taken from a different plant and is typical for the plant. (After Gross.)

Cross overs occasionally occur resulting, for example, in the F_4 pure red early family shown in Table 32. But if these two were the only genetic factors involved in the cross, no "constant" families of intermediate flowering time could result from the cross. As a matter of fact more than half the F_4 families are of this constant intermediate type, which shows that one or more other factors, independent of the chief factor for flowering time, must be concerned in the result. Hoshino supposes that a single supplementary factor (not

TABLE 32

Variation in flowering time of two pure varieties of garden peas, one Early White, the other Late Red; and a classification, both as to color and as to flowering time, of two hundred and thirty F_4 families produced by crossing the two varieties, these F_4 families being all regarded as " constant " in flowering time because of their low variability, as low as that of the parent varieties. Only the position of the *mean* of each F_4 family is given in the table, not its range as in the case of the parent varieties.

Days to Flowering	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Early White Parent	1	2	11	7	9	13	7	..	1	..	..	..	..	..	..	..	..
Late Red Parent	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
F_4 White Families	..	..	1	13	5	2	..	3	18	12	15	14	13	12	3	..	..
F_4 Mixed Families, White or Red	..	..	..	1	1	1	..	1	1	..	1	1	4	2	..	..	..
F_4 Red Families	..	..	..	1	..	..	..	..	1	1	3	12	13	4	6	2	..
Total " Constant " F_4 Families	..	..	1	15	6	3		4	20	13	19	27	30	18	9	2	
			25					142									

Days to Flowering	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
Early White Parent	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Late Red Parent	..	..	..	..	5	11	10	11	10	7	10	1	..	3	2	1
F_4 White Families	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
F_4 Mixed Families, White or Red	..	..	..	..	1	3	..	..	..	..	..	..	..	..	..	..
F_4 Red Families	5	3	3	2	10	13	3	10	8	1	1	..	..	..	..	..
Total " Constant " F_4 Families	5	3	3	2	11	16	3	10	8	1	1	..	..	..	..	..
	63													= 230		

linked with flower color or with the chief factor for flowering time) will account for the case. In accordance with this view, four true-breeding combinations of the factors for flowering time might be expected, and it is possible that their modes fall in Table 32 on 35 days, 40 days, 44 days, and 54 days respectively, all of which show high frequencies. Another possibility is that several modifying factors acting in various combinations produce the wide ranging group of 142 "constant" intermediate families and that linkage among these modifying factors is responsible for the apparent discontinuity between the intermediate and the early and the late groups. Certainly more than one supplementary or modifying factor is in evidence. For it is to be remembered that in Table 32, the F_4 distribution is not that of individual plants varying round particular modes, but each frequency indicated is itself the mode of a family, "constant as to that particular modal length of time between sprouting and flowering. Accordingly the "constant" varieties resulting from the cross are not *four only*, as a two factor scheme would demand, but their number is very great, since they range with only two apparent breaks all the way from the original early to the original late variety. Such a result could be produced only by numerous modifying factors, which in action supplement, or else inhibit, the action of the chief gene for flowering time so clearly linked with red flower color in transmission. No other "factorial" explanation seems admissible.

CHAPTER XXIII

GENETIC CHANGES AND THE CHROMOSOMES

In one way our views concerning heredity have been considerably simplified by the discovery that blending inheritance may be included in the category of Mendelian inheritance. One mechanism will now suffice for all kinds of inheritance, this mechanism being found in the chromosomes. In them, we may reasonably suppose, is found the material basis of every inherited character. When the inheritance is of the simplest kind, involving presence or absence of color or some similar character, we assume that a genetic change has occurred in a single, definite locus in a particular chromosome, and that this single change is responsible for the observed inherited variation. Other characters depend on two or more genes, which may lie at different loci in the same chromosome, or even in different chromosomes. Thus the gray coat of a rabbit is an inherited character which depends on at least five different genes, each of which apparently lies in a different chromosome. These are (1) a color factor, (2) a black factor, (3) an extension factor, (4) an agouti factor and (5) an intensity factor. Each of these factors or genes behaves as an independent unit in transmission. We know of their existence only because each of them has been observed to occur in two or more alternative forms. For a gene which remains unchanged remains unknown. We do not know how many undiscovered genes are concerned in producing the gray coat of a rabbit, nor in what linkage-systems (chromosomes) they lie. These few have revealed themselves by their striking variations. By various combinations of the different forms of these five genes, we get all the known color varieties of gray, black, yellow, and white rabbits. When it comes to the inheritance of size differences among rabbits, we suppose that genes affecting size are involved and that they also are located in the chromosomes. But it is clear that the size genes must be numerous since the inheritance of size is blending, and they are probably located in many different chromosomes or even in all the different chromosomes. That genes do affect size is shown by the typical Mendelian behavior of the characters tall and short in crosses of peas, and brachydactyl and normal in human families. The case studied by Hoshino in which late flowering in peas was found to be coupled with red flower color is important because it shows that a gene which affects a quantitatively varying character, one which blends in heredity, is located in the same chromosome with a color gene. There is no reason to think that any genes occur elsewhere in the gamete than in the chromosomes.

An apparent exception occurs in the case of a plant, *Mirabilis*, the cultivated four-o-clock, studied by Correns. A single plant of this species arose in his cultures, which had white-margined leaves, the white areas being due to an abnormal condition of the normally green plastids, which are cytoplasmic (not nuclear) structures. Sometimes entire branches arose on this plant (or its descendants) which were white, and which contained only colorless plastids, and others which were green containing normal colored plastids. White branches produced only white seedlings when self-pollinated and green branches produced only green seedlings. When flowers on the two sorts of branches were intercrossed, the seeds borne on white branches still produced only white seedlings, and those borne on the green branches produced only green seedlings, which thereafter bred true. The white seedlings perished because without chlorophyl they could not live. The case has been explained as one in which inheritance is exclusively maternal, by means of the egg but not by means of the pollen. Further it is a cytoplasmic structure, the plastids of the egg, which determine the plastid character of the offspring, the nucleus not being concerned in the process. Here then we seem to have a case of cytoplasmic inheritance in which nuclear genes are not concerned. But a more careful study of the case makes it seem probable that we are here dealing with a pathological condition of the cytoplasm rather than with true inheritance. Consider a similar case in animals. The organism which produces Texas fever in cattle is introduced into the blood of cattle by the bite of a diseased tick. Among ticks, the disease passes from mother to offspring *in the cytoplasm of the egg.* The sperm is too small to carry the disease germ, and so the disease does not pass from father to offspring in the sperm. In reciprocal crosses between diseased and healthy ticks, if such could be made, we should observe exactly the same mode of transmission as in the four-o-clock crosses between white branches and green branches. The offspring would always show the condition of the mother, never that of the father. But we should hesitate to describe the transmission of a foreign organism in the egg of a tick as inheritance, and the same hesitancy should be shown regarding the transmission of diseased chloroplastids in the cytoplasm of *Mirabilis.*[1]

Leaf-variegation, quite similar in appearance to that just described, but of truly genetic origin, occurs also in *Mirabilis* and was studied simultaneously by Correns. This is transmitted alike in egg-cell and pollen, as a recessive character, which shows that the gene concerned is probably borne in the nucleus. In certain other plants (Antirrhinum, Melandrium) leaf-variegation is a dominant character transmitted equally by both sexes. In fact, in a great majority of cases, variegation is inherited as an ordinary Mendelian character, either dominant or recessive, and so may be explained as due to genes contained in the nucleus. The exceptional cases are cases of cell pathology rather than of inheritance.

If then, as seems probable, genes located in the chromosomes constitute the sole vehicle of inheritance, it follows that heritable variations can arise only from changes in the genes. Such changes are called "mutations," of which we can distinguish the following varieties:

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[1] Similar cases of "maternal inheritance" have been studied by Baur in Antirrhinum, by Gregory in Primula, by Ikeno in Plantago, and by Winge in Humulus.

(1) Change in a single gene, ordinary unit-character variation, mutation in the sense of Johannsen and Morgan.

(2) Doubling of the normal chromosome number, presumably resulting in a duplication of every gene of the normal gamete, the duplicate condition being handed on permanently from generation to generation. This is the "gigas" type of mutation first observed by De Vries in the case of Oenothera, later in Primula by Gregory, and in the nightshade and the tomato by Winkler.

(3) Addition of a single extra chromosome to the regular number in the gamete, probably by duplication of a single chromosome. This is the "lata" type of mutation as observed in Oenothera, and it is related to the phenomenon of non-disjunction as observed by Bridges in the case of the sex-chromosome in eggs of Drosophila.

(4) Loss of a definite part of the sex-chromosome of Drosophila, has been described by Bridges under the name "deficiency." This involved the simultaneous disappearance from a single chromosome of at least two neighboring genes.

Of these four varieties of mutation, the last two may be regarded as rare and more or less pathological phenomena, the second leads occasionally to the sudden origin of a new variety of flowering plant, and may have functioned in the evolution of some of the lower plants (mosses, algae) and lower animals, but beyond a doubt the first mentioned variety of mutation, spontaneous change in single genes, is the usual and continuously operative method by which genetic changes arise in both animals and plants. To this we must look for that unceasing variability of organisms which furnishes the material for natural selection to operate upon and for men to work with in the improvement of the domestic animals and cultivated plants.

CHAPTER XXIV

GENETIC CHANGES IN ASEXUAL REPRODUCTION IN PARTHENOGENESIS, AND IN SELF-FERTILIZATION

The frequency of occurrence of variation in single genes apparently is very different in different species of animals and plants, and in different modes of reproduction. It is supposed to be commonest in organisms which reproduce only sexually but it must be remembered that sexual reproduction favors the spread of any genetic change which happens to occur, whereas under asexual reproduction a mutation, however favorable, has no chance to spread from the family in which it originated to others of the same species. Accordingly mutation (in single genes) may seem to be less common than it really is, in organisms which are propagated asexually. It is only when systematic search is made for genetic variations that we gain any adequate idea of how commonly they occur. Jennings was the first to take this matter up in connection with the asexual reproduction of the protozoan, paramecium. He was unable to detect any genetic changes in size in races of paramecium reproducing by fission, but in a soft-bodied animal like paramecium in which body size is constantly changing, measurement of size is not an easy matter. Later Jennings sought more favorable material for study and apparently found it in a shelled protozoan, Difflugia. This has a definiteness and rigidity of form which is wanting in paramecium. Its shell can be measured with great exactness and the number of spines which it bears can be counted, and their length measured. In the case of Difflugia Jennings found that differences in size, number of spines, and length of spines may be observed among the asexually produced descendants of a single individual, that in consequence of selection these differences become strengthened and divergent races are thus created. Hegner has observed the occurrence of similar genetic changes in Arcella. It is evident that on the theory that genes are the exclusive vehicles of inheritance, it must be supposed that genes are undergoing change rather frequently in the asexual reproduction of Difflugia and Arcella.

In the asexual reproduction of plants genetic changes known as bud-variations occasionally occur. East (1910) has observed, in the reproduction of the potato by tubers, changes in the shape, color, or depth of eyes of the tubers, such as are known to behave as simple unit-character variations in reproduction by seed. It seems probable therefore that they have arisen as changes in single genes occurring in asexual reproduction. In the propagation by budding of citrous fruits and of prunes, according to Shamel, genetic changes of commercial importance occur with so great frequency that it seems desirable to take budding stock only from carefully selected trees within the variety. The variations noted affect especially the shape and size of the fruit, or the vigor and productiveness of the tree. Shamel describes thus the recent origin of a new and improved variety of the French prune. (See Fig. 133.)

> In 1904, in a French prune tree growing in an orchard near Saratoga, Cal., one branch high up in the tree was found bearing very large fruits. There is no question as to its being a true bud variation. Several grafts were secured from this branch and placed in bearing peach trees in order to secure early evidence as to whether this variation, or bud sport, could be propagated. The fruits produced by these grafts were found to be identical to those borne by the original branch. The large fruits possessed all of the desirable characteristics of the smaller fruits of the ordinary French prune and, in addition, possessed the desired improvement in size.
>
> In order to give this strain a commerical test Mr. Coates bought 10 acres containing about 1000 peach trees for experimental trials of the large prune variety. These trees were five years old in 1914 at the time of their purchase. The large-fruited French prune variety was budded into every other row of the peach trees with the usual method practiced in top-working citrus and other fruit trees.
>
> The top-worked trees with the improved French prune strain, called No. 1418 for convenience during the experimental stages, are in alternate rows with the ordinary or other selected strains of the parent variety. In other words, in the 10-acre experimental orchard there is one row of No. 1418 followed by a row of the parent variety, and so on throughout

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Fig. 133. Origin of a new and improved variety of French prune by a bud-variation. Top row, leaves, fruit and seed of the new variety; bottom row, leaves, fruit and seed of the parent variety, shown on the same scale. (After Shamel.)

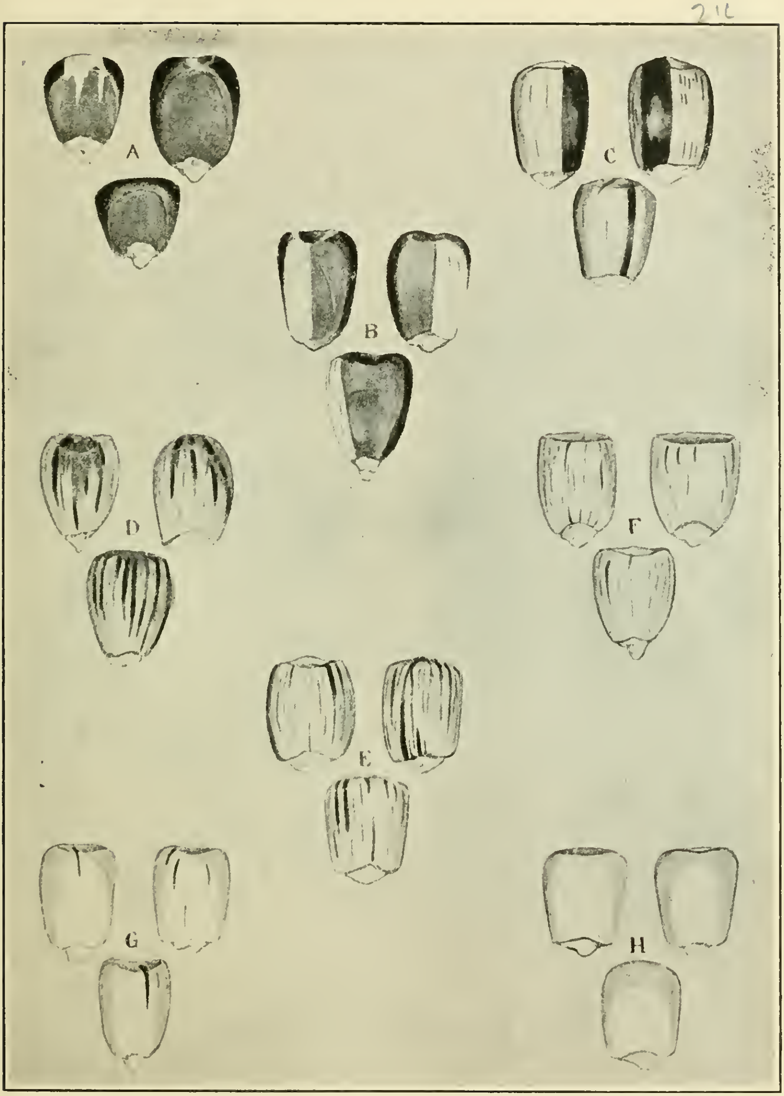

FIG. 134. Eight different types of variegated seeds of maize, which behave in general as allelomorphs one to another. But mutation from one type to another is common, only the end types of the series, A and H, being as stable as ordinary Mendelian allelomorphs. (After Emerson.)

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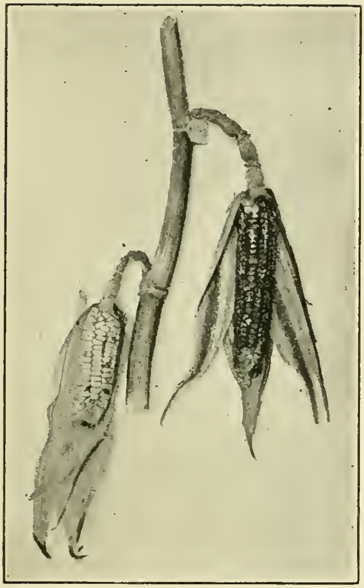

Fig. 135. Bud variation (mutation) in a plant of maize. The lower ear bears chiefly light colored seeds, the upper ear bears chiefly dark colored seeds. Each kind, as a rule, reproduces its own sort. (After Emerson.)

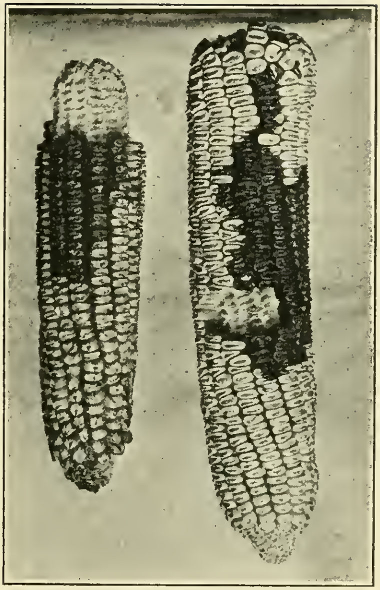

Fig. 136. Bud variation (mutation) in single ears of maize. Each ear bears patches of very dark seeds among the generally light colored seeds. Dark seeds and light seeds reproduce each its own sort, as a rule. (After Emerson.)

> the entire orchard. The conditions are comparative and furnish the basis for a fair comparison of the No. 1418 strain trees with those of the parent variety.
>
> The yield of the No. 1418 trees in the experimental planting has been more than double that of the comparative trees. The No. 1418 fruits are about twice the size and weight of the comparative fruits. They are more uniformly distributed throughout the tree than is the case with the fruits borne by the comparative trees. Furthermore, the fruits are more uniform in size, shape and other characteristics than are the fruits of the ordinary variety. So uniform are the No. 1418 fruits that they appear to have been graded mechanically as to size as they lie on the ground after falling.
>
> The No. 1418 trees appear to be more vigorous growing and develop larger leaves than do the comparative trees. The leaves of the trees of this strain appear to be thicker and have a tougher feel than do the leaves of the trees of the parent variety. In looking down the rows one notices that the larger trees of the No. 1418 strain, with their more luxurious and abundant foliage, stand out markedly as compared with the trees and leaves of the parent variety.
>
> The fruits of the No. 1418 strain average about 25–30 to the pound as compared with an average of from about 50–60 to the pound as is the case of the fruits of the parent variety.

The increased size of leaves and fruit and the great vigor of the tree, suggest that in this case a "gigas type" of bud-mutation has occurred rather than change in a single gene. Cytological study might reveal whether this is the case or not.

In plants with variegated leaves, such as Pelargonium (Baur) and Coleus (Stout), it is easy to change the racial proportion of green to white or green to colored areas by vegetative selection, that is by selection from among the vegetatively propagated offspring of a single mother plant. Apparently in such cases what is varying is the plastid content of the cytoplasm of cells rather than their nuclear structure, but the studies of Emerson and of Hayes upon variegation of the seed-coat in maize show that in this case there is a close correlation between the somatic variation (seen in the seed-coat) and the variegated character transmitted by the embryo within the seed, so that selection on the basis of the former is attended by genetic change of a corresponding sort within the gametes. It cannot be doubted therefore that, in practically all cases of variegation in plants, real genetic changes are involved whenever selection on the basis of vegetatively produced individuals or structures is found to change the racial character. Such a relation has been observed to hold in all cases thus far carefully studied.

In regard to variegated seed-coat in maize, Emerson and Hayes are agreed that the chief genetic changes occur in one and the same gene, which results in producing a series of multiple allelomorphs. Hayes recognizes four allelomorphs in the same series, Emerson "at least nine or ten." The number is probably limited only by the ability of the observer to discriminate them. Besides variation in a single gene, Hayes assumes additional "slight germinal variations," probably to be understood as changes in other genetic loci, possibly located in other chromosomes and functioning as "modifying factors." Emerson finds that some *states* of the chief gene for variegated seed-coat in maize are apparently more stable than others, since some members of the multiple allelomorph series are observed to mutate less frequently than others. Thus, "self-colored and colorless races are," he says, "as constant probably as most Mendelian characters," but the truly variegated or intermediate types mutate much more frequently, from one type of variegation into another, or even into the more stable self-colored and colorless types.

Parthenogenesis in animals, like vegetative reproduction in plants, when as commonly it occurs without the formation of gametes, affords an opportunity to observe how common genetic changes are. For in such cases no reduction of the chromosomes occurs, there is no segregation of duplicate genes, and there is no opportunity for the production of new character combinations as a result of union of gametes in fertilization. Genetic changes can in such cases occur only under conditions comparable with those of bud-variation in plants. Banta has observed for long periods, extending into hundreds of generations, the successive parthenogenetic generations of small crustacea known as water fleas (Simocephalus, Daphnia) with a view to detecting genetic changes, if such occur. His attention has been centered upon the characters which distinguish females (the ordinary parthenogenetic individuals) from the more rare males. He has observed the occurrence as mutations in *Simocephalus vetulus* and in several different strains of *Daphnia longispina*, of what are called "sex intergrades," individuals intermediate in character between males and females as regards the sex-differentiating characters both primary and secondary, or showing various combinations of the several characters which ordinarily distinguish the sexes.[1] That these variations are due to real genetic changes is shown by their occurrence in parthenogenetic lines descended (asexually) from a common mother individual; that their occurrence is not rare is shown by the fact that five out of six lines of *Daphnia* under observation in the year 1918 were observed to give rise to strains of sex intergrades. Further, such changes did not occur in single lines once only and cease thereafter. Six lines were propagated from the descendants of a single mutant sex intergrade, and selected, three toward normal femaleness, three toward maleness. The selection is characterized as "somewhat effective." "In most later generations," says Banta, "the stock in the strains selected away from the intergrade characters has been moderately or only slightly intergrade, while in some cases the stock has been almost wholly normal female. In the strains selected to make them strongly intergrade, the stock has usually been strongly intergrade. . . . In general there is a fairly pronounced difference between the characters of the stock in strains selected toward femaleness and in strains selected toward a more

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[1] Banta enumerates five easily recognized secondary sex-characters in Daphnia. See Fig. 137. These are (1) *Body size*, greater in females than in males; (2) *outline of the head*, forming a beak in the female but not in the male; (3) *size and character of the first antenna*, well developed in males but rudimentary in females; (4) *outline and hairiness of ventral anterior margin of carapace*, which in males forms almost a right angle and is hairy, but in females is rounded and hairless; (5) *character of first thoracic appendage*, in males with a hook-shaped finger-like projection, in females without hook and branched into many long terminal filaments.

strongly intergrading condition." This fact shows that minor genetic changes have occurred subsequent to the original mutation either in the same genetic locus, or loci, or in other genetic loci. Banta has shown that the degree of intergradeness is considerably influenced by environmental conditions, but that the facts are as stated, when all needed control observations are made. This leads to the strong conviction that genetic changes probably occur with considerable frequency in the parthenogenesis of animals as well as in bud-variation among plants.[1] There is, however, some negative evidence on record. Ewing selected for forty-four parthenogenetic generations a species of plant louse, *Aphis avenæ*, which was observed to vary as to length of body, length of antennæ, and length of cornicles (honey-dew tubes). All the observed variations were apparently due to environmental conditions, because no permanent modification of the race was effected by selection. The variation curve went up and down with change in environmental conditions (temperature and the like) but returned to normal when normal conditions were restored. Hence it appears that genetic variations affecting size were not occurring with any considerable frequency, if at all, in the particular characters studied at the particular time they were studied. This is not surprising when we consider what a specialized organism a plant louse is, adapted and limited to a particular host plant. But a single positive case, like that studied by Banta, outweighs any number of negative cases so far as concerns

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[1] Banta (1919) has also studied the effects of selection, in pure line cultures of *Simocephalus vetulus*, upon the sensitiveness of this species to light stimulation, as measured by its reaction time. The selection experiment was continued for 54 months, 181 parthenogenetic generations. In the first two-month period, no difference could be detected in the average reaction time of plus selected and minus selected strains of the same pure line, but subsequently the two strains gradually diverged in reaction time so that "in the final ten generations the strain selected for greater reactiveness to light had a reaction time less than one-third as large as that for the strain of the same line selected for reduced reactiveness to light." No differences in general vigor between the selected lines could be detected. The change was a specific one in relation to light reactiveness and had been attained gradually.

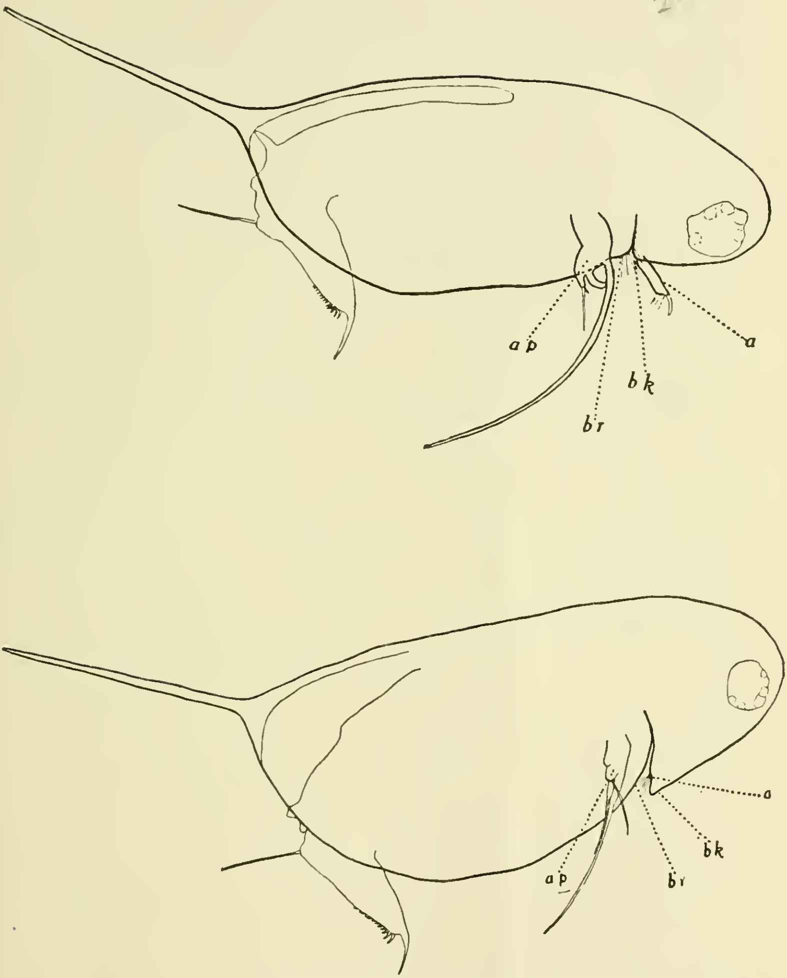

Fig. 137. Male (above) and female (below) of Daphina longispina. Note striking differences as regards *a*, antenna; *br*, breast (ventral anterior margin of carapace); *bk*, beak; *ap*, first thoracic appendage. Sex intergrades may have any combination or intermediate condition of the male and female characters shown. (After Banta.)

showing the possibility of the occurrence of genetic change outside of sexual reproduction.[1]

Self-fertilization among plants is almost as favorable as parthenogenesis or as vegetative reproduction for showing genetic changes, if they occur. For in self-fertilization both egg and pollen gametes are furnished by the same parent individual. Johannsen first advanced the view that when such a parent individual is homozygous for all genetic factors, no genetic changes will be observed among the descendants, which will continue generation after generation to constitute a "pure line." He substantiated this view by studies of size variation in successive generations of self-fertilized beans. He found in a number of cases that no change in size resulted from selecting in successive generations either the largest or the smallest beans borne on the same mother plant and concluded that such plants were homozygous for all genetic factors affecting size of seed, and that the observed variations in size upon which his selections had been based were due to environmental agencies such as the position of the bean in the pod and the consequent amount of material available for storage in the seed, which conditions were not subject to inheritance.

The case is very different if one selects by size beans borne on a plant heterozygous for genetic size factors (as for example an F_1 plant from a cross between a large-seeded and a small-seeded race of beans). Under those conditions races differing in average seed-size are quickly segregated (Emerson). Johannsen's observations show that genetic variations affecting the seed-size of beans are not of frequent occurrence, yet he has himself recorded the occasional occurrence

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[1] A very puzzling case of genetic change in parthenogenesis is recorded by Nabours. He observed in grouse locusts (*Apotettix*) the development of offspring from unfertilized eggs which showed unmistakable segregation of characters and even crossing-over among linked characters for which the mother was heterozygous. All the offspring, however, were of the female sex, indicating that the eggs from which they developed had not undergone reduction as regards the sex determinant, though it would appear that they *must* have undergone reduction as regards other characters. Cytological study of such material should prove interesting.

of mutation within a pure line of beans. That such mutations must occasionally occur or at least have occurred in times past is shown by the very existence of races differing in genetic constitution. By crossing these we can produce intermediates of any desired size. This shows that the genetic differences between them are numerous (on the multiple factor hypothesis) and numerous genetic differences have, most probably, not originated at one time or place. Studies of other self-fertilizing plants, such as peas, oats, wheat and tobacco, support the view that genetic variations in such species are rare as compared with the variability to be secured by artificially crossing different varieties, in which the beneficial genetic changes of centuries may have accumulated. All these are immediately made available for recombining in every possible way with the genetic variations accumulated in any other variety, when the two are artificially crossed. Any advantageous genetic variations which have made their appearance in a self-fertilizing plant, from the time it was taken into cultivation to the present time, are likely to be found in varieties now in cultivation, since if such variations had survival value they would naturally increase and come to predominate in the crops of successive years, even if no conscious selection was exercised. Accidental cross-pollinations, such as are known to occur occasionally in any species normally self-fertilized, would give opportunity for combination to arise of two or more advantageous genetic variations, distinct in origin. Subsequent self-fertilization for ten or more generations would establish in homozygous lines all possible combinations of the genetic factors introduced in the accidental cross. Thus it happens that a field crop of any self-fertilizing plant contains a great number of pure lines, each considered by itself a pure-breeding homozygous variety. In such cases the work of the plant breeder is very simple. He has only to isolate the varieties which nature gives him ready-made and test these out to determine which can most profitably be grown in a particular region or under a particular set of field conditions. In farm practice elimination from the seed planted of all but the best pure lines, may greatly increase the total yield. This in many cases has actually been done. The work of determining what are the best pure lines and of increasing these to the exclusion of all others is the main work of the plant breeder. It is a work which will have to be done over again generation after generation, because impurities will creep in from accidental crossing with inferior varieties or from the occasional origin within the pure line of new genetic changes for the worse, for quite as many of this sort occur, probably, as of those which are for the better. Besides discovering and isolating, as pure lines, homozygous strains of favorable genetic variations, as they occur in commercial field crops, the plant breeder has a second important function to perform in connection with plants normally self-fertilized. He may, by artificially crossing varieties, combine the excellent qualities which they severally possess. It often happens that favorable variations which have arisen in the crops of one country are unknown in those of another country. The plant breeder may bring together the best varieties of all countries, determine the good qualities of each and then by suitable crosses combine these in new varieties adapted to special conditions or particular regions. Never in the history of the world has this been done on so extensive a scale or with greater success than in the United States at the present time.

To return to the point of our departure, how common in occurrence are genetic changes in self-fertilizing plants? An answer to this question can be made only in relative terms. It is scarcely safe to assume that they *never* occur. The very existence of numerous genetically different pure lines in every self-fertilized crop shows that genetic changes *have occurred* in the past, and if so they are doubtless occurring today. Some refer all such multiplicity of varieties to past hybridizations of species genetically different, but this is only referring to a more remote period the genetic changes which are involved in the origin of the hypothetical species themselves. The genetic changes must have occurred *sometime* if related species really had a common origin as we, under the Darwinian theory, suppose.

Moreover, a cultivated plant, regularly self-fertilized, the sweet pea, whose historic origin from a single wild species is known, exists today in hundreds of true-breeding varieties differing one from another in genetic constitution. All these genetic changes have occurred within a few centuries and in most if not in all cases within what were at the time probably "pure lines."

A common answer to the question proposed is that genetic changes in pure lines are *comparatively* rare. Rare in comparison with what? With the genetic variations already existing in the same species. But the latter are accumulations of the genetic changes of centuries, or in the case of cultivated wheat, of thousands of years. Is it surprising that in comparison with such accumulations of variations, the variations observed contemporaneously to occur in pure lines are relatively few? Practically, it would be, as has often been said, a "waste of time" to look for the occurrence of favorable genetic changes within pure lines of self-fertilizing plants, so long as a wealth of untested varieties exists ready made in every commercial variety of such crop, and an even greater number of new varieties may be created by crossing the best existing varieties. But this is not to be regarded as evidence that genetic changes have not come about in the past exactly as they are coming about today, within lines pure or otherwise.

CHAPTER XXV

GENETIC CHANGES IN BISEXUAL REPRODUCTION

How common are genetic changes in ordinary bisexual reproduction? This question also can be answered only in relative terms. Few organisms have been studied intensively enough and for enough generations in succession to enable us to answer the question intelligently. *Drosophila melanogaster* has probably been studied more thoroughly than any other species, these studies, because of the rapid reproduction of Drosophila, extending over hundreds of successive generations. No other organism has yielded such a great number of known distinct genetic variations, but at first their discovery came rather slowly. Improved technique and training on the part of observers enabled them to recognize more and more genetic changes. Those discovered within ten years have mounted in number into the hundreds. There is reason to think that a goodly proportion of these genetic changes have actually occurred (not merely been discovered) during the period of laboratory study of Drosophila at Columbia University. Some of them have been observed to occur independently at different periods and in unrelated stocks of flies. This indicates that in the best-known genetically of all organisms the genes are extremely numerous and are subject to rather frequent changes, for we are acquainted only with such genes as have revealed themselves by undergoing change. The first discovered gene was that for white eye. In all eight different allelomorphic forms of this gene have now been described, viz., (1) white, (2) tinged, (3) buff, (4) eosin, (5) cherry, (6) blood, (7) coral, and (8) red. They form a series of grades of increasing intensity of red pigmentation, each one having made its appearance independently of the others. Bridges has made an intensive study of *minor* genetic variations in one of these seven grades, viz., eosin, the middle one of the series. He finds that in a pure culture of eosin, the intensity of the pigmentation may vary from a "deep pink darker than eosin" to a "pure white," through the modifying action of eight other factors, "in origin entirely independent of one another" and located each at a different genetic locus, four being in chromosome II and one in chromosome III, the others not having been definitely located. Seven of the eight modifying factors act as diluters or lighteners of unmodified eosin, one only acting as a darkener. They are in the order of their darkening (or lightening) effects, (1) dark, (2) pinkish, (3) cream c, (4) cream b, (5) cream a, (6) cream III, (7) cream II, and (8) whiting. "Each of these genes arose by mutation," while the stocks were under continuous study, "by the transformation of the materials of a particular locus into a new form having a different effect upon the developmental processes." The eye-color mutations observed to occur in Drosophila since Morgan's discovery of *white eye* are so numerous that Bridges classifies them in per cents, as 60 per cent general or non-specific modifiers of eosin, such as vermilion and pink, 22 per cent specific modifiers of eosin, and 18 per cent allelomorphs of eosin. He continues, "It is probable that mutation (change in single genes) is very much more frequent than appears, since a great many mutations are of very slight somatic effect and would pass undetected except that certain characters such as eosin eye-color, truncate wings, beaded wings, and a few others, are peculiarly sensitive differentiators for eye-color and wing-shape genes, etc." Here we have a picture of genetic mutability in the most carefully studied of organisms, occurring contemporaneously, which affords all the material needed for selection either natural or artificial to act upon in either darkening or lightening the eye-color by a series of progressive steps, if such change should be found advantageous or desirable.

Among organisms reproducing sexually, the evening-primrose has probably been studied more intensively than any other except Drosophila. But it is impossible to say in the case of Oenothera to what extent variation in single genes is occurring, because those who, following De Vries, have studied "mutation" in this multifarious genus of plants, have directed their attention, almost without exception, to the major variations which they have called "mutations," and have neglected or denied the existence of minor genetic variations, such as have been studied in much detail in Drosophila. In some cases, such as the "gigas" and the "lata" types of mutation, irregularities of cell-division seem to have resulted in duplication of entire chromosomes, or of the entire set of normal chromosomes. As a complementary phenomenon we should expect entire chromosomes to be lost from the germ-cell in other cases, and this may possibly be the explanation of some classes of Oenothera mutants whose associated cytological conditions have not been determined. In the presence of such striking genetic changes it is not surprising that variations in single genes have scarcely been detected, although the "nanella" and "rubri-calyx" mutants may be mentioned as manifesting simple uni-factorial Mendelian inheritance. It seems probable that when the minor variations of Oenothera are studied as intensively as its peculiar "mutations" have been studied, they will be found to be not less frequent in occurrence.

In domesticated mammals and birds, where asexual reproduction, self-fertilization, and parthenogenesis are unknown, and where so much racial or family hybridization is constantly being carried on with a view to increasing vigor or variability, it is difficult to say how much of the genetic variability is of contemporaneous origin and how much of it has been handed down in the stock from previous generations. Theoretically, it should be possible to make any stock of animals homozygous for practically every gene by inbreeding continued for twenty or more generations, mating brother with sister, parent with offspring, cousin with cousin, or uncle with niece (Jennings). If this is done and genetic variation is subsequently observed to occur, this must have originated after the stock had been purified. By this means we get an idea of how frequently genetic changes are happening. Such purification of stock has rarely been undertaken. Miss King has inbred rats, brother with sister, for 25 generations and the resulting stock has been studied as to genetic character chiefly in respect to sex ratio. In the course of the inbreeding, selection was made in two different lines for opposite changes in the sex ratio; in Series A for a high ratio of males to females, and in Series B for a low ratio of males to females. The result in 6,274 young of the 25 generations of the A series was a ratio of 122.3 males to 100 females. In 5,893 young of the B series, the ratio was 81.8 males to 100 females. These very different results were secured within the first 10 or 12 generations of selection, after which progress in the direction of the selection was negligible. This indicates that the genetic factors responsible for the changes were already in existence in the stock at the beginning of the selection and were gradually sorted out and rendered homozygous in the early part of the selection period, and that new genetic changes appreciable in amount did not appear subsequently.

Selection was made simultaneously for large size in the course of the inbreeding experiments of Miss King and this resulted in producing inbred races which were larger than the unselected stocks from which they were derived. The maximum size was attained as early as the seventh inbred generation, possibly earlier, as the seventh generation is the earliest one for which comparable data are available. The inbred races maintained throughout the entire period, up to the twenty-fifth inbred generation, their superiority in size over the control stocks from which the inbred strains had originated, but no evidence was found that genetic size factors had changed in the period between the seventh and twenty-fifth inbred generations. Observations were made also on fecundity as indicated by size of litter in the inbred rats. No change was observed in this character as a result of the inbreeding. The average size of litter was for the inbred series 7.5 young, for the stock albinos used as a control, 6.7

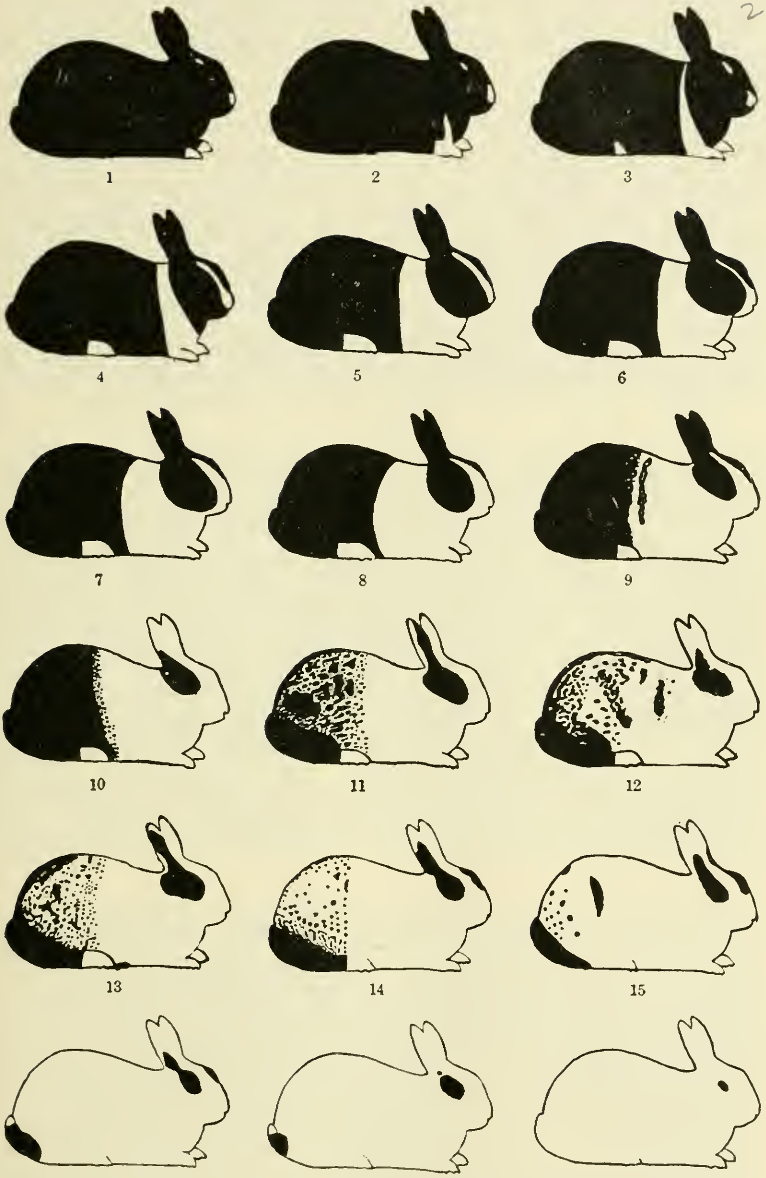

Fig. 138. Grades 1–18 of white spotting as seen in Dutch rabbits. By systematic selection the average grade of a race of Dutch rabbits may be gradually but permanently changed either in a plus or in a minus direction. Dutch spotting is allelomorphic with English (Fig. 123).

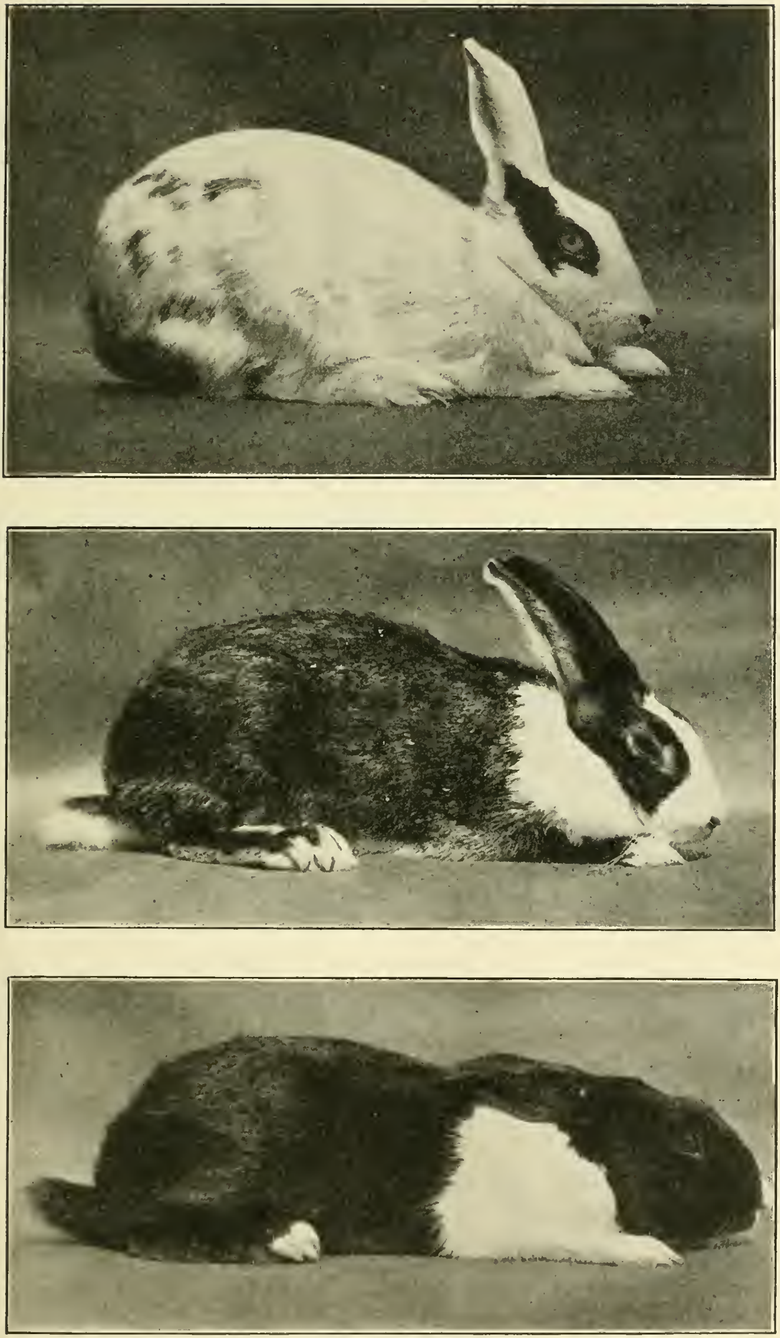

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Fig. 139. Typical examples of three races of Dutch rabbits, each having a different and characteristic amount or distribution of white spotting. The top figure represents the "white" race; middle figure, the "tan" race; lowest figure, the "dark" race. Each is allelomorphic with the others in crosses but segregates in a slightly modified form.

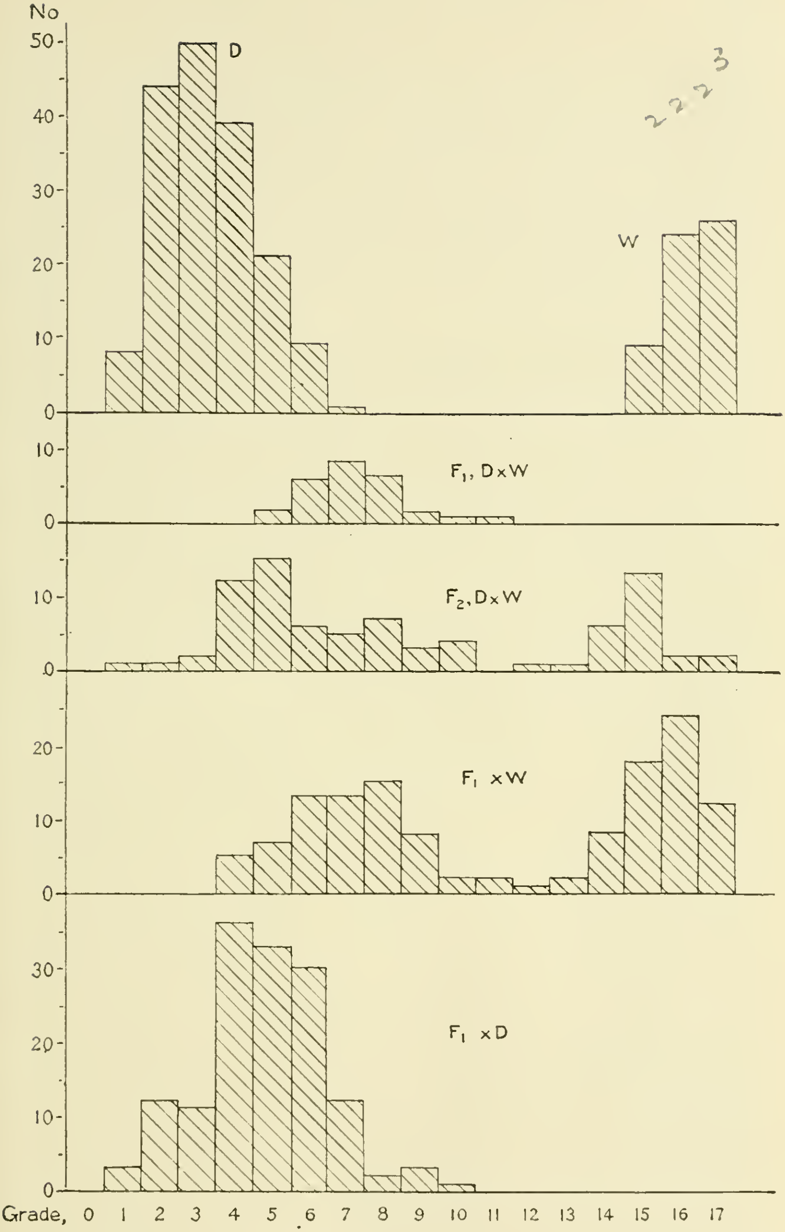

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Fig. 140. Graphic presentation of the variation in grade of two races of Dutch rabbits, "dark" (D) and "white" (W), and results of intercrossing them. At the top is shown the grade distribution of each uncrossed race; below is shown the grade distribution of F_1 animals, of F_2 animals, and of animals produced by back-crosses of F_1 with each parent race. Note that the extracted D or W groups diverge less from each other than the uncrossed D and W groups.

young per litter. At the beginning of the inbreeding experiment strains of large, vigorous, rapid-growing and fecund animals were isolated from the general stock, and those characters seem to have been maintained without diminution under the continuous selection exercised in choosing as breeders the largest and best nourished individuals from each litter, but no evidence is forthcoming of further progressive genetic changes.

In hooded rats inbred, but not exclusively in brother-sister matings, for twenty generations, selection has been made successfully for change of the hooded pattern in opposite directions, to make the race as white as possible in one line, and as dark as possible in another line. (See Tables 27 and 28.) Genetic variability decreased somewhat during the first seven or eight generations, which probably sufficed to eliminate most of the genetic variability originally present in the stock as modifying factors. But subsequently the variability as measured by the standard deviation showed little change up to the end of the experiment in generation 21 when the selected races died out owing to the prevalence of disease and infertility. The case seems to be best interpreted as one in which minor genetic changes are continually occurring, so that selection utilizing these may move the racial mode and mean either in a plus or in a minus direction without encountering impassable limits short of an all white or an all black condition. There is a strong parallelism between the variability of the white-spotting pattern in rats and other mammals and the variability of variegated seed-coat in maize and of variegated foliage in a great many species of plants. In both sets of cases an unstable mosaic of alternative characters exists, pigmentation and nonpigmentation; somatic variation in the relative proportions of the balanced characters is constantly occurring, and germinal variation of a similar nature very commonly occurs at the same time as the somatic variation, so that selection on the basis of the somatic variation effects germinal change in the race. The variability (or "mutability") in the case of plants with variegated seed-coat or foliage extends into end stages of the series which are wholly colored or wholly colorless, which stages seem to be more stable than the intermediate (mosaic) stages, as pointed out by Emerson. It is to be regretted that in the selection experiments with rats similar end stages were not reached before the selected races perished. In the case of Dutch rabbits (Figs. 138–140) the all-white condition has been recorded once, and the all-colored condition is often found in animals known to be either heterozygous or homozygous for some form of white spotting.

Two different explanations of cases of this class in animals and plants have been suggested. (1) On one view the chief genetic locus mutates frequently producing multiple allelomorphs more or less stable (Emerson), but these multiple allelomorphs may be supplemented in action by minor modifying genes (Hayes). (2) On another view the chief gene is as stable as other genes and the ordinary genetic variability is due exclusively to modifying genes (MacDowell, Pearl, Sturtevant). If the chief gene is really less stable in the case of these mosaic characters than in ordinary cases, as the descriptive term used by DeVries, "ever sporting characters," would seem to imply, at least in the case of plants, it may be because a mosaic condition exists at the genetic locus itself. In variegated plants the character of the mosaic in particular parts of the plant corresponds roughly with the character of variegation transmitted by flowers arising in those same parts of the plant whether egg-cells or pollen-cells are the vehicles of transmission, which suggests actual variation in the genetic locus involved rather than change in modifying genes. (See Figs. 135, 136.)

MacDowell inbred, brother with sister, a race of Drosophila possessing a recessive Mendelian character, extra bristles, for 49 generations, selecting meanwhile in different lines for high and for low number of extra bristles. For about eight generations the selection was effective after which no material change was observed attributable to the selection. MacDowell concludes that at the beginning of the experiment a number of genetic factors modifying bristle number were present in the stock in heterozygous condition. Selection attending the inbreeding served to eliminate certain of these from one race and to establish them in homozygous condition in the other race, after which no genetic changes would be observed unless they arose *de novo*. As MacDowell was unable to detect any such changes, he concludes that none were occurring. Payne has carried out a similar selection experiment for changed number of bristles, in another race of Drosophila, starting with the descendants of a single "mutant" individual with "reduced" bristle number, which appeared in an "extra-bristle" strain. Selection was made among the descendants of a single pair of flies and was carried in brother-sister matings in a minus selected line for 64 generations, and in a plus selected line for 60 generations. Toward the end of the experiment, the flies of the minus line, in from 96 to 100 per cent of all cases, were without bristles. This degree of purity was attained gradually during the first seventeen generations of minus selection, after which no further genetic change was observed. But in the plus selection, toward the normal number of bristles, four, in other races of Drosophila, progress continued longer, reaching its maximum in the 55th generation when 64 per cent of the individuals possessed four bristles. The two selected lines, plus and minus, had thus become very different as a result of selection. Payne finds evidence that two or possibly three genetic factors affecting bristle number were present in the plus line, two of them being sex-linked, but that in the minus line only a single factor was present. (Figs. 141, 142.)

Zeleny inbred a race of Drosophila possessing a dominant character, bar eye, meanwhile selecting for high and for low grades of the character (number of ommatidia). During the course of the selection two striking mutations were observed of the gene under study, one a reverse mutation to "full" (normal) eye, the other a mutation in the direction of selection toward a more reduced condition of the eye, and called "ultrabar." The average size of the eye in these three allelomorphic states of the "bar" gene is as follows: Full (normal) eye, 849.8 facets; bar eye, 75.6 facets; ultra-bar eye, 23 facets. Zeleny also observed lesser mutations of the gene for bar, which made their appearance during 42 carefully controlled generations of selection for low and for high facet number in brother-sister matings. Aside from mutations in the gene for bar, Zeleny observed genetic differences between his high selected and low selected lines which he ascribes to "accessory factors outside of the sex chromosome in which the bar gene is located." These when present in heterozygous state are speedily sorted out by selection, which "ceases to be effective after three to five generations." "There is, however, no limit to the possibilities of selection if the occasional mutants are included in the series, and two at least of these, reversal to full and ultra-bar, have been shown to be changes in the bar gene itself."

We may conclude that the amount of genetic change which is occurring at the present time is greater as regards some characters than as regards others, and is probably greater in some organisms than in others. But in any group of organisms capable of interbreeding, which has been divided for any length of time into non-interbreeding groups (races, breeds, or strains) genetic differences of one sort or another will probably be found to have arisen, when an intensive study of the matter is made. If so, we must conclude that genetic changes are probably occurring with appreciable frequency in most, if not in all organisms. But it should be stated emphatically that the amount of variability to be detected by selection within pure lines is in all cases small as compared with that which can be secured by crossing different strains, breeds or varieties, which have long been established within the species. For in pure line selection only genetic changes occurring during the process of selection are likely to be revealed, but following a variety cross, all possible recombinations may be expected of the genetic changes which have occurred since the two parent groups diverged from each other.

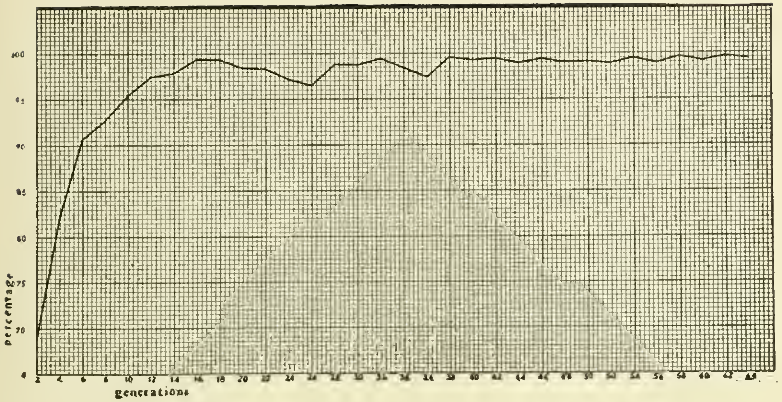

FIG. 141. Results of selection for a reduced number of bristles continued for 64 generations among the inbred descendants of a single pair of flies. The heavy line shows the percentage of flies without bristles in each generation. Note that little change occurs after the 17th inbred generation. (After Payne.)

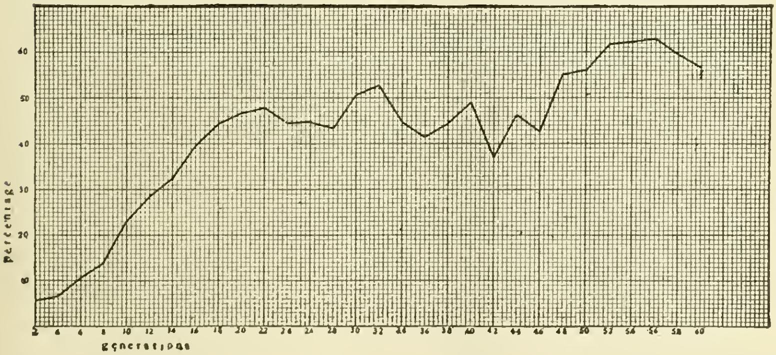

FIG. 142. Results of selection for an increased number of bristles made throughout 60 inbred generations upon the same initial stock as is mentioned in the description of Fig. 141. The heavy line shows the percentage of four-bristled (normal) flies in each generation. Note the progressive increase which continued as late as generation 55. (After Payne.)

CHAPTER XXVI

INBREEDING AND CROSSBREEDING

It is the opinion of most experienced animal breeders that close inbreeding should be avoided because it has a tendency to decrease the size, vigor and fecundity of the race in which it is practiced. Many even believe that it leads to the production of abnormal individuals or monstrosities. On the other hand some of those who have had greatest success in producing new or improved breeds of domesticated animals have practiced the closest kind of inbreeding and attribute their success in part to this fact.

In human society we find a nearly unanimous condemnation of the marriage of near-of-kin. Nearly all peoples, civilized or uncivilized, forbid it. Only exceptionally, as in the case of the royal families of ancient Egypt and ancient Peru, has the marriage of brother and sister been sanctioned. The underlying reason in such cases was a belief that the family in question constituted a superior race whose members could find no fit mates outside their own number. There was probably no thought that inbreeding itself was beneficial but only a desire to conserve the superior excellence believed to reside in certain individuals. The same considerations, probably have led to the occasional practice of inbreeding in animal husbandry, viz., the desire to conserve and perpetuate the superiority of particular individuals.

If we inquire into the biological foundation of the idea that inbreeding is harmful, we come upon seemingly conflicting evidence. No generalization can be drawn which is applicable to all organisms.

By inbreeding we mean the mating of closely related individuals. As there are different degrees of relationship between individuals, so there are different degrees of inbreeding. The closest possible inbreeding occurs among plants in what we call self-pollination, in which the egg-cells of the plant are fertilized by pollen-cells produced by the same individual. A similar phenomenon occurs among some of the lower animals, notably among parasites. But in all the higher animals, including the domesticated ones, such a thing is impossible because of the separateness of the sexes. For here no individual produces *both* eggs and sperm. The nearest possible approach to self-pollination is in such cases the mating of brother with sister, or of parent with child. But this is less close inbreeding than occurs in self-pollination, for the individuals mated are not in this case *identical* zygotes, though they may be *similar* ones.

It has long been known that in many plants self-pollination is habitual and is attended by no recognizable ill effects. This fortunate circumstance allowed Mendel to make his remarkable discovery by studies of garden peas, in which the flower is regularly self-fertilized, and never opens at all unless made to do so by some outside agency. Self-pollination is also the rule in wheat, oats, and the majority of the other cereal crops, the most important economically of cultivated plants. Crossing can in such plants be brought about only by a difficult technical process, so completely adapted is the plant to self-pollination. And crossing, too, in such plants is of no particular benefit, unless by it one desires to secure new combinations of unit-characters.

In maize, or Indian corn, however, among the cereals, the case is quite different. Here enforced self-pollination results in small unproductive plants, lacking in vigor. But racial vigor is fully restored by a cross between two depauperate, unproductive individuals obtained by self-fertilization, as has been shown by Shull. This result is entirely in harmony with those obtained by Darwin, who showed by long-continued and elaborate experiments that while some plants do not habitually cross and are not even benefited by crossing, yet in many other plants crossing results in more vigorous and more productive offspring; that further, the advantage of crossing in such cases has resulted in the evolution in many plants of floral structures, which insure crossing through the agency of insects or of the wind.

In animals the facts as regards close fertilization are similar to those just described for plants. Some animals seem to be indifferent to close breeding, others will not tolerate it. Some hermaphroditic animals (those which produce both eggs and sperm) are regularly self-fertilized. Such is the case, for example, with many parasitic flatworms. In other cases self-fertilization is disadvantageous. One such case I was able to point out some twenty years ago, in the case of a sea-squirt or tunicate, Ciona. The same individual of Ciona produces and discharges simultaneously both eggs and sperm, yet the eggs are rarely self-fertilized, for if self-fertilization is enforced by isolation of an individual, or if self-fertilization is brought about artificially by removing the eggs and sperm from the body of the parent and mixing them in sea water, very few of the eggs develop, — less than 10 per cent. But if the eggs of one individual be mingled with the sperm of any other individual whatever, practically all of the eggs are fertilized and develop.

In plants much attention has been given to the problem of self-sterility by East, Stout, Dorsey, and others. The case of native American plums is as simple as any. All varieties investigated by Dorsey were found to be self-sterile. If self-pollinated, they set no fruit, either because the pollen grains fail to germinate or because the pollen tubes, if formed, grow too slowly to reach and fertilize the ovules. Not only are all varieties self-sterile, some are also cross-sterile, *i. e.*, sterile when crossed with each other. It is probable that such varieties have inherited a similar genetic constitution, so that the pollen of one reacts toward the pistil of another as toward pistils of its own plant. In support of this view it may be said that East and Park found that the F_2 plants produced by crossing *Nicotiana Forgetiana* with *N. alata* fell into four groups, all the plants in each group being mutually cross-sterile but fertile with any plant of the other three groups. The obvious conclusion is that the plants of each group were similar in constitution as regards factors affecting fertility, and that some *dissimilarity* is necessary to enable the pollen of one individual or variety to grow vigorously on the stigma of another individual or variety. The phenomenon of self-sterility accordingly involves the principle of heterosis. (See Chapter XXVII.)

In the great majority of animals, as in many plants, self-fertilization is rendered wholly impossible by separation of the sexes. The same individual does not produce *both* eggs and sperm, but only one sort of sexual product. But among sexually separate animals the same degree of inbreeding varies in its effects. The closest degree, mating of brother with sister, has in some cases no observable ill effects. Thus, in the case of a small fly, Drosophila, my pupils and I bred brother with sister for fifty-nine generations in succession without obtaining a diminution in either the vigor or the fecundity of the race, which could with certainty be attributed to that cause. A slight diminution was observed in some cases, but this was wholly obviated when parents were chosen from the more vigorous broods in each generation. Nevertheless crossing of two inbred strains of Drosophila, both of which were doing well under inbreeding, produced offspring superior in productiveness to either inbred strain. Even in this case, therefore, though inbreeding is tolerated, crossbreeding has advantages.

In the case of many domesticated animals, it is the opinion of experienced breeders, supported by such scientific observations as we possess, that decidedly bad effects follow continuous inbreeding. Bos (1894) practiced continuous inbreeding with a family of rats for six years. No ill effects were observed during the first half of the experiment, but after that a rapid decline occurred in the vigor and fertility of the race. The average size of litter in the first half of the experiment was about 7.5, but in the last year of the experiment it had fallen to 3.2, and many pairs were found to be completely sterile. Diminution in size of body also attended the inbreeding, amounting to between 8 and 20 per cent.

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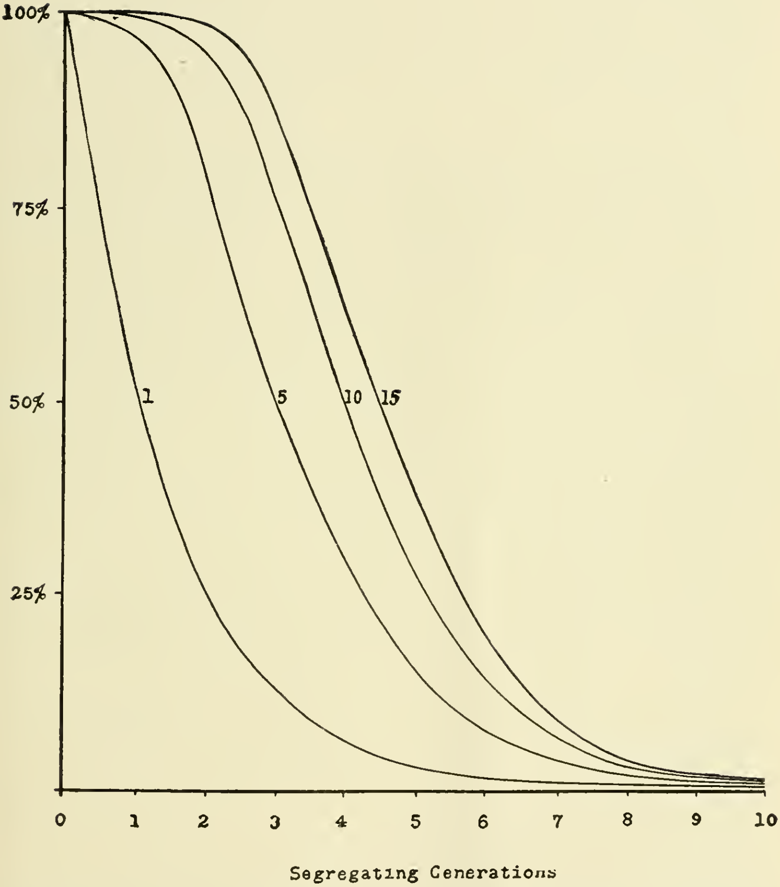

Fig. 143. Graphs showing the progressive reduction of heterozygous individuals in a population of self-fertilized plants, starting with all individuals heterozygotes. Four cases are shown, in which the number of independent allelomorphs is respectively 1, 5, 10, or 15. (After East and Jones.)

Experiments made by Weismann confirm those of Bos as regards the falling off in fertility due to inbreeding. For eight years Weismann bred a colony of mice started from nine individuals, — six females and three males. The experiment covered twenty-nine generations. In the first ten generations the average number of young to a litter was 6.1; in the next ten generations, it was 5.6; and in the last nine generations, it had fallen to 4.2.

But recent inbreeding experiments with rats carried on at the Wistar Institute by Dr. Helen King give results quite at variance with those of Bos and Weismann. She finds, as was found to be the case in Drosophila, that races of large size and vigor and of complete fertility may be maintained under the closest inbreeding, if the more vigorous individuals are selected as parents. By this means she seems to have secured races of rats which are relatively immune to injurious effects from inbreeding. My own experience with rats inbred within lines of narrow selection for seventeen generations is that races of fair vigor and fecundity can be maintained under these conditions, but that when two of these inbred races are crossed with each other, even though they had their origin in a small common stock many generations earlier, an immediate and striking increase of vigor and fecundity occurs. This is quite similar to the result observed in the case of Drosophila, and is quite in harmony with the results obtained by Shull in maize; it indicates that by careful selection races may be secured which are vigorous in spite of inbreeding, but that nevertheless an added stimulus to growth and reproduction may be secured in such cases by crossbreeding.

In the production of pure breeds of sheep, cattle, hogs, and horses inbreeding has frequently been practiced extensively, and where in such cases selection has been made of the more vigorous offspring as parents, it is doubtful whether any diminution in size, vigor, or fertility has resulted. Nevertheless it very frequently happens that when two pure breeds are *crossed*, the offspring surpass either pure race in size and vigor. This is the reason for much crossbreeding in economic practice, the object of which is not the production of a new breed, but the production for the market of an animal maturing quickly or of superior size and vigor. The inbreeding practiced in forming a pure breed has not of necessity *diminished* vigor, but a cross does temporarily (that is in the F_1 generation) *increase* vigor above the normal. Now why should inbreeding unattended by selection decrease vigor, and crossbreeding increase it? We know that inbreeding tends to the production of homozygous conditions, whereas crossbreeding tends to produce heterozygous conditions. Under self-pollination for one generation following a cross (involving one unit-character only), *half* the offspring become homozygous; after two generations, three-quarters of the offspring are homozygous; after three generations seven-eighths are homozygous, and so on. So if the closest inbreeding is practiced there is a speedy return to homozygous, pure racial conditions. We know further that in some cases at least heterozygotes are more vigorous than homozygotes. The heterozygous yellow mouse is a vigorous lively animal; the homozygous yellow mouse is so feeble that it perishes as soon as produced, never attaining maturity. Crossbreeding has, then, the same advantage over close breeding that fertilization has over parthenogenesis. It brings together differentiated gametes, which, reacting on each other, produce greater metabolic activity. East and Jones have suggested that the superiority in vigor of crossbred over inbred individuals is roughly proportional to the number of genetic differences between the races crossed. This idea is worthy of an experimental test.

Inbreeding, also, by its tendency to secure homozygous combinations, brings to the surface latent or hidden recessive characters. If these are in nature defects or weaknesses of the organism, such as albinism and feeble-mindedness in man, then inbreeding is distinctly bad. Existing legislation against the marriage of near-of-kin is, therefore, on the whole, biologically justified. On the other hand, continual crossing only tends to *hide* inherent defects, not to exterminate them; and inbreeding only tends to bring them to the surface, not to *create* them. We may not, therefore, lightly ascribe to inbreeding or intermarriage the *creation* of bad racial traits, but only their manifestation. Further, any racial stock which maintains a high standard of excellence under inbreeding is certainly one of great vigor, and free from inherent defects.

The animal breeder is therefore amply justified in doing what human society at present is probably not warranted in doing, — viz., in practicing close inbreeding in building up families of superior excellence and then keeping these pure, while using them in crosses with other stocks. For an animal of such a superior race should have only vigorous, strong offspring if mated with a healthy individual of any family whatever, within the same species. For this reason the production of "thoroughbred" animals and their use in crosses is both scientifically correct and commercially remunerative.

The early plant hybridizers found that frequently (but not always) hybrids produced by the crossing of distinct species or genera are characterized by remarkably vigorous growth and large size, superior to that of either parent. But these same large vigorous hybrids produced little or no seed. Vegetative and reproductive activity are to some extent complementary and opposed activities of the plant. A vigorously growing young fruit tree may be brought into bearing early if it is cut partly in two, or a ring of bark is removed from it in the growing season, thus checking its growth. Under such circumstances fruit buds are formed. In many hybrid plants, in which the vegetative vigor is great, partial or complete sterility exists. This, however, is not invariably the case. The offspring of a cross between geographic varieties of the same species are usually both vigorous and fertile, but the offspring of widely separated species or genera may be lacking in vigor as well as fertility. With increasing diversity of the parents the following series of conditions obtains:

1. The mating of parents belonging to the same pure race

and closely related to each other has on the whole the same effect as self-fertilization. It brings together gametes which transmit the same characters, which are doubtless chemically alike, and no particular increase of vigor results when they unite. It is on a par with asexual reproduction by parthenogenesis, fission, budding, or vegetative multiplication. There is in consequence no change in the germinal constitution, or relatively little. There is neither increase of vigor nor loss of vigor.

2. The mating of closely related individuals within a normally intercrossing population such as a breed of domesticated animals, or a human population, is apt to cause some loss of vigor. So much of the vigor of the population as is due to its crossed (or heterozygous) character, will tend gradually to disappear, as homozygous conditions are obtained in consequence of inbreeding. The greater the number of characters in which a population varies, the slower will be the attainment of a fully homozygous state in consequence of inbreeding. If sufficient vigor is retained after a fully homozygous state has been reached, then the closest inbreeding (or even self-fertilization, when this is possible) should cause no further loss of vigor. There is no reason to think that monstrosities are produced by inbreeding (as for example deformities, feeble-mindedness, insanity) except in so far as such maladies may be due (1) to the lack of sufficient vigor on the part of the organism to complete its normal development, or (2) to the appearance in a homozygous state of a recessive condition unseen in the heterozygous parents.

3. The mating of individuals belonging to distinct geographical races of the same species of animal or plant usually produces offspring larger or more vigorous than either parent and fully fertile. The same result follows when distinct breeds of domesticated animals or distinct varieties of cultivated plants are crossed. The offspring are equal to or superior to the parents in vigor and not less uniform in character. But the F_2 generation from such a cross does not retain the superiority of the F_1 generation, for it shows great variabil-

ity in all respects, which in economic animals or plants is very undesirable. For the characters in which the two pure breeds differed undergo recombination in all possible ways in the F_2 offspring. Even a back-cross of an F_1 individual with one of the pure races would produce offspring quite variable and including undesirable combinations, since each F_1 individual would form the maximum number of different kinds of gametes. Hence crossing of pure breeds of domesticated animals may in special cases be advantageous but should never be carried beyond the F_1 generation unless the breeder is setting out on the slow and tedious process of producing and fixing a wholly new breed. In that case he must be prepared to produce and sacrifice many worthless animals for the sake of obtaining in the end a few of possibly superior value. For such an undertaking the imagination and the patience of an inventor are required.

4. When animals or plants of widely separated species or genera are crossed, one of two results follows: Either the offspring are of remarkable vigor but of impaired fertility, or the offspring lack both vigor and reproductive capacity. In the former category comes one very important economic cross, that of the horse with the ass, producing a very valuable animal, the mule. The economic importance of mules is indicated by the large numbers produced in the United States, South America, Europe and Africa, and by the fact that the market price of a mule averages higher than the price of either a horse or an ass. Nevertheless a mule is absolutely incapable of reproduction. It has well developed sexual glands and sexual instincts, but the sexual cells degenerate before reaching full maturity. If mules were capable of reproduction, they would probably be less valued than they now are, for F_2 and F_3 individuals would doubtless then be produced, and these would lack the uniformity and vigor of the F_1 individuals which alone exist at present.

Crosses of cattle with the American bison produce hybrids which are sterile in the male sex only, the females being fertile with either parent species. By use of these fertile female hybrids, three-fourths bloods may be produced which are almost as variable as a true F_2 generation. If the products of this cross are shown to possess economic advantages over domestic cattle (which seems very doubtful) a fertile hybrid race will doubtless be established in the near future. How this can be done is shown in experiments made by Dr. Detlefsen and myself in crossing the guinea-pig with a wild Brazilian species of cavy, *Cavia rufescens*. The F_1 individuals surpass either parent species in size and vigor, but the males are fully sterile, the females, however, being fertile. After two back-crosses of female hybrids with the guinea-pig a few fertile males were obtained, whose descendants were also fertile. But they possess certain Mendelizing characters derived from the wild parent, *Cavia rufescens*. The skeletal characters of the hybrids are a blend. The great vigor of the F_1 hybrids is not shown in the fertile hybrids obtained by back-crossing. As regards size and vigor they are not superior to guinea-pigs. If the Mendelizing color characters possessed economic value, the hybrid race could now be easily continued. As in the case of the cattle-bison cross, the economic value of the F_1 generation is not sufficient to warrant the expense of its continued production.

Hybrids which are feeble as well as sterile have, of course, no economic value. They are scientifically interesting as showing how, when the difference between gametes becomes too great, they can no longer form a vigorous zygote. Few, if any, animal hybrids of this sort are known, but many plant hybrids of this sort have been produced, among them being some of the first produced hybrids obtained by crossing different species of Nicotiana (tobacco). See Fig. 26*a*, East's repetition of Kölreuter's pioneer experiment.

5. When organisms are crossed which differ more widely than do ordinary species, so that they are referable to different genera or families, the production of a hybrid organism does not follow, apparently because the uniting gametes are too unlike to be capable of continued existence together in the same cell. Nevertheless a *parthenogenetic* development of the

egg-cell may result from its fertilization by the foreign sperm. Thus when the egg of a sea urchin is fertilized with the sperm of a sea lily, an animal of a wholly different class of echinoderms, the egg begins development following a fusion of the sperm and egg nuclei, but the nuclear substance introduced by the sperm soon degenerates and disappears. The egg, however, having once started to develop, continues to do so, producing an organism showing only characters of the maternal species. Its development is as truly parthenogenetic as when induced by chemical or osmotic means, as is now known to be possible in the case of the eggs of many marine and of some fresh-water animals. Thus the unfertilized egg of a frog may be made to develop by chemical means (or even by puncturing the superficial layer of the egg with a needle), a process we may call artificial or induced parthenogenesis. Now in crosses of species too widely separated to produce a hybrid individual, the sperm may merely induce parthenogenesis. This method of inducing parthenogenesis is being used by plant breeders of the United States Department of Agriculture to obtain orange seedlings which it is hoped may be superior to the mother plant in certain respects, though the progeny will inherit none of the qualities of the pollen plant. It is hoped merely that there may occur in the parthenogenetic offspring some segregations or variations of the characters found in the mother plant.

What might be called male parthenogenesis has been reported in crosses of strawberries made many years ago by Millardet and also in a cross between Mexican teosinte, a plant related to maize, and a coarse grass of the southern United States. (Collins.) In such cases a cross-fertilized seed produces a plant which shows only characters of the pollen parent. It is supposed that the egg nucleus has taken no part in the production of an embryo, but that this has arisen wholly from nuclear material of the pollen tube.

Considering all the facts, changes in heterozygosity alone seem an insufficient explanation of the effects of crossing and inbreeding respectively. It is necessary to suppose further that gametes as well as zygotes vary in vigor. Some can exist as *gametes alone*, so great is their natural vigor. Here there can be *no* heterozygosity. Examples are found both in animals and in plants (honeybee drone, fern gametophyte). Others can exist only as zygotes, so feeble are they (the majority of the higher animals and plants). Still others cannot exist as homozygotes, but only as heterozygotes, because they are still feebler (the yellow mouse, the aurea snapdragon).

The experience of Miss King in inbreeding rats brother with sister for twenty-five generations, shows that heterozygosity is not indispensable to vigor even in bisexual reproduction, for she did not observe any evidences of decline in vigor, size or fecundity, yet in all probability great increase in homozygosity took place, since variability decreased.

Pearl (1915) has attempted to devise a precise measure of inbreeding based on the number of times that the same individual or individuals appear in the pedigree of a particular animal. Thus, in bi-parental reproduction each individual has two parents, each of these also had two parents, which may or may not be the same pairs. If the parents were brother and sister, then *their* parents were *one* pair, not two. Thus the maximum number of different ancestors would be two parents, four grandparents, eight great-grandparents, etc. Such would be the condition when no inbreeding had occurred. But occurrence of the same individual more than once in a pedigree would show a certain amount of inbreeding, and the extent of the inbreeding would increase with every repetition of an individual in the pedigree. Pearl makes this the basis of his "coefficient of inbreeding," which is intended to express the relation between the possible (maximum) number of different ancestors and the actual number of different ancestors, each individual being counted only once, no matter how many times it is mentioned in the pedigree.

The chief utility of such a coefficient is to show what approach to homozygosity of genetic factors has probably been made in the production of a particular individual, as a consequence of mating together related individuals among his direct ancestors, but this the coefficient of inbreeding can not do with great exactness because even with the closest possible inbreeding (self-fertilization) the approach to homozygosity in individual cases is quite a matter of chance. Thus, East and Jones say, forcefully and quite correctly, "The rate at which complete homozygosity is approached depends on the constitution of the individuals chosen. Theoretically in any inbred generation the progenitors of the next generation may be either completely heterozygous or completely homozygous or any degree in between, depending upon chance. The only condition which must follow in self-fertilization is that no individual can ever be more heterozygous than its parent, but may be the same or less. Thus it is seen that artificial inbreeding, as it is practiced, may theoretically never cause any reduction in heterozygosity, or it may bring about complete homozygosity in the first inbred generation. In other words the rate at which homozygosity is approached may vary greatly in different lines." . . . "Although nearly complete homozygosis is theoretically brought about by seven generations of self-fertilization, the attainment of absolute homozygosity is a difficult matter and in practice it may never be reached." . . . "Continued selective mating is necessary to bring about homozygosity. Intermittent inbreeding alternating with periods of outcrossing, which is the prevailing state of affairs with many organisms, cannot maintain any high degree of homozygosity." These statements show that the coefficient of inbreeding, though it appears to be very precise, like Galton's law of ancestral heredity, is subject to similar limitations. It indicates what is true of populations in the mass, but has small utility as an indicator of what happens in individual cases. When it is applied to the case of a particular Jersey bull it may be very much less reliable as an index of probable performance than the judgment of an experienced cattle breeder.

It is nevertheless of value to know what the tendency of a particular system of breeding is, if persistently followed, as regards homozygosity, for homozygosity implies fidelity to type in transmission and is probably what the animal breeder means by "prepotency," so far as he has any clearly defined idea in mind when he uses the term. Inbreeding tends automatically to replace heterozygous germinal conditions by homozygous conditions in the inbred population and the "closer" the degree of inbreeding the stronger is this tendency. Jennings has worked out formulæ for calculating the probable percentage of homozygosity in populations inbred after a particular system of matings for any number of generations. The results in three systems of matings for a series of from 10 to 25 inbred generations are shown in Table 32*a*. The progress toward homozygosis, it will be observed is rapid in self-fertilization, heterozygotes being only one-tenth of one per cent after 10 generations of inbreeding. The elimination of heterozygotes is equally rapid when

TABLE 32*a*

Probable Percentage of Homozygosity, under Different Systems of Inbreeding, in Populations at the Outset Entirely Heterozygous. (From Data of Jennings and Fish.)

Generations of Inbreeding	Self-fertilization, or Back-cross to the same Homozygous Parent	Brother-sister Matings	Generations of Inbreeding	Brother-sister Matings
1	50.00	50.00	12	94.31
2	75.00	50.00	13	95.40
3	87.50	62.50	14	96.28
4	93.75	68.75	15	96.99
5	96.87	75.00	16	97.56
6	98.43	79.69	17	98.03
7	99.22	83.59	18	98.40
8	99.61	86.72	19	98.71
9	99.80	89.26	20	98.96
10	99.90	91.31	21	99.15
11	....	92.97	25	99.64

back-crosses are made in every generation with the same homozygous parent race. In brother-sister matings, the next nearest degree of inbreeding, progress toward homozygosity is much slower, twenty-five generations of such matings accomplishing no more than eight generations of self-fertilization.

CHAPTER XXVII

HYBRID VIGOR OR HETEROSIS

Plants or animals which maintain normal size and vigor under self-fertilization or close inbreeding may nevertheless show an added vigor when outcrossed, that is when mated with individuals of races genetically different from their own. This is called heterosis, because it is supposedly due to *heterozygosis*, the cross-bred state of genetic factors. The mule has already been mentioned as a familiar example among animals, in which hybrid vigor is shown. Many similar examples are on record for hybrid plants. For example East and Hayes describe a cross between two different wild varieties of tobacco (*Nicotiana rustica brazilia* and *N. rustica scabra*) showing that reciprocal crosses produce F_1 plants taller than either parent variety. See Table 32*b*.

TABLE 32*b*

Variation in Height of Plants of *Nicotiana rustica brazilia* (349), of *N. rustica scabra* (352), and of their Reciprocal F_1 Hybrids

(*After East and Hayes*)

Variety or cross	Class centers in inches																		
	24	27	30	33	36	39	42	45	48	51	54	57	60	63	66	69	72	75	78
349	4	10	22	14	7	..	..	..	..	..	..	..	..	..	..	..	..	..	..
352	..	..	..	..	..	..	2	1	5	11	16	17	6	..	..	..	..	..	..
352×349, F_1	..	..	..	..	..	..	..	..	..	1	3	0	5	5	5	6	1	1	..
349×352, F_1	..	..	..	..	..	..	..	..	..	..	..	3	5	2	4	6	5	1	2

In maize, which is normally cross-fertilized and so maintained as a field crop in a state normally heterozygous, self-fertilization for a number of generations serves automatically to eliminate most of the heterozygosity (see Fig. 143) and consequently produces races of size and vigor less than

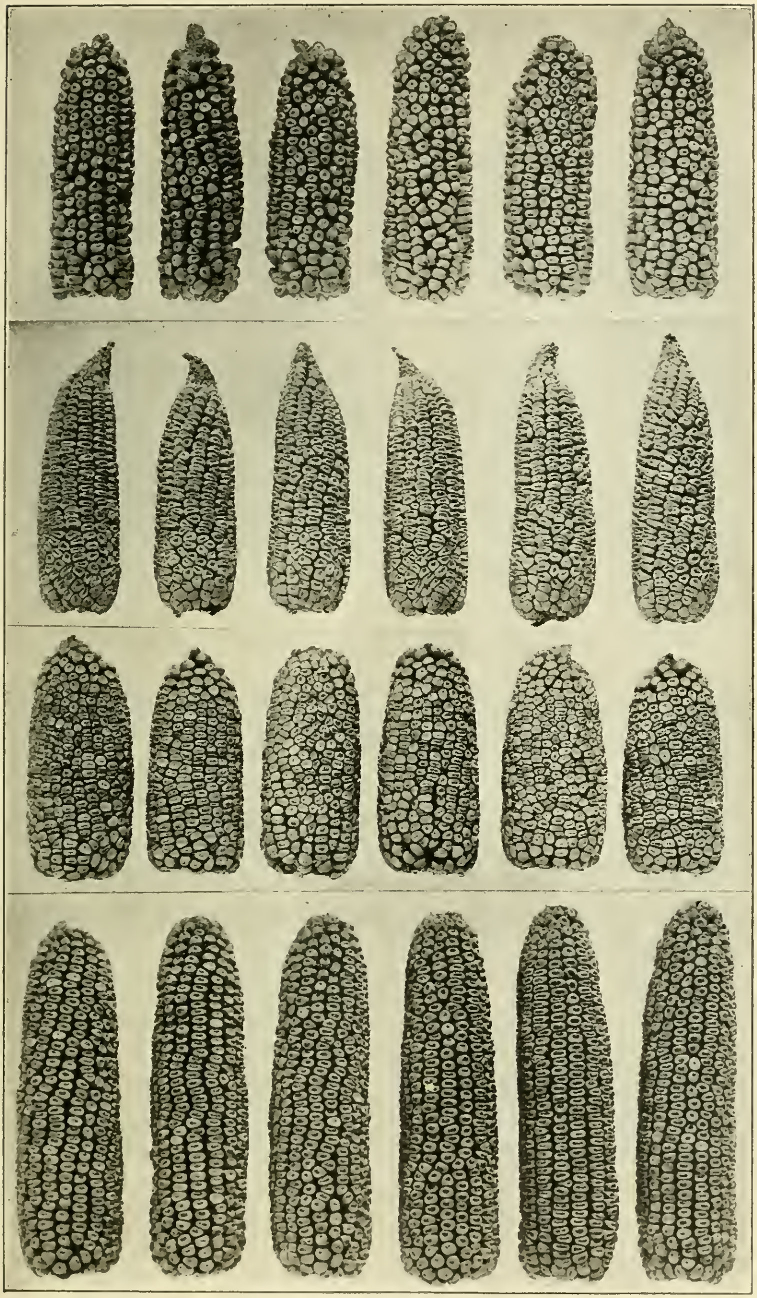

FIG. 144. Four characteristically different inbred strains of maize after eleven generations of self-fertilization. Note the remarkable uniformity of each strain. (After East and Jones.)

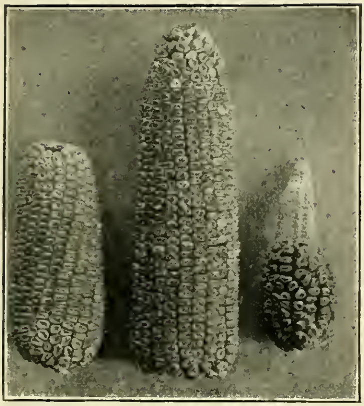

FIG. 145. Two ears of maize self-fertilized for six generations and between them an ear of their F_1 hybrid. (After East and Jones.)

FIG. 146. Two plants of maize self-fertilized for eleven generations, and between them, plants of their F_1 hybrid showing greatly increased size and productiveness.

FIG. 147. A field of maize showing remarkably uniform and vigorous plants, representing a first generation cross between two inbred strains. (After East and Jones.)

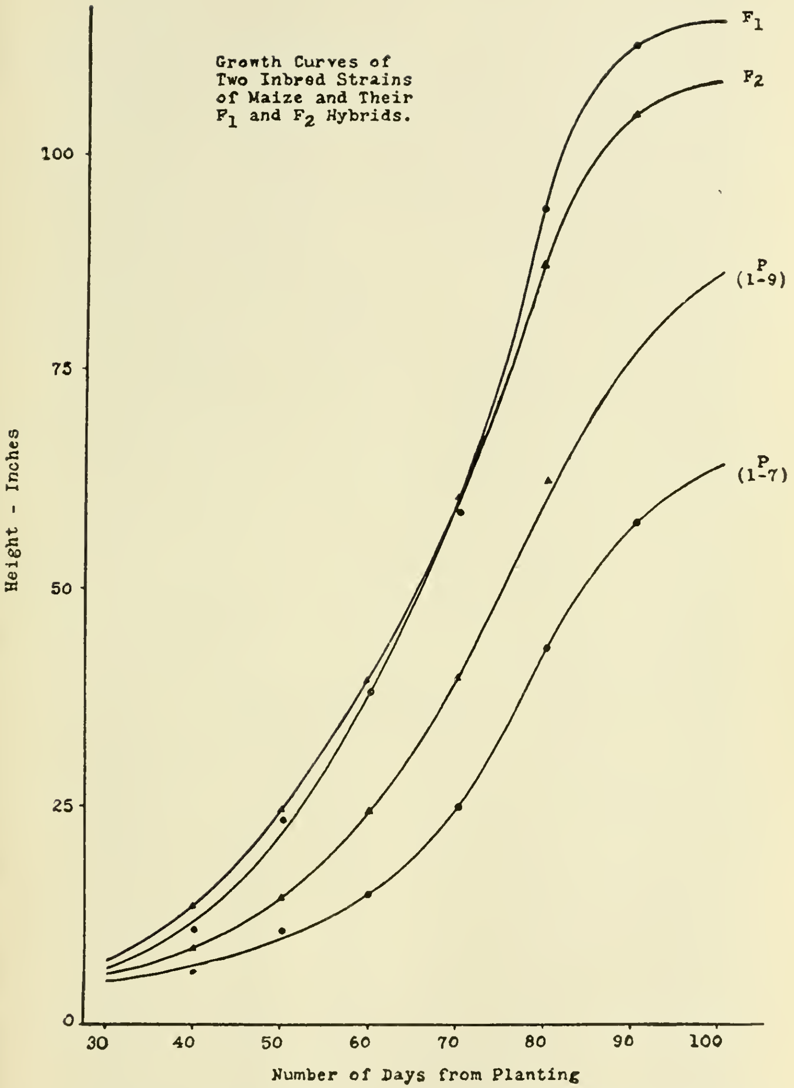

Fig. 148. Graphs showing growth curves of two inbred strains of maize, P (1–7) and P (1–9), and of their F_1 and F_2 hybrids. Note that both F_1 and F_2 are at all ages much taller than either inbred parent race, but that F_1 is considerably taller than F_2, as the plants approach maturity. (After East and Jones.)

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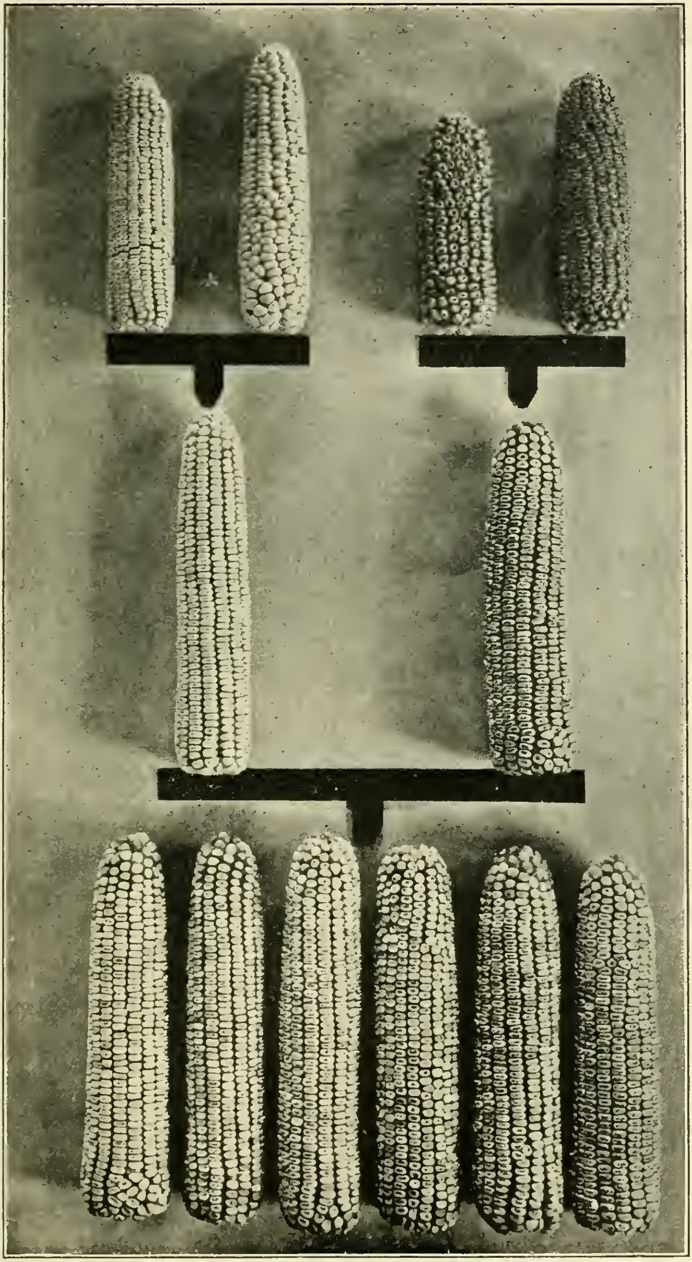

FIG. 152. Diagram showing a method of double crossing maize to secure maximum yield from seed plot and general crop. Four different inbred strains (shown in the top row) are crossed in pairs, producing the two vigorous but unrelated F_1 hybrids shown in the middle row. By crossing these with each other, an entire crop of F_1 seed of high productiveness is secured. (After East and Jones.)

normal but very uniform in character (Fig. 144). But if two of these inbred strains are crossed with each other a great increase in size results in F_1, which as it accompanies restoration of the original heterozygosis may reasonably be ascribed to its agency (see Figs. 145–147). If a second generation of the crossed corn is raised by planting seeds taken from F_1 plants, there is found to be a falling off in vigor (see Fig. 148). The F_2 plants start out well owing to the large amount of food materials stored in the plump F_1 seeds, but ultimately they fall behind F_1 plants in vigor of growth so that they attain a height considerably less, though still much in excess of the inbred parent races. This is in harmony with the view that heterosis is the cause of hybrid vigor, for heterosis should be at a maximum in F_1 and should decline in F_2 exactly as the height of the maize plants is seen to do in this cross. A case in which ordinary (blending) size inheritance is complicated by heterosis is seen in crosses made between *Cavia Cutleri* from Peru and races of guinea-pigs which we will call B and C. The growth curve of each of the parent stocks is shown in Fig. 149. In each case males are heavier than females except for the first few weeks of life when the females are heavier. Races B and C are nearly twice as heavy in adult weight as *Cavia Cutleri*.

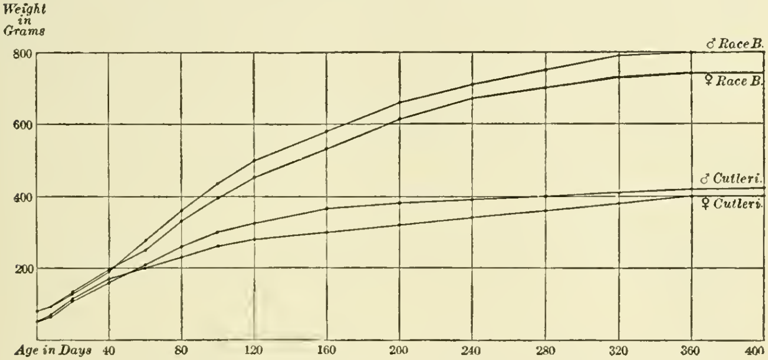

FIG. 149. Growth curves of race B guinea-pigs and of *Cavia cutleri.*

Growth curves of the F_1 and F_2 hybrids are shown in Figs.

150 and 151, where they can be compared with the growth curves of the respective parent races. In each case F_1 surpasses either parent race in size, but F_2 is intermediate between them. So far as heredity is concerned, the inheritance is blending, but F_1 shows an increase in size due to hybridization. It seems to be due not to heredity at all, strictly speaking, but to heterosis, and it begins to disappear as the F_1 hybrids are bred together producing an F_2 which theoretically is only half as heterozygous as F_1 (Table 32*a*). It might be expected to decline still more in later generations.

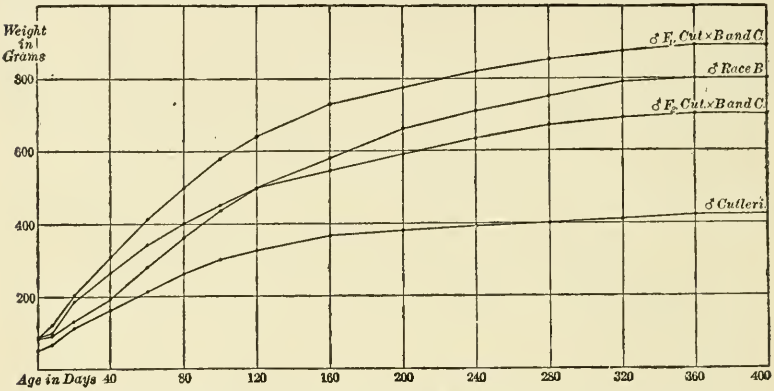

Fig. 150. Growth curves of race B and *Cavia cutleri* males and of their F_1 and F_2 male hybrids.

Animal breeders have long utilized the principle of heterosis in the production of mules and in the "grading" of cattle, hogs, and sheep for meat production. Plant breeders are likewise seeking to take advantage of this same principle for improving field crops in quantity, quality and uniformity of yield. In particular East and Jones have suggested the following novel methods of breeding maize. First, a standard variety should be inbred (self-pollinated) for several generations, in the course of which it will automatically resolve itself into a number of genetically different pure lines (Fig. 144). Any lines inherently weak will become extinct or may be discarded. Those which remain will contain the best combinations of genetic factors originally present in the variety, but will lack any vigor due to heterosis and so will be less productive than the original variety before it was inbred. It will accordingly not be profitable to propagate these pure lines as field crops, and further the amount of seed which they will yield if cross-pollinated will not be large. Hence to produce a large quantity of cross-bred seed will be expensive. But from a small number of F_1 plants a very large yield of F_2 seed might be obtained at small expense, since F_1 plants are extremely productive. The aim should be therefore to cross-breed F_1 plants. This can be done by securing four different inbred lines and crossing these in pairs, A with B, C with D. There will result two unrelated and vigorous F_1 groups, AB and CD which may now be planted in alternate rows. One of them, if detasseled, will be naturally pollinated by the other and consequently all the seed which it produces will be crossbred, representing combinations of factors found in AB with the allelomorphic factors in CD. Such seed, if planted, will produce a field crop of maximum yield, since all plants will be cross-bred F_1 individuals, though produced by F_1 plants. This last fact will keep down the cost of producing the seed because the yield will be heavy, half the total crop from the area planted (see Fig. 152).

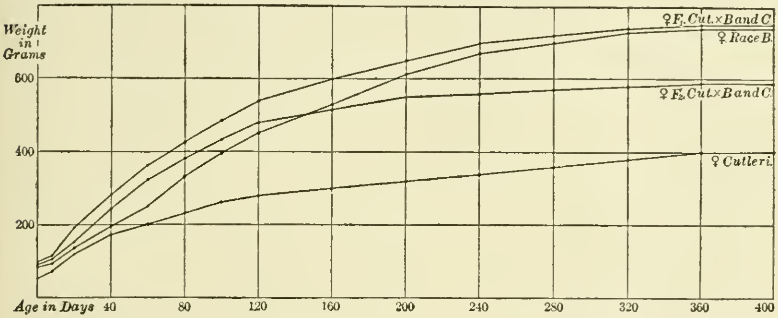

FIG. 151. Growth curves of race B and *Cavia cutleri* females and their F_1 and F_2 female hybrids.

CHAPTER XXVIII

GALTON'S LAW OF ANCESTRAL HEREDITY AND HIS PRINCIPLE OF REGRESSION

Galton (1889) was the first to recognize the distinction between alternative and blending inheritance. But he sought nevertheless to unify the two categories of cases and finally formulated in 1897 a generalized "law of ancestral heredity" which he believed would include both. In seeking such a general law of heredity he had studied a representative case each of blending and of alternative inheritance. The former was found in family statistics of human stature, the latter in the coat color of Basset hounds. The latter we should now describe as a case of Mendelian inheritance involving simultaneously white spotting, and a color pattern (bi-color). Stature inheritance is well described by Galton's term, "blending," but is now understood to involve multiple Mendelian factors whose action is cumulative.

In either case, Galton would have admitted that the entire inheritance is from the parents through the two gametes which unite to form the zygote, so that strictly speaking there is no inheritance from generations more remote than the parents. But he would have maintained quite correctly that a better idea can be had of what the gametes on the average will transmit, if one knows the character of several generations of ancestors than if one knows the character of the parents alone, and in this sense we may be said to inherit from ancestors more remote than our parents. Galton believed that the apparent influence of each generation of ancestors diminished as its remoteness increased, each more remote generation having only half the influence of the next later one. In his own words: "The two parents contribute between them, on the average, one-half, or (0.5); the four grandparents, one-quarter, or $(0.5)^2$; the eight great-grandparents, one-eighth, or $(0.5)^3$, and so on. Thus the sum of the ancestral contributions is expressed by the series $(0.5) + (0.5)^2 + (0.5)^3$, etc.] which being equal to 1, accounts for the whole heritage."

If one attempts to make use of this law by basing upon it predictions as to the character of the offspring in particular kinds of matings, it works fairly well when blending characters are under consideration, but fails completely when ordinary Mendelizing characters are under consideration. See Castle (1903). As a useful generalization it is now pretty generally discredited.

Regression was a name given by Galton to the apparent *going back* of offspring from the condition of their parents toward that of more remote ancestors, or more correctly toward *the general average of the race.* Thus he observed that very tall parents have children *less* tall than themselves, while very short parents have children *taller* than themselves. In either case the children regress toward the general average of the race, and the regression is greater the more pronounced the deviation of the parents from the general average of the race. Also in sweet peas, Galton observed that when very large seeds are planted, the crop harvested averages smaller in size than the seeds planted; and that when small seeds are planted, the crop averages *larger* in size. Regression occurs in both cases toward the mean of the race. Galton regarded regression as a feature of ancestral heredity; but Johannsen has shown, as regards size of beans, that regression is due to a lack of agreement between somatic and genetic variations, the latter being more conservative, and that when selection is made within a line pure genetically, no regression occurs. Davenport confirms this view in the case of human stature, showing that the children of parents genetically pure for tall stature do not regress toward mediocrity, as Galton supposed all classes of a population to do. Galton's law of ancestral heredity and his principle of regression are now chiefly of historical interest, but it is well to keep them in mind when generalizations based on similar reasoning are brought forward. (See Chapter XXVI.)

CHAPTER XXIX

SEX DETERMINATION

Certain facts presented in an earlier chapter show that there is a close connection between sex-linked inheritance and sex determination, since only male-determining gametes or only female-determining gametes are able to transmit sex-linked characters in particular crosses. We must now consider more fully the facts and theories of sex determination. In all the higher animals and plants a discontinuous variation occurs as regards sex, every individual being either male or female. The distribution of males and females in successive generations presents many analogies with Mendelian inheritance. This idea occurred to Mendel himself, as is shown in his posthumously published letters. Bateson suggested it independently in 1902, and this idea was more fully elaborated by Castle (1903). The view is now generally accepted that a factor concerned in sex determination is in all the higher animals and plants inherited in accordance with Mendel's law. What in such cases is the distinction between male and female individuals?

The essential difference between a female and a male individual is that one produces eggs, the other sperm. All other differences are secondary and dependent largely upon the differences mentioned. If in the higher animals (birds and mammals) the sex glands (*i. e.*, the egg-producing and sperm-producing tissues) are removed from the body, the superficial differences between the sexes largely disappear. In insects, however, the secondary sex characters seem to be for the most part uninfluenced by presence or absence of the sex glands. Their differentiation occurs independently, though simultaneously, with that of the sex glands, evidently depending on the genetic (chromosome) constitution of the cells in each part of the body. When the constitution of cells

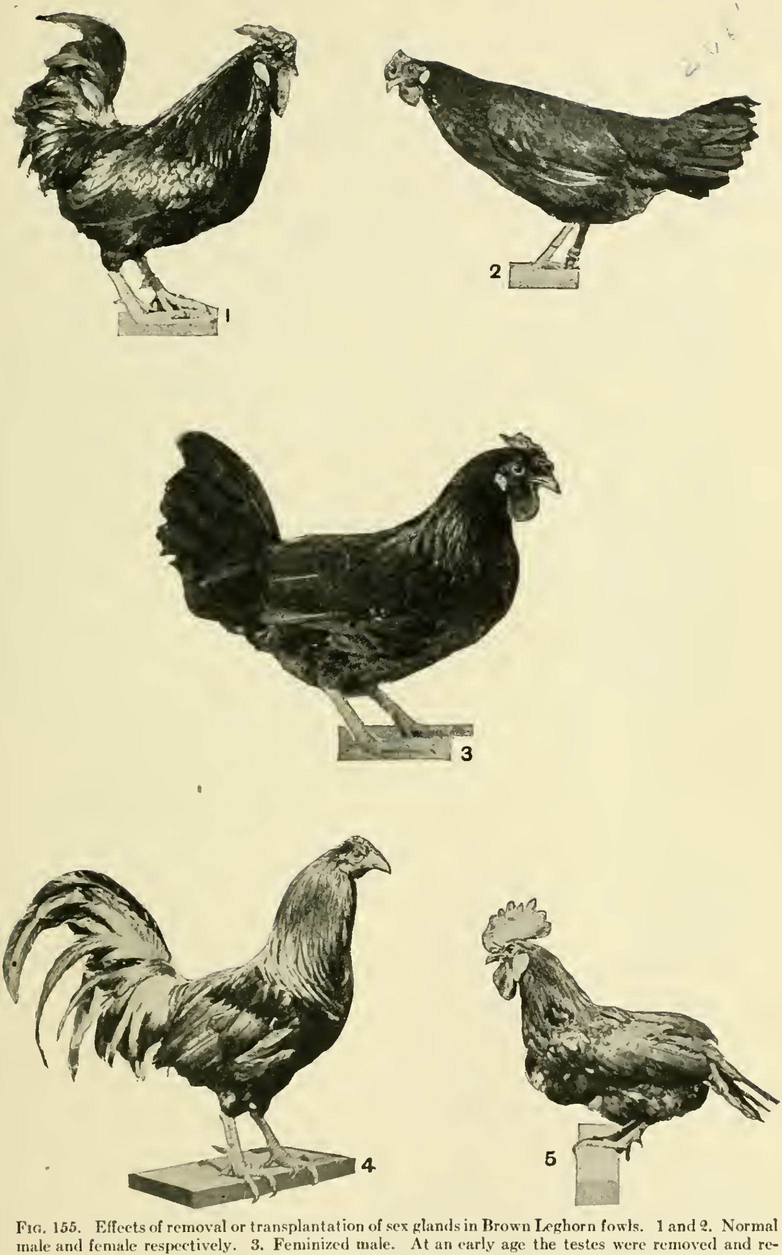

FIG. 155. Effects of removal or transplantation of sex glands in Brown Leghorn fowls. 1 and 2. Normal male and female respectively. 3. Feminized male. At an early age the testes were removed and replaced by ovaries. 4. Castrated male, three years old. Notice undeveloped comb and wattles, but characteristic male hackle feathers, tail feathers and spurs. 5. Castrated female. Notice well-developed comb and wattles but characteristic female plumage. (After Dr. H. D. Goodale.)

in different parts of the body differs in respect to sex-linked characters, a sex-mosaic results known as a gynandromorph. Morgan and Bridges have made an exhaustive study of such mosaic individuals found in their cultures of Drosophila. One of the simplest types, a bilateral sex-mosaic, is shown in Fig. 153. The right half of this fly shows male characters, viz., shorter wing, black-tipped abdomen, sex-comb on first leg. The left side of the fly shows the contrasted female characters. The right eye was also white, a character inherited in the single X-chromosome derived from the white-eyed mother of the fly. The left eye was red resulting from the presence (in the female part of the body) of an X-chromosome bearing red-eye, derived from the red-eyed father, which is dominant over the white-eye borne by the X-chromosome furnished by the mother.

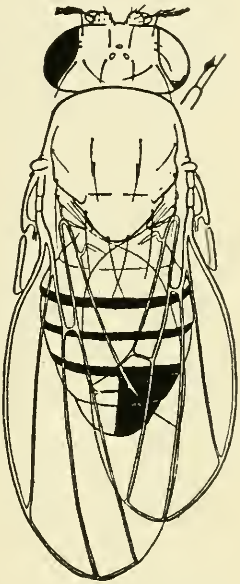

FIG. 153. A sex-mosaic, or gynandromorphic, Drosophila. The right half of the body shows male characters, viz. comb on first leg, short wing, and black-tipped abdomen. The left half of the body shows female characters, viz. long wing and light-tipped abdomen. Note also that the right eye was white, the left eye red. See text. (After Morgan.)

Three different explanations have been offered in recent years for the origin of sex-mosaic insects. These are expressed diagrammatically in (Fig. 154). The first, A, was offered by Boveri. It suggests that an egg which has undergone maturation, and which accordingly retains a single X-chromosome may, on account of delayed fertilization, undergo nuclear division before fertilization is complete, so that it becomes binucleate before fusion of egg and sperm nuclei has occurred. The sperm now fuses with one of the egg's two nuclei. That nucleus and its descendants will be 2X (female), but the unfertilized nucleus, if it develops by itself will be X (male). A body mosaic as to sex will result, part male, part female. The case shown in (Fig. 153) could be accounted for on this hypothesis, but many other cases in Drosophila cannot, for which reason Morgan and Bridges favor a different explanation. B and C (Fig. 154) are explanations of sex-mosaics offered at different times by Morgan. In B it is supposed that two sperms have entered the egg, one of which united with the egg-nucleus and produced a female (2X), hybrid as to sex-linked characters, the other developing by itself produced male parts showing only characters of the father. This explanation evidently will not fit the case of (Fig. 153) because the male side of the fly inherits from the *mother*, not the father. An alternative explanation, C, is offered by Morgan for such cases as this. It is supposed that the egg has been normally fertilized but that in a division of the fertilized nucleus, one division product of an X-chromosome gets left behind at the middle of the spindle. Thus one daughter nucleus gets two X-chromosomes (female) and the other only one (male). Whether the male part shows maternal or paternal characters will depend on which X-chromosome (maternal or paternal) was eliminated. Explanation C is thus an alternative to A for cases in which the male part of the mosaic shows maternal characters, and it also affords an explanation (alternative to B) of cases in which the male part of the mosaic shows paternal characters.

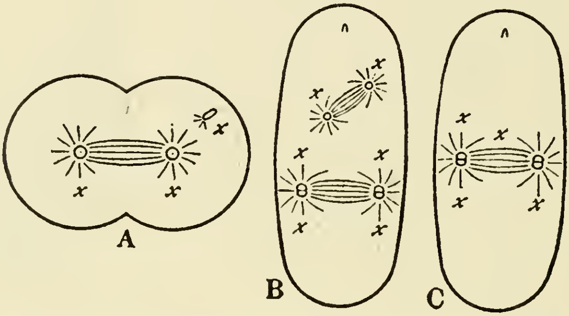

Fig. 154. Three different explanations which have been offered to account for the production of gynandromorphs (sex-mosaics or sex-intergrades) in Drosophila. See text. (After Morgan.)

In contrast to the case of insects, the dependence of secondary sex differences in mammals and birds upon the presence of the gonads acting through secretions (hormones) is clearly shown by the experimental work of Steinach and Goodale. The former castrated immature male rats and guinea-pigs and then introduced into the bodies of the castrated males ovaries of the female of the same species. The transplanted ovaries became established and caused remarkable changes in the castrated animals. Their mammary glands, which are rudimentary in the male, became greatly enlarged. The body remained small as in females and the fur soft. Their behavior too was more like that of females than of males.

Goodale (1916) performed a similar experiment on male brown Leghorn chicks with like results. (See Fig. 155.) Goodale (1911[a], 1913) found also that mere removal of the ovaries from female birds (hens and ducks) causes them to assume, to a considerable extent, the quite different appearance of males and that castrated males fail to develop many of the normal male characteristics. It is accordingly clear that some secretion of the ovary normally acts as an inhibitor against the development of male plumage in birds, and that in males a secretion of the testis is necessary for full development of the secondary sex characters.

Morgan has shown that what in female fowls acts as an inhibitor to the development of male plumage is not a secretion of the egg-cells proper but a secretion of certain "luteal cells" normally present in the ovary. He finds that in Sebright bantams, which breed has hen-feathered males, "luteal cells" are present in the testis of males as well as in the ovary of females. Consequently when Sebright bantam males are castrated they become "cock-feathered," that is they grow the long tail-feathers and the hackle feathers characteristic of males in other breeds of fowls. In crosses of Sebright bantams, in which the cocks are hen-feathered, with black-breasted game bantams, in which the cocks are normal, Morgan found that hen-feathering behaved as a non-sex-linked dominant character probably involving two distinct genetic factors.

To recapitulate, we have in fowls this relationship of plumage and other secondary sex characters to the gonads or their secretions. Fowls of both sexes will develop the same plumage characters, viz., the full plumage of normal males, if no secretions interfere. In females such an inhibiting secretion is normally produced by luteal cells present in the ovary, and in hen-feathered males luteal cells in the testis produce a similar secretion. If luteal cells are introduced into castrated males (in transplanted ovaries) the birds become hen-feathered. Likewise if the luteal cells are removed (with the ovary) from a female, she becomes "cock-feathered." If the luteal cells are removed (with the testes) from a hen-feathered cock, he becomes cock-feathered. Hence "hen-feathering" in either sex is due to the secretion of luteal cells, not to the sex-cells proper. But the developed condition of comb and wattles normally seen in males is due to a different secretion formed by the testis. For this condition disappears in castrated males and is not attained in feminized males into which ovaries have been introduced.

In male sheep a secretion of the testis seems to act as a stimulant to horn development, for male sheep regularly have larger horns than females (Fig. 97) and in some breeds, for example the merino, males only have horns. (See Figs. 101 and 103.) Early castration of the male in such breeds results in hornlessness.

Finally Lillie (1916) has shown that in cattle hormones in the blood of the developing male, if allowed to enter the circulation of the developing female, so interfere with the growth of the ovary as to render its possessor sterile. This is the explanation of the "free martin," a sterile female calf born as a twin to a male calf. The twins in this case begin their development, each from a separate fertilized egg, but become later so closely crowded together in the uterus of the mother that their foetal blood vessels unite, allowing the blood from one embryo to pass freely over into the other. A sterilizing influence on the female results, the ova in the body of the female embryo failing to grow, but no reciprocal influence on the male has been noted, nor is the sex of the female changed but merely her sexual development repressed.

An interesting case of sex control through secretions has recently been discovered in a mollusk, Crepidula. The individuals of this species normally function as males when they are small, at that time developing sperm, but when grown to larger size they develop eggs and function as females. Since eggs and sperm are not developed simultaneously in the same individual, the eggs are regularly cross fertilized. Gould has shown that if a small Crepidula is isolated from other individuals it remains a "neuter," but that if it is brought within a few millimeters of a large (female) individual, it proceeds to develop as a male and liberates sperm. The action is supposed to result from substances given off into the sea water from the body of the nearby female. As the individuals of Crepidula remain in one place practically throughout their adult life, this curious adaptation has manifest advantages to the species.

The egg or larger gamete (the so-called *macro-gamete*) in all animals is non-motile and contains a relatively large amount of reserve food material for the maintenance of the developing embryo. This reserve food material it is the function of the mother to supply. In the case of some animals, for example flatworms and mollusks, the food supply of the embryo is not stored in the egg-cell itself, but in other cells associated with it, which break down and supply nourishment to the developing embryo derived from the fertilized egg. Again, as in the mammals, the embryo may derive its nourishment largely from the maternal tissues, the embryo remaining like a parasite within the maternal body during its growth, feeding by osmosis. But in all cases alike the mother supplies the larger gamete and the food material necessary to carry the zygote through its embryonic stages. The father, on the other hand, furnishes the bare hereditary equipment of a gamete, with the motor apparatus necessary to bring it into contact with the egg-cell, but without food for the developing embryo produced by fertilization. The gamete furnished by the father is therefore the smaller gamete, the so-called *micro-gamete.*

From the standpoint of metabolism, the female is the more advanced condition; the female performs the larger function, doing all that the male does in furnishing the material basis of heredity (a gamete), and in addition supplying food for the embryo. As regards the reproductive function, the female is the equivalent of the male organism, plus an additional function, — that of supplying the embryo with food. When we come to consider the structural basis of sex, we find, often in differences in chromosome number, reasons for thinking that here, too, the female individual is the equivalent of the male plus an additional element.[1] The conclusion has very naturally been drawn that if a means could be devised for increasing the nourishment of the egg or embryo, its development into a female should be thereby insured, while the reverse treatment should lead to the production of a male.

In a few cases it has been found possible by indirect means to control the state of nutrition of the eggs and so to control the sex of the individual which develops from it. Thus in the rotifer, Hydatina senta, parthenogenetic eggs of two sorts are produced, which are either male-producing or female-producing, the former being smaller. Whitney has shown that when a colony of Hydatina is fed for a generation exclusively on the green flagellate, Dunaliella, practically all the mothers lay male-producing eggs, but a continuous diet of the colorless flagellate, Polytoma, leads to the production of female eggs. The effect in each case is seen not in the first generation, but in the second generation of offspring. The female fed on Dunaliella has *grandsons;* the female fed on Polytoma has *granddaughters.* The diet of the mother is immaterial.

In pigeons, eggs are produced in clutches of two each, and in wild species these commonly develop, one into a male, the

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[1] But in the poultry type of sex-linked inheritance it is evident that the male is more liberally equipped with certain genes, in which he is duplex while the female is simplex.

other into a female. Riddle has shown that the female-producing egg is the larger of the two and contains the larger amount of potential chemical energy. If the eggs are removed from the nest as fast as laid, the female is induced to lay a larger number of eggs than she would otherwise have laid and the majority of these are female-producing. Toward the end of the season nothing but females may come from eggs the production of which is forced in this way.

In such cases sex is subject to a certain amount of control through the state of nutrition of the egg itself. But, neither in this case nor in that of most other animals is the state of nourishment of the single eggs directly affected by nourishment of the mother.

In certain cases (Daphnia) poor nutrition of the mother may diminish the number of eggs which she liberates, without increasing the proportion of males among the offspring produced, since nourishment of the individual egg is not lessened, for the eggs under such circumstances resort to cannibalism, devouring one another, and those which survive are fully nourished.

Attempts to influence the sex of an embryo or larva by altered nutrition of the embryo or larva itself have proved equally futile. Practically the only experimental evidence of value in favor of this idea has been derived from the study of insects, and this is capable of explanation on quite different grounds from those which first suggest themselves. It has sometimes been observed, as by Mary Treat for example, that a lot of insects poorly fed produce an excess of males. In such lots, however, the mortality is commonly high, and more females die than males, because the female is usually larger and requires more food to complete her development.

A delayed fertilization of the egg has in certain cases, notably frog's eggs, been shown to increase the percentage of male offspring. This is not due to any change in the spermatozoa, as experiment clearly shows, but merely to the relative staleness of the egg. If the fertilization of the frog's egg is delayed three or four days after its passage into the uterus, more male offspring occur. It is possible that the chemical composition of the egg changes when fertilization is delayed, the total energy content decreasing and so diminishing the probability that the egg will develop into a female. Riddle's work with pigeons suggests such an interpretation.

Further frog's eggs may by various means be caused to develop parthenogenetically. Loeb (1918) has raised twenty leopard frogs from unfertilized eggs artificially stimulated into development by the prick of a needle. Among these frogs both sexes were represented and the chromosome number was found to be diploid. Accordingly sex differentiation in this case would seem not to have depended upon chromosome reduction of the ordinary sort. Again King (1912) has shown that keeping toad's eggs out of water for several hours after fertilization raises the percentage of female young from fifty to over seventy. Hence it may be, as Riddle thinks, that the natural sex tendencies of the gametes may under certain conditions be overbalanced or counteracted by other agencies influencing metabolism, the eggs perhaps developing parthenogenetically without passing into the haploid chromosome state of ordinary gametes.

What are we to understand by the expression, "natural sex tendencies of the gametes"? Obviously what is meant is the genetic constitution of the gametes, that is their content of genes. But we have seen that strong reasons exist for believing that genes are found exclusively in the chromatin. If this is so, "natural sex tendencies of the gametes," can mean only composition of the gametes as regards chromatin. One of the most important generalizations reached in recent years by cytologists is this, that the chromatin composition of the gamete does in reality determine its natural sex tendencies.

In a great many animals, possibly in all, the chromosome composition of the individual's cell-nuclei bears an interesting relation to its sex. Thus in bees, ants, wasps, and related insects, as well as in small crustacea and rotifers, only females develop from fertilized eggs, *i. e.*, from zygotes, whereas males develop from unfertilized eggs which have the nuclear constitution of gametes, and which, in some cases at least, are capable of actually functioning as gametes. It would seem that in such cases the female must have a *duplex* chromosome composition, since two gametes have united to produce it, whereas the male can be only *simplex*, since he represents a developed gamete.

The case of the honeybee affords a familiar example. The mother bee, or "queen" of the hive, lays eggs which are capable of development either with or without fertilization. The mother is able to produce or to withhold fertilization according to circumstances, for she has in a sac connected with the oviduct a supply of sperm received at mating. The eggs pass the outlet of this sac as they are laid. The outlet of the sac is controlled by muscles which relax when an egg is to be fertilized, permitting sperm to come in contact with the egg, but closing the outlet tightly when the egg is not to be fertilized. Fertilized eggs are laid in cells of the regular size in the wax comb, but unfertilized eggs are laid only in cells of a larger size known as drone cells. The fertilized eggs develop into females, even if they are moved from ordinary cells to drone cells; but the unfertilized eggs produce males, even if they are transferred to cells of ordinary size, in which case, however, they will become small-sized drones because of the limited amount of space in which they complete their growth. Fertilized eggs developing in cells of ordinary honeycomb size produce female bees with imperfectly-developed sex organs, known as workers. They are the individuals that gather honey and pollen and feed the young of the colony. A fertilized egg, which produces a larva that receives special care and nourishment and develops in a cell of unusual size, gives rise to a *queen*, a fully developed female capable of mating and laying great numbers of eggs, but without the structural peculiarities or instincts of workers. From these facts it will be clear that, in the bee, fertilization determines sex, though environment (size of cell, food of the larva) may determine many other characteristics of the individual. As regards their origin, the female is a zygote produced by the union of two gametes, the male is derived from a gamete developing by itself. So far as chromosome constitution is concerned, the female is duplex, the male simplex.

In small crustacea, and rotifers, the case is slightly different. The female here, too, is duplex and the male simplex, but the conditions of their origin are less simple, for the mother here produces three different kinds of eggs. The first kind never passes into the simplex state of ordinary gametes, but retains the duplex number of chromosomes, omits the reducing cell-division, and begins development at once unfertilized and duplex. It forms a female, like the mother in all respects. The other two types of eggs undergo reduction and pass into the condition of gametes, with the simplex chromosome number. They differ in size. The smaller-sized egg develops unfertilized into a male (simplex) individual, which forms simplex sperm just as the male bee does, by omitting a reduction division in spermatogenesis. The larger-sized egg (winter egg) is incapable of further development without the stimulus of fertilization. When fertilized, it develops into a female individual, since in consequence of fertilization it contains the duplex chromosome number.

The cases of bee and rotifer agree in this, that the female regularly has the duplex chromosome condition, the male the simplex condition, a difference completely parallel with that between *Oenothera Lamarckiana* (which has fourteen chromosomes) and its mutant *gigas* (which has twenty-eight).

In plant lice the difference between the sexes as regards chromosome number is not so great. Here the female merely has one or two chromosomes more than the male, recalling the mutant *Oenothera lata*, which has one more chromosome than the parent species, *Lamarckiana*. The male however in plant lice develops from an unfertilized egg, *partially* reduced in chromosome number. The female arises either from an egg *unreduced* and so with the full duplex number of chromosomes, and which develops without fertilization into a female, or from a reduced egg (a true gamete) which has been fertilized and thus brought back to the duplex condition.

If one were inclined to be facetious, he might say that in all these lower animals, *duplicity* is synonomous with femaleness, *simplicity* with maleness!

It should be noted in passing that among plants as well as among animals, an unfertilized gamete may undergo multiplication and growth while in the simplex, reduced condition. The ordinary fern plant is a zygote with a duplex chromosome number. But it produces reproductive cells (spores) containing the reduced (simplex) chromosome number, and these after growing into a small inconspicuous little plant, known as a prothallus, produce the functional gametes (egg and sperm-cells) without further reduction. Union of these, egg with sperm, produces duplex zygotes again, which develop into the ordinary fern plant.

In many animals in which males and females alike arise from fertilized eggs, there occurs nevertheless a difference in chromosome number between males and females, the female always containing the higher number, as in the parthenogenetic plant lice. One of the best-known cases is that of the common squash bug, Anasa tristis, first worked out by E. B. Wilson, but since fully confirmed by the observations of others. In this animal the body-cells of the female contain twenty-two chromosomes, those of the male twenty-one. Historically this is a famous case, the first one in which the mechanism of sex determination was definitely ascertained. The egg, according to Wilson, always undergoes reduction to the simplex chromosome number, eleven. But reduction in the male is less simple because the male contains an odd number of chromosomes, viz., twenty-one. All the sperm cells cannot receive the same number of chromosomes at the reduction division, unless the odd chromosome splits, but this it refuses to do. The division occurs into cells with eleven chromosomes, and those with ten. Both metamorphose into sperm cells. The 10-chromosome sperm cells, if they fertilize an egg, cause it to develop into a male, since Egg 11 + Sperm 10 = 21, the number characteristic of the male. But the 11-chromosome sperm fertilizing an egg causes it to develop into a female, since Egg 11 + Sperm 11 = 22, the female number. The first man to suggest a relation between the odd chromosome and sex determination (McClung) supposed of course that the extra chromosome must go to produce a male, the more important sex, and he called it a *male sex-determining chromosome*, but it turned out otherwise. The extra chromosome is really a *female* sex determinant. When a difference exists between the sexes in chromatin content, it is regularly the female that has the larger supply. The significance of this we may inquire into further.

In some cases, several of which are described by Morgan, the number of chromosomes is found to be the *same* in both sexes, but one of the chromosomes in the female is regularly *larger* than the corresponding chromosome in the male. This indicates that the female, in this case also, contains some chromosome element not found in the other sex.

But Wilson and his pupils have shown that in species in which the female contains two X-chromosomes and the male one such chromosome, a new chromosome may appear in the male, a so-called Y-chromosome, which the female does not normally possess. What its precise function is has not yet been ascertained.

Finally, in many animals no difference has been detected between the chromosome composition of the two sexes, but this does not preclude the existence of such a difference, even though it has not yet been discovered.

To summarize the foregoing, there are many known facts which support and none which contradict the idea that the female has a greater chromatin content than the male and, either by reason of this fact or independently of it, has greater anabolic activity in reproduction, producing macro-gametes, gametes stored with food. Micro-gametes, those not stored with food but generally possessed of locomotive ability, are the distinctive product of males.

Morgan (1913) assumes that the chromatin element, which occurs in the female but not in the male, is the specific cause of femaleness, that is, of egg production, and so speaks of the odd chromosome (when this occurs) as a sex-chromosome, or an X-chromosome. But a moment's reflection will show (as Morgan himself once suggested) that *quantity* of such substance may be quite as influential as quality in determining sex, since by hypothesis *one* X-chromosome produces a male and *two* X-chromosomes a female, in species such as the squash bug. The essential thing in sex determination is probably not so much the possession of some particular sort of material as the attainment of a particular grade of anabolic capacity, femaleness implying a higher grade than maleness, since in the former condition macro-gametes are produced, whereas in the latter micro-gametes are produced.

That maleness and femaleness are only different grades of reproductive capacity is indicated by a study of organisms in which the two functions are combined. In many of the lower animals and in most of the higher plants, the same individual is capable of producing both macro-gametes and micro-gametes. Sometimes these are produced simultaneously but in separate gonads, as in flatworms and leeches among animals, and in "perfect" flowering plants. Such parents are true and simultaneous hermaphrodites. Sometimes the individual may function at first as a male and later as a female, a condition known as successive hermaphroditism. This is found in certain worms and mollusks and in the prothallia of certain ferns and mosses. This condition is also approached in flowering plants such as cucumbers, melons, and squashes, which at first produce only male blossoms but later produce those of both sexes. In other cases the individual may function *chiefly* as of one sex but partially as of the other sex. This condition is found in polygamo-dioecious plants and exceptionally in such animals as crayfish, mollusks, worms, and even frogs and fishes, which, in a particular part of an ovary may develop sperms, or in a particular part of a testis may develop eggs.

Such facts as these indicate that maleness and femaleness are merely different grades of one and the same form of reproductive activity. This is not inconsistent with their behavior as Mendelian alternatives in heredity, for in color inheritance different grades of pigmentation, of spotting, etc., frequently behave as Mendelian allelomorphs. So probably different degrees of sexual distinctness behave in heredity, for in the plant, Lychnis, Shull has shown that femaleness is allelomorphic not only with maleness but also with hermaphroditism, the three conditions being triple allelomorphs. A similar interpretation may perhaps be given to conditions found in certain mosses as discussed by Collins.

PART II

EUGENICS

CHAPTER XXX

HUMAN CROSSES

MANKIND consists of a single species; at least no races exist so distinct that when they are crossed sterile progeny are produced. The widest possible human crosses are comparable with the crossing of geographical varieties of a wild species of animal, or with the crossing of distinct breeds of domesticated animals. The race horse and the draft horse differ as much in bodily conformation and temperament as do the most diverse races of mankind.

Offspring produced by crossing such races do not lack in vigor, size or reproductive capacity. But these are not the only qualities which we desire either our horses or our citizens to possess. It is a *particular combination* of qualities which makes a race horse useful, and a different combination which makes a draft horse useful. Crossing the two will produce neither one type nor the other. The progeny will be useless as race horses and they will not make good draft horses. A second generation of offspring will be more variable but will rarely approach the specialized type of either the race horse or the draft horse, and will be too heterogeneous in character to serve any single purpose well. For such reasons as these, pure breeds of domesticated animals are rarely crossed unless a new type of animal is desired to meet special needs and conditions. Even then many animals of small value must be produced and discarded and this process must be continued for generations before the new type can be established. For such reasons wide racial crosses among men seem on the whole undesirable. There is no question about the physical vigor of the offspring, provided the parents are free from disease. The statement is often made that mixed races are feeble, but if this is ever true it is not because they are mixed, but because the specimens that mix are feeble. Mating out of the race, when mates within the race are available, is *prima facie* evidence that the individual so mating is a social outcast. It is not surprising that the progeny of such individuals are sometimes feeble. If the parents were diseased, licentious, or feeble-minded, it is natural that the children should be of like character.

Of course not all racial crossing implies such conditions. Frequently Europeans, when pioneers in a new country and without mates of their own race, have married native women. Such men have not always been social outcasts; frequently they have been men of great energy, ability, and courage both physical and moral, and free from disease. When, in such cases, the mothers belonged to a race with capacity for civilization, the results have been good. Examples may be found among the Indian citizens of our southwest states. But human racial crossing in general is a risky experiment, because it interferes with social inheritance, which after all is the chief asset of civilization. Physically and also intellectually, according to Professor Osborn, we are no whit superior to the men of twenty-five thousand years ago. All the advantage which we have over them lies in the accumulated experience of the human race since then.

All this we as individuals learn from our mothers and fathers, or in the schools, the churches, the markets, or the courts of justice. Wide racial crosses unsettle the foundations of these agencies of enlightenment. At times it is necessary that some of these agencies be disturbed in order that we may lay their foundations deeper and broader, but racial crossing leads rather toward the discarding of all foundations of civilization than to improving them.

Such crosses, therefore, as of Europeans with Asiatics or Africans can not be recommended as agencies for the improvement of the human race. Physically Europeans on one hand and Asiatics or Africans on the other, are sufficiently diversified among themselves to allow the maximum benefit from intercrossing, without resorting to crosses with a distinct branch of the human family. Socially the effects of such crosses on a large scale are too disturbing to be recommended. This country has seen a sufficiently extensive experiment of that sort in its southern states, the outcome of which we shall not know fully for several generations yet. It is desirable that each nation should have the fullest intercourse with every other in commerce and in the exchange of ideas. This is mutually beneficial to all, but the obliteration of all racial differences within the human family is not to be expected or desired.

What has been said thus far refers only to crosses between the widely separated branches of the human family and even as regards such cases may be accepted with reservation, since there is room for a difference of opinion concerning such matters, which are not primarily biological, but sociological.

What opinion one holds will also depend upon his point of view. From the viewpoint of a superior race there is nothing to be gained by crossing with an inferior race. From the viewpoint of the inferior race also the cross is undesirable if the two races live side by side, because each race will despise individuals of mixed race and this will lead to endless friction. About the only conditions under which a racial cross of this sort could be fairly tested would be those under which Pitcairn Island was populated. Here more than a century ago a few English sailors and a few Polynesian women founded a population still in existence and flourishing. Neither pure race was present to create social distinctions or racial antipathy. The story of this hybrid human race is a romantic one.

In the year 1788 the Englishman, John Bligh, who as sailing master had been round the world with Captain Cook on his second voyage, was commissioned by the British Government to go to Tahiti, secure plants of the bread-fruit tree and introduce them into the West Indies. To this end he was given command of the ship *Bounty*. Bligh proved a harsh and oppressive captain, and on his way from Tahiti to Jamaica the crew mutinied. They put the captain with eighteen of his crew into the ship's launch and themselves turned back to Tahiti. The captain and his companions after three months of hardship all reached land (Timor, three thousand six hundred miles from where they started) safely, and were taken back to England. The British Government sent out a warship to punish the mutineers and part of them were captured on Tahiti. But their leader and nine other sailors had already escaped to Pitcairn Island in company with eighteen natives, six men and twelve women. Their place of refuge remained a secret for twenty years, when it was accidentally discovered by an American sealing ship which visited the island in 1808. Pitcairn Island is the southernmost island of the Low Archipelago in latitude 25° S. and longitude 180° W. It is about two miles long and one mile wide, and consists of a mountain surrounded by coral reefs. For ten years after the landing of the refugees, disorder and lawlessness prevailed. In 1808 the sole survivors were one Englishman by the name of John Adams (formerly Alexander Smith), eight or nine women, and several children. It is related that the elements of disorder being removed Adams instilled ideas of morality and religion into the others, with the result that the settlement prospered. In 1815 when the ship *Britain* visited the island, the captain was impressed with the peace and good order prevailing. In 1839 the island became a British dependency. In 1855 the number of inhabitants had increased to two hundred and the island was becoming too small for them. They therefore petitioned the British government to be removed to Norfolk Island, which was done the following year. Since then some of them have returned to Pitcairn Island whose present population is about one hundred and twenty-five. The population of Norfolk Island in 1901 was eight hundred and seventy, mostly descendants of the Pitcairn Islanders.

Here then on these two islands is a race of probably one thousand persons at the present time, originated more than a century ago by a cross between English men and women of Tahiti. The experiment has gone far beyond the F_1 generation and would afford unique material for a study of the effects of race-crosses uncomplicated by race-antipathies. So far as present information goes the results have been excellent both biologically and sociologically. It is to be hoped that some student of eugenics will give the case careful and critical study.

Another successful experiment in human racial crossing has been recently studied and described by a German, Fischer,[1] who chronicles the origin of a tribe in German Southwest Africa of mixed Boer and Hottentot blood. This arose from the intermarriage with native Hottentots of a few Boers dissatisfied with British rule in South Africa, who penetrated far northward among hostile tribes, and were thus forced to combine with each other against a common enemy. Their descendants, intermarrying, formed a distinct cultural group entirely surrounded by pure native stocks and wholly isolated from contact with Europeans. Pride in their ancestry and cultural inheritance held them together and prevented mixing with neighboring tribes. After this had gone on for several generations they came within the German zone of colonial influence (again British at present under the fortune of war). Very likely the group as such will presently disappear, but the experiment has progressed far enough to show that under conditions which do not interfere with cultural inheritance crossing of racial stocks as widely separated as Europeans and Africans has no evil consequences, but produces a vigorous, sound race. Fischer finds evidence of Mendelian inheritance of physical characters among these people, but critically examined, this evidence is substantially like that available from other sources. Some characters, such as hair and eye-colors show fairly good segregation. As regards skin-color, proportions of the skeleton, features, etc., the hybrids are intermediate between the parent races, but more variable. It is probable that intelligence and other psychic traits are inherited in this way.

Racial crosses, if so conducted as not to interfere with social inheritance, may be expected to produce on the whole intermediates as regards physical and psychic characters.

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[1] "Die Rhehobothen Bastarden," 1911.

This seems to have been the result in Central and South America and in the West Indies, where racial crossing has taken place to a very great extent. A similar outcome seems likely to occur in Africa, as that continent is further overrun by European races. The leading racial stocks of Asia seem at the present moment to have such physical, mental, and cultural vigor that they are not likely to amalgamate with European races.

CHAPTER XXXI

PHYSICAL AND MENTAL INHERITANCE IN MAN

THE same laws govern inheritance in man as in other animals and in plants, but our knowledge of human heredity is less accurate than that of animals and plants, because we are in the human field debarred from experiment. The best we can do is to observe and compare the traits of individuals in successive generations and thus to ascertain with what known laws of heredity these cases best agree. For the discovery of new laws of heredity, human data can have little value because of our inability to experiment. Nevertheless the interest in human heredity is so general and the number of competent observers so large, including as it does a great many physicians and other men of science, that we may look forward to a very complete cataloguing of human heredity as fast as general categories of inheritance phenomena are established by the experimental study of other organisms. Already we have in hand a great amount of material bearing on human heredity, gathered chiefly by medical men, much of it within the last fifteen years. A considerable part of this is unreliable because of the careless or biased way in which it has been gathered, or the uncritical treatment which it has received in publication. But still there remains a considerable body of valuable information, which shows that man is subject to heredity in every aspect of his physical and mental make-up.

Two comprehensive attempts have been made to gather and analyze data concerning human inheritance, one in England at the Eugenics Laboratory of the University of London, founded by Galton and presided over by Karl Pearson, the other and more recent one at the Eugenics Record Office, Cold Spring Harbor, New York, directed by Dr. C. B. Davenport. Pearson's data are recorded in the "Treasury

TABLE 33

Inherited Characters in Man

1. *Blending*

General body size, stature, weight, skin-color, hair-form (in cross-section, correlated with straightness, curliness, etc.) shape of head and proportions of its parts (features).

2. *Mendelian*

	Dominant	Recessive
Skin and hair	Dark.	Blonde or albino (probably multiple allelomorphs).
	Spotted with white.	Uniformly colored.
	Tylosis and ichthyosis (thickened or scaly skin).	Normal skin.
	Epidermolysis (excessive formation of blisters).	Normal skin.
	Hair beaded (diameter not uniform).	Normal hair.
Eyes	Front of iris pigmented (eye black, brown, etc.).	Only back of iris pigmented (eye blue).
	Hereditary cataract.	Normal.
	Night blindness (when not sex limited).	Normal.
	Normal.	Pigmentary degeneration of retina.
Skeleton	Brachydactyly (short digits and limbs).	Normal.
	Polydactyly (extra digits).	Normal.
	Syndactyly (fused, webbed, or reduced number of digits).	Normal.
	Symphalangy (fused joints of digits, stiff digits).	Normal.
	Exostoses (abnormal outgrowths of long bones).	
	Hereditary fragility of bones.	Normal.
Kidneys	Diabetes insipidus (excessive production of urine).	Normal.
	Normal.	Alkaptonuria (urine black on oxidation).
Nervous System	Huntington's chorea.	Normal.
	Normal.	Hereditary feeble-mindedness.

3. *Mendelian and Sex-Linked*

(Appearing in males when simplex, but in females only when duplex.)

Dominant	Recessive
Normal.	Gower's muscular atrophy.
Normal.	Haemophilia (bleeding).
Normal.	Color blindness (inability to distinguish red from green).
Normal.	Night blindness (inability to see in faint light).

4. *Probably Mendelian but Dominance Uncertain or Imperfect*

Defective hair and teeth or teeth alone, extra teeth, a double set of permanent teeth, hare-lip, cryptorchism and hypospadias (imperfectly developed male organs), tendency to produce twins (in some families determined by the father, in others by the mother), left-handedness, otosclerosis (hardness of hearing owing to thickened tympanum).

5. *Subject to Heredity, but to what Extent or how Inherited Uncertain*

General mental ability, memory, temperament, musical ability, literary ability, artistic ability, mathematical ability, mechanical ability, congenital deafness, liability to abdominal hernia, cretinism (due to defective or diseased thyroids), defective heart, some forms of epilepsy and insanity, longevity.

of Human Inheritance" (1909). The data collected by the Eugenics Record Office have been published in part in a series of bulletins and monographs which is being rapidly extended.

We may provisionally distinguish inherited human traits as (1) blending (probably involving multiple factors); (2) clearly Mendelian (involving a single genetic factor); (3) Mendelian and sex-linked; (4) probably Mendelian but with dominance imperfect or uncertain, and (5) hereditary, but to what extent or how, uncertain.

The grounds on which a category of blending characters may be based have already been discussed. If they are valid for animals and plants, they are also valid for man. Here belong characters which show intermediate inheritance in F_1 and also in F_2, but with greater variability in F_2 than in F_1. Size and stature are good examples. The greater variability of F_2 shows that the blending was not perfect in F_1 and that multiple factors are probably involved. Indications of segregation more or less complete were observed by Davenport in his studies of skin-color and hair-form inheritance in negro-white crosses, which supports the idea that multiple factors are involved, or one or more chief factors associated with modifying factors. The well known lack of correlation between skin-color and hair-form in mulattoes of the F_2 or later generations certainly indicates the existence of independent factors affecting these characters.

As regards shape of the head, anthropologists have long distinguished between long-headed and round-headed races or types within mixed races. These may be convenient terms for purposes of classification, but it by no means follows that the types are alternative in heredity. Without positive evidence to the contrary, it is safe to assume from what we know of skull shape in animals and in negro-white crosses that skull shape is in all cases blending (multiple factorial) in inheritance. Salaman (1911) himself an English Jew, has described the Jewish type of countenance as recessive to the Anglo-Saxon type in mixed marriages in England on classifications of the offspring as of Jewish or Gentile type, made for him by Jews, but the evidence is far from satisfactory and not based on any clearly defined differences. If measurable characters were considered, it is probable the inheritance would be found to be blending, and the classification adopted in his tables to have been based on blending in many characters rather than on simple segregation in any one.

It is to be noted that in man, as in wild species of animals and plants, characters which *blend* in heredity are in no case abnormal or monstrous conditions, but are such as distinguish one member of a perfectly normal population from another.

The case is very different when we come to the category of simple Mendelian characters, whether or not sex-linked. Here a great majority of the characters listed refer to abnormalities or monstrosities. As regards variation in the color of hair, skin and eyes, we have, in these, recessive or loss variations, similar to those of other mammals, producing a graded series of probable allelomorphs ranging from black to albino.

Retrogressive variation of eye pigmentation leads from "heavily pigmented iris (back and front)" through more faintly pigmented conditions to "iris pigmented only behind," the ultimate recessive, blue. Spotting with white, affecting skin and hair pigmentation, or affecting only the pigmentation of the iris (Bond, 1912) are unit-character variations completely parallel with those of rodents. Nearly all other known Mendelizing characters in man are more or less pathological. They include a variety of hereditary malformations or "diseases" affecting skin, eye, skeleton, kidneys or nervous system. (See Table 33.)

Many characters (mostly loss variations) are probably Mendelian in inheritance, but not enough is known concerning their behavior to permit of a positive statement in the matter. (See Table 33, 4.)

In Section 5 of Table 33 are included many important characters known to be to some extent hereditary, but in accordance with what law is still uncertain. Especially important are such characters as general mental ability, mental capacity in special directions, hereditary epilepsy and insanity, and longevity. It would be a mistake to cover up our present ignorance concerning the inheritance of these characters by classifying them either as unifactorial or as multifactorial. We shall presently examine into the evidence that the more important of these are inherited.

Hair-form. This character has been studied by Dr. and Mrs. Davenport, whose findings may be briefly summarized. Hair having a circular cross-section is straight. But if the hair is elliptical in cross-section, it has a tendency to become curly. Grades of departure from the straight condition are formed with increase in flattening of the hair in cross-section as follows: (1) straight, (2) wavy, (3) curly, (4) kinky (Africans). Crosses produce intermediates or show imperfect dominance of curliness, with segregation more or less complete in later generations.

Hair and skin-color. Hair-color is in general correlated with skin-color, the darkest shades of hair-color being found only in persons with dark skin. Whole races of mankind have only black hair and dark skin (known as "black, brown, red or yellow"). A dark skin is an adaptation to life in a tropical country or one having much intense sunlight. Fair-skinned races are unable to endure life in the tropics unless the body is protected from the direct rays of the sun. Dark-skinned races, however, have a natural protection against the effects of direct sunlight. From an evolutionary standpoint the white races are possibly retrogressive variations, "loss" variations. In a population of Europeans, the darker shades of hair and skin-color are either completely or incompletely dominant. It is not at all uncommon to find a mixture of dark-haired and light-haired children in the same family, provided one or both parents are dark-haired, but when both parents are light-haired, the children are all light-haired. This result shows that the lighter shades of hair-color are recessive in relation to the darker shades. An exact estimate is often difficult to make because persons with light hair in childhood often have much darker hair when adult, and further, the hair may later become gray or even white, which makes direct comparison with the hair of younger persons impossible.

Extremely pale conditions of hair, skin and eye pigmentation are known as albinism and occur in all races, even in negroes and American Indians. Albinism is clearly a recessive character in relation to normal pigmentation. The various shades of blonds probably correspond physiologically and as regards inheritance with the graded series of albino allelomorphs found in guinea-pigs. Each darker shade is dominant to the lighter shades, any two in the entire series being allelomorphs of each other. This is known to be the case in rodents and probably holds for European races of mankind. In other races of mankind blond variations are rare, even more so than extreme albinism. Here again we have a condition parallel with that found in most rodents, in which the albino variation is known, but not other members of the graded series of retrogressive allelomorphs.

In a cross between a negro and a white person, children are produced of an intermediate, but frequently variable skin-color, and are known as mulattoes. Mulattoes mating *inter se* produce an F_2 generation of highly variable skin-color but rarely pure white. Davenport has concluded that two independent Mendelian factors affecting skin-color are involved. This explanation would lead us to expect one in sixteen of the F_2 mulatto offspring to have skin as white as a European, even though his negro ancestry might show in other characteristics, such as curly hair, broad nose, thick lips, etc. It is difficult to get any wholly satisfactory evidence either for or against this explanation. That published by Davenport can scarcely be considered conclusive, for the data studied are derived from a population in which illegitimacy, by Davenport's own statement, is as high as 72 per cent. On the whole, it seems probable that segregation of skin pigmentation in mulattoes is either incomplete or rarely complete, because multiple or modifying factors are involved.

A clearly and sharply defined Mendelian factor which involves spotting with white occurs in many human families, as in domesticated animals. In some families a lock of white hair (usually above the middle of the forehead, or on top of the head) is inherited as a Mendelian dominant (transmitted only through affected individuals). Irregular spotting of the body with unpigmented areas has been shown to be hereditary as a dominant character in a family of Louisiana negroes (exhibited in Europe and America), and a similar variation is inherited in the same way in a white family in Minnesota, one or more of whom have studied at the University of Minnesota.

CHAPTER XXXII

HEREDITY OF GENERAL MENTAL ABILITY, INSANITY, EPILEPSY, AND FEEBLE-MINDEDNESS

One of the first investigations carried on in the laboratory of Pearson related to the inheritance of ability as indicated by the " class lists " (rank lists) of Oxford. The investigation of the relative rank of two thousand five hundred pairs of fathers and sons showed that a distinct correlation exists between them. If the father took high rank the son also ranked high, and *vice versa,* in a considerable percentage of cases. Expressed numerically the correlation in the Oxford lists was found to be .31 where 1.00 would express exact agreement in rank and 0 would express only chance agreement. Between four thousand two hundred brothers the agreement was closer still, viz., .40. Closer resemblance was indeed to be expected, since in this case the mothers as well as the male ancestors were the same. The conclusion reached is that mental capacity, as indicated by rank attained at the University, is inherited; that the proverb " like father, like son " applies in the long run to scholarship, as well as to physique. This is a conclusion which every experienced teacher would have anticipated. It is interesting to find that it has full statistical warrant.

But the further question arises whether success in study has any relation to success in life outside of schools. Of this question an investigation was made in Pearson's laboratory. Rank in the Oxford B. A. examinations was compared with subsequent rank in the professions, the Church and the Law. The measure of success in the Church was taken to be the holding of a high office in the Church or of a first-class scholastic appointment. It was found that the higher the classification of a man at the Oxford examinations, the brighter were his prospects of attaining distinction in the Church.

Rank in Oxford Examinations	Percentage Distinguished
First class	68
Second "	37
Third "	32
Fourth "	29
Pass degree	21
No degree	9

Of those who attained a first-class degree, 68 per cent obtained official distinction, etc.

The results of the investigation as regards lawyers were found to be very similar. The measure of success here was taken to be the holding of public office under the government.

Of the first class men,	46% were so distinguished.
" " second " "	33%.
" " third " "	22%.
" " fourth " "	20%.
Pass degree men,	16%.
No degree men,	15%.

The general conclusion reached is that the "promise of youth" as indicated by scholarship is in general justified by the "performance of manhood" in the professions. The objection might be offered that appointments in church and state may be influenced by a man's university rank, but this is offset by results obtained in America, where this is certainly not true.

Insanity. Considerable work has been done in Pearson's laboratory in the study of the heritability of insanity. David Heron made a study of the inheritance of insanity as indicated by three hundred and thirty-one family histories collected during a period of thirty years by the superintendent of an asylum patronized by middle-class people of Perth, Scotland. See Table 34.

If insanity is treated as due to one and the same thing in all cases, it is obvious that the inheritance is not Mendelian; *i. e.*, insanity does not behave as a simple Mendelian unit-character, either dominant or recessive. But that insanity is in some way inherited is obvious, for it occurs much oftener in these families than in the general population, where it is between 1 and 2 per cent. But in these families 21 per cent of the offspring of sane parents are insane, and a still higher percentage of the offspring of insane parents are insane.

The correlation coefficient used as a measure of the strength of the inheritance of insanity lies between .52 and .62. For comparison it may be said that the correlation coefficient between parent and child in the case of pulmonary tuberculosis was found by Pearson to be about .50; for deaf-mutism [1] it was found to be .54; for stature .50; for intelligence between .49 and .58.

TABLE 34

Data on Inheritance of Insanity (*Heron*)

	Children		
Parents	Insane	Sane	% Insane
Both sane	314	1179	21
One insane	93	299	24
Both insane	4	4	50

Heron concludes that insanity on the whole is inherited about as strongly as other mental and physical characteristics.

But insanity cannot be regarded as a simple defect which can accordingly be eliminated from a population altogether, as could albinism. Insanity is a general name for a great variety of conditions of mental lack of balance and many different factors may enter into it. Not every family stock in which it occurs is to be regarded as unsound. But the intermarriage of families in which insanity occurs, and, still more, inbreeding within a family containing insanity is likely to increase the percentage of insane offspring and so should be avoided.

Two American investigators (Rosanoff and Orr) more friendly than the biometric school to Mendelian theory, have

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[1] Dr. Fay's U. S. data.

attempted to eliminate several categories of insanity and to find out more precisely what the law of inheritance of the remaining sort is. They eliminate cases possibly due to injury to the brain, alcoholism, syphilis, tumors, apoplexy and the like. Their material consisted of cases in the state hospital for the insane at Kings Park, N. Y. Careful inquiry was made as to the pedigree of all patients whose insanity was not referable to other than genetic causes. Seventy-two families were thus investigated, representing two hundred and six different matings, with a total of one thousand ninety-seven offspring. These are tabulated to test the hypothesis that insanity is a Mendelian recessive unit-character, as follows:

TABLE 35

Data on Inheritance of Insanity (*Rosanoff and Orr*)

Parents	Matings	Children		
		Neuropathic	Normal	Expected
Both insane	17	54	10*	All insane.
Only one insane, DR × RR	93	190	239	1:1
Only one insane, DD × RR	14	..	45	All sane.
Both normal (but tainted), DR × DR	62	107	215	1:3
Both normal (only one or neither tainted), DR × DD (?)	20	..	77	All sane.

* Eight have not yet passed "age of incidence."

The table seems in a general way to substantiate the hypothesis advanced, that insanity is a recessive character, especially the first category of matings where only insane progeny are expected. But when we look into the method of gathering the data and of compiling the table we become somewhat skeptical of this conclusion. The data have the scientific value of gossip, consisting of answers made by "informants" to leading questions designed to bring out any weakness in the pedigree. Like inquiries made concerning any individual in the community would show him an unmistakable victim of insanity. The authors frankly admit that " of the four hundred and thirty-seven persons classed by them as neuropathic, only one hundred and fifteen, or 26.3 per cent, presented at any time in their lives indications for commitment to sanitariums or hospitals for the insane." Three-fourths, therefore, of their persons insane for pedigree purposes would be classed as fully normal, if they occurred in families free from insane hospital patients. Such classification has little scientific value.

In dealing with the pedigrees the authors class as neuropathic persons whose only offence, aside from having an insane relative, are the following: " Crank "; " easily excited, nervous temperament "; " very nervous "; " erratic, excitable "; " nervous, little things bothered her, worried a great deal "; but in one case, which goes beyond all others, the individual is classed as insane on the following grounds: " money mad, very cruel, very miserly though wealthy, left much of his money to his housekeeper." To the layman this does not read like the characterization of an insane person; change the word housekeeper to hospital and it might describe a philanthropist and captain of industry.

It seems that, in the light of this investigation, if critically viewed, and in the light of Heron's investigation, very doubtful whether insanity in general is inherited as a Mendelian unit-character. Very likely there are different varieties of insanity independently inherited. That insanity is inherited, however, there can be no doubt. Heron quotes Pearson's family records as including seventeen cases in which one or both parents were insane. In only one case were all members of the family who attained the age of fifty or over free from insanity. When both parents were insane, Pearson's records give 66 per cent of insane offspring; when only one parent was insane, forty per cent of the offspring were insane, whereas in the general population only 1 or 2 per cent are insane. Hence with insanity in one or both parents, the percentage of insane progeny increases; on this all investigators agree.

The practical conclusion is obvious: insane persons should not be permitted to marry; indeed legislation forbids this in most countries. Further it would be well to avoid marriage into families in which insanity is common. It need not be assumed, however, that every person who has had an insane relative is an unfit mate. For such a conclusion, if enforced, would soon bring human breeding to a standstill.

Epilepsy. As regards the inheritance of epilepsy and feeble-mindedness the evidence is much clearer. By epilepsy we understand such nervous troubles as manifest themselves in the simplest cases in momentary loss of consciousness, and in extreme cases in marked convulsions. Much so-called epilepsy is probably due to infection with syphilis, congenital or otherwise, in which case its inheritance would be apparent only.

TABLE 36

Epilepsy and Feeble-Mindedness in Epileptic Families

(*Davenport and Weeks*)

Parents	Children			
	Number of Matings	Epileptic	Feeble-Minded	Normal
Both epileptic	1	3	..	..
One epileptic, one feeble-minded	5	8	6	..
Both feeble-minded	6	5	16	..
One epileptic, one insane	3	1	4	9*

* One "neurotic."

But if we leave out of account this possible complication, the inheritance seems to be that of a simple recessive Mendelian character. Davenport and Weeks (Eugenics Record Office, Bull. No. 4) have tabulated records concerning inmates of the New Jersey State Village for Epileptics at Skillman, N. J., which show one case, in which, both parents being epileptic, their three children were epileptic also. In five matings between an epileptic and a feeble-minded person fourteen children were produced, eight epileptic and six feeble-minded. In six cases feeble-minded persons married each other producing sixteen feeble-minded and five epileptic offspring. These cases indicate that the epilepsy and feeble-mindedness here dealt with were merely different manifestations due to a single cause, either a common infection or a common form of defect inherited without specific infection.

That insanity is probably due to a variety of causes and not the same ones as epilepsy or feeble-mindedness is shown by matings of the insane with epileptic or feeble-minded persons. Davenport and Weeks report three matings of an insane person with an epileptic or feeble-minded person, which produced fifteen adult offspring. Of these nine, or a majority, are described as normal, one as epileptic, and four as feeble-minded, while one is classed as "neurotic." This result indicates that the insane parent in most of these cases did not transmit the same abnormality or pathological condition as the epileptic or feeble-minded parent. Insanity in the family is racially less serious than epilepsy, possibly because less often due to congenital infection.

Feeble-mindedness. The most complete study of the inheritance of feeble-mindedness that has ever been made is that published by Dr. H. H. Goddard of the Vineland New Jersey Training School for Feeble-minded, who has recently published his results in book form (Macmillan & Co., 1914). He has studied the family histories of three hundred and twenty-seven families which sent pupils to the Vineland School. These family histories are published in detail, though not of course by name, and include in many cases photographs of the pupil or of his written work. In every case the family pedigree is charted to show the occurrence of mental or physical peculiarities in ancestors or any pertinent facts concerning their lives. The information was obtained from the parents of pupils, from family physicians, friends or neighbors, partly through printed questionnaires, partly through personal interviews by trained investigators. This method of obtaining information is of course capable of uncritical use, as already pointed out, but seems to have been employed with circumspection and in some cases with independent verification by Dr. Goddard.

The importance of such an investigation as this is shown, according to Goddard, by many facts.

First. Feeble-mindedness is much commoner than most persons suppose, understanding the feeble-minded to include all persons congenitally of such low intelligence that they are either unable to care for themselves or are incapable of managing their own affairs with ordinary prudence. Goddard believes that the feeble-minded are individuals of arrested or undeveloped mentality and are thus quite different from the insane, who show pathological mentality. A feeble-minded person has the undeveloped mind of a child; an insane person may have attained mental maturity and then lost it again, his mentality having degenerated. Feeble-mindedness and insanity may coexist in the same individual but they are due to distinct agencies. Feeble-mindedness, according to Goddard, characterizes a large proportion of such persons as become public charges as paupers, drunkards, or criminals.

The method now generally employed of grading the intelligence of individuals is known as the *Binet* test, from the Frenchman who devised it. It consists of giving the individual a series of standardized tasks to perform of increasing difficulty as regards the demands on intelligence. The results of these tests are graded in terms of the average performance of normal children of particular ages. Thus a feeble-minded person may show the mentality of a normal child of any age from one year to twelve years, and is spoken of as mentally of age one, two, three, etc. Tests of intelligence made by the Binet method upon juvenile criminals in various state reformatories show that a large proportion of the inmates are of abnormally low intelligence, *i. e.*, are feeble-minded. In *New Jersey* the proportion reported feeble-minded as indicated by Binet tests is 46 per cent; in Ohio 70 per cent; in Virginia 79 per cent; and in Illinois 89 per cent. Probably 50 per cent would be a conservatively low general estimate of the youthful criminals who are feeble-minded. Goddard says, " It is easier for us to realize this if we remember how many of the crimes that are commited seem foolish and silly. One steals something that he cannot use and cannot dispose of without getting caught. A boy is offended because the teacher will not let him choose what he will study, and therefore he sets fire to the school building. Another kills a man in cold blood in order to get two dollars. Somebody else allows himself to be persuaded to enter a house and pass out stolen goods under circumstances where even slight intelligence would have told him he was sure to be caught. Sometimes the crime itself is not so stupid but the perpetrator acts stupidly afterwards and is caught, where an intelligent person would have escaped. Many of the ' unaccountable ' crimes, both large and small, are accounted for once it is recognized that the criminal may be mentally defective. Judge and jury are frequently amazed at the *folly* of the defendant — the lack of common sense that he displayed in his act. It has not occurred to us that the folly, the crudity, the dullness, was an indication of an intellectual trait that rendered the victim to a large extent irresponsible."

This same line of explanation Goddard applies with much plausibility to drunkenness in relation to feeble-mindedness. It is well known that drunkenness and feeble-mindedness are often associated, and people have concluded that drunkenness *causes* feeble-mindedness. Goddard believes the reverse of this to be true that feeble-mindedness occasions drunkenness, because the individual has not enough intelligence and will power to resist temptation when it arises.

Another social evil, prostitution, Goddard finds to be due in large measure to feeble-mindedness. Binet tests made in an Illinois reformatory of girls committed for immorality showed 97 per cent of them to be feeble-minded. A Massachusetts Commission reports that Binet tests applied to three hundred immoral women under detention in that state proved 51 per cent of them to be feeble-minded, while the rest had the mentality of children aged nine to twelve years.

If Dr. Goddard is right in the opinion that feeble-mindedness is responsible for much crime of various sorts, for much drunkenness and pauperism, it would seem that the easiest way to attempt to diminish these evils would be by attempting to diminish feeble-mindedness. Hence the importance of his undertaking to get at the causes of feeble-mindedness.

Dr. Goddard divides his three hundred and twenty-seven cases, as regards the probable causes of the observed feeble-mindedness, into six groups:

1. Hereditary	164
2. Probably hereditary	34
3. Neuropathic ancestry (a possible cause)	37
4. Accident (to mother or child, as disease)	57
5. No cause assignable	8
6. Unclassified	27
	327

From this table it will be seen that he regards the feeble-mindedness as clearly hereditary in half of the families studied, while it is "*probably* hereditary" in 10 per cent more. Heredity then is the largest single discoverable cause for feeble-mindedness. Neuropathic ancestry and accident are also recognized as probable causes in a small percentage of cases each, but it is not to be expected that feeble-mindedness so produced would prove hereditary. He can find no evidence that hereditary feeble-mindedness is caused by a variety of agencies to which it is frequently referred, as for example to alcoholism, tuberculosis, syphilis, insane, epileptic or paralytic ancestry, etc.

Most feeble-mindedness, then, is due to heredity, but how did the character become hereditary? How did it originate? Goddard does not attempt to answer this question, but he does make clear his view that the feeble mind is an undeveloped childish mind. His observations show that the physical vigor of the feeble-minded equals that of normal individuals and that the feeble-minded are even more fecund than normal individuals owing to their lack of normal prudence and self-control. It might be supposed, therefore, either that they represent a primitive, animal-like condition of the human race, which has survived down to the present time, or that they represent a retrogressive (loss) variation. The manner of inheritance of the condition is of interest in connection with this question, for evolution by loss usually results in the production of recessive variations.

Goddard's evidence indicates that feeble-mindedness is a recessive unit-character. In his family records one hundred and forty-four matings of feeble-minded *inter se* have produced seven hundred and forty-nine children of whom four hundred and eighty-two are of ascertained mentality. Of these, all but six are recorded as feeble-minded. These few exceptions to theoretical expectation might be explained as being of ancestry other than that assigned. A case reported from an Ohio institution illustrates the point well. "In a white family, the father and mother are both feeble-minded. They have twelve children, all feeble-minded but two. These two are normal (as regards intelligence) but they are colored."

TABLE 37

Data on the Inheritance of Feeble-Mindedness

Mating	Children		
	F-M	N	
F × F	476	6	
F × N	193	144	(N heterozygous ?). Some families tabulated here belong above, probably.
F × N	..	68	(N homozygous ?).
N × N	39	83	(Both heterozygous ?). Some belong above, probably.
N × N	..	116	(One or both homozygous ?).

The data of Goddard indicate clearly that feeble-mindedness is inherited as a recessive Mendelian character, but one which like albinism may occur in many different grades, the higher grades probably tending to dominate. The feeble-minded are frequently deficient in physical strength and vigor. However, many of them seem to possess unusually good physique. Goddard compares them to savages with strong bodies but childish minds. The high-grade feeble-minded, known as "morons," with mentality of eleven or twelve years, are capable of being useful members of society in manual or mechanical occupations not demanding too much planning or initiative. But it is evident that as they are easily influenced and imposed upon and more than ordinarily fecund, since they do not exercise the prudence and self-restraint of normal individuals, their numbers are likely to increase unduly, unless some restraint is put upon them. A self-governing democracy with universal suffrage is seriously threatened by a large increase in the unintelligent portion of its population, and is justified in adopting strong measures to counteract it. This is often urged as an argument for restricted immigration without due regard for the distinction between low intelligence and illiteracy. Many of our immigrants who are illiterate, because they have never had an opportunity to attend school, are people of unusual intelligence and energy. Their illiteracy is usually speedily removed when they get within reach of American schools and the next generation is represented among the most earnest students in our universities and later among the successful men in the professions. But the person of low intelligence, whether literate or illiterate is more dangerous to society than the intelligent illiterate, because he and his descendants for all time will require parental protection and care from the state to prevent them from becoming criminals, paupers, idlers, and purchasable voters.

To prevent the natural increase of the feeble-minded, Goddard recommends their segregation, so far as possible, in schools and institutions under state control. This is already being done to some extent in many of the states, but altogether too few individuals have yet been segregated to insure a decrease in the proportion of feeble-minded in the population. Many have hitherto been unrecognized as feeble-minded, who are classed as backward pupils in school, and later as truants, drug fiends, drunkards, criminals, tramps or prostitutes. A proper recognition of the source from which these classes are recruited and of what really ails them should lead to more intelligent efforts to reduce their number.

When segregation is impracticable, the feeble-minded should be looked after in their homes, as children are looked after. They should not be allowed to marry unless first sterilized. In the case of males this is now possible by a very simple surgical operation, vasectomy, unattended by risk or serious consequences to health. In the case of females segregation during the reproductive period is probably more to be recommended than sterilization.

CHAPTER XXXIII

THE POSSIBILITY AND PROSPECTS OF BREEDING A BETTER HUMAN RACE

The suggestion that the human race might be improved by the methods of the stock breeder is a very old one. Plato advanced it in his *Republic* as the only practicable basis for the production of a permanent and superior governing class within the ideal state. The family had no place in his scheme.

It was his proposition that the best of both sexes should be mated with each other and should be given every encouragement to the production of offspring, the young being taken at birth into a state nursery and their identity lost so far as the parents were concerned. Inferior persons, on the other hand, were to be kept from reproducing, as far as possible, and their progeny destroyed. Realizing that such favoritism would cause no end of trouble, if known, Plato said that what was done should be kept a secret from all but the magistrates themselves, and " an ingenious system of lots must be contrived in order that inferior persons may impute the manner in which couples are united to chance and not to the magistrates."

The eugenics system of Plato has probably never had a full and fair trial, but if we may believe the account of Plutarch, in his life of Lycurgus, something very like it actually existed in Plato's time in Sparta, and it was probably the Spartan system that Plato had in mind. Sparta was practically an armed camp, in which a military class ruled with great severity the subject native races, holding them in subjection by force of arms and compelling them to work the land for the benefit of their conquerors. The Spartans subjected themselves, both men and women, to the severest discipline. Gymnastics and war were their exclusive occupations. Family life scarcely existed among the Spartans. The men lived together in a sort of camp or club, very frugally, and ready for instant warfare. Marriage was recognized as an institution for the production of soldiers merely. The child belonged to the state, rather than to its parents. The magistrates decided whether it should be reared or not. Plutarch says concerning Lycurgus, founder of the Spartan constitution:—"Lycurgus was of a persuasion that children were not so much the property of their parents as of the whole commonwealth, and therefore, would not have his citizens begot by the first-comers, but by the best men that could be found; the laws of other nations seemed to him very absurd and inconsistent, where people would be so solicitous for their dogs and horses as to exert interest and pay money to procure fine breeding, and yet kept their wives shut up, to be made mothers only by themselves, who might be foolish, infirm, or diseased; as if it were not apparent that children of a bad breed would prove their bad qualities first upon those who kept and were rearing them, and well-born children, in like manner, their good qualities."

The Spartan system of eugenics seems to have attained its object, the production of superior children, but we must remember that with it was combined a system of life-long physical education and military discipline which has rarely if ever been equalled, so that it is impossible to say how much of the result obtained was due to breeding and how much to training of the youth.

Further the Spartan system succeeded only so long as Sparta was a small, isolated community, without wealth, luxury, or leisure, and using iron for money. Foreign conquest was the undoing of Sparta. She could conquer in a fight but she could not govern except as she governed her Helots — by enslaving them. Upon contact with the rest of the world, life was found to have other attractions than fighting, and the old discipline was relaxed.

Moreover, what the Spartan system produced was a single type of man, the soldier. The memory of Athens is sacred for other types of manhood and achievement, art, literature, philosophy and science, the greatest intellectual achievements of mankind up to that time, but in these Sparta had no share. Her eugenics was of the same type as that of the animal breeder. It aimed to produce a single specialized type of superior excellence. In this it succeeded, but at the sacrifice of all else. In this, again, it resembles animal husbandry, which produces a type of animal more useful to man, but wholly dependent upon him, and unable to maintain itself if thrust back into the struggle for existence with other animals.

The civilization for whose continuance Plato planned came to an end. We do not know why. Historians differ widely in their views as to why Greece and Rome fell. But one suggestion is that in their later days the inferior classes increased more rapidly than the superior ones and the general average was thereby lowered. Now it is conceivable that this may have happened in one of two ways. If each class reproduced its kind, then the lower classes must have reproduced faster than the upper ones. This is what is assumed to have occurred by those who consider modern nations to be threatened in a similar way.

On the other hand it is possible that there was no real germinal difference between the so-called upper and the lower classes. The classification of ancient society may have rested on economic rather than biological grounds and the downfall have been due to economic causes rather than to racial changes. If this is true then the more rapid reproduction of those low in the social scale was not in itself harmful to the race, that is would not have caused a lowering of its biological level, and economic causes must be sought to explain the decay of ancient civilization. The question is one for historians to deal with, but its answer must be borne in mind when the fate of ancient civilizations is cited as a warning to us.

A belief that biological decline is occurring or is likely to occur among modern nations has given rise to the modern eugenics movement. This movement was started by Francis Galton, who, adopting Darwin's theory of evolution, sought to apply it to human society. His studies of family histories had convinced him that both physical and mental traits are largely matters of inheritance. He reasoned that the existing biological status of society could be maintained only if all classes of society reproduced at the same rate; that improvement would result if the biologically *best* individuals reproduced faster than others, but that deterioration would result if the biologically inferior individuals reproduced faster than others. He sought to devise measures which would encourage early marriage and the rearing of large families by the best and most competent members of every profession and trade. His suggestions met chiefly with ridicule at the time, but are coming now to be taken more seriously.

No one can deny that our country's population is increasing fast enough, the only danger is that the biologically poorest elements in the population may increase faster than any other. The declining birth rate is not in itself serious, but the differential character of its decline is serious. The most intellectual and cultured elements in the population breed slowest. Professor Cattell says that a Harvard graduate has on the average three-fourths of a son and a Vassar graduate one-half of a daughter. If this continues college graduates may look forward to the early extinction of their line as an element in the American population.

As elements in the differentially declining birth-rate we may recognize (1) late marriages, shortening the reproductive period and (2) voluntary limitation of the number of children. Voluntary limitation occurs for a variety of reasons such as expense, health, etc., but chiefly because of selfishness and luxury, causes which were operative in the decline of Greece and Rome as they are among modern nations.

The more complex human life becomes, the less attention is given to its perpetuation. In a small community family life is dominant and the rearing and education of children are its most important occupations. But as community life becomes more complex family life sinks into a subordinate position. The more intellectual and cultured the individual is, the more does he find outside the home to interest and attract him. The consequence is that home life suffers. It is slighted or shunned altogether by those who are best qualified to be parents, and the rearing of children is left to those considered too dull for other activities. In consequence the majority of the children produced in a cultured and progressive city population are produced by its least cultured and progressive members. This is the condition which today confronts the leading nations of the world and has given rise to the eugenics movement. If this condition is interpreted from the standpoint of the animal breeder, it means that the average capacity of the population for intellectual pursuits, for culture and for progress is bound to decline. For this amounts to selecting for breeding, not the best, but the *culls* of the flock, and every breeder knows that this means deterioration.

If a great city can in each generation import a fresh stock of youths from the country or from foreign countries, all may go well, but it is questionable whether this can continue indefinitely. Already many of our rural New England communities are said to be running out of good human stock. For generations they have been sending their best to the cities and to the developing West. Many of those left behind are lacking in energy or ambition, perhaps also in intelligence, and a European peasant population is rapidly replacing them. Will this new population be a fit substitute for the old Anglo-Saxon stock ? Time alone will tell. If it is a sound stock which has hitherto lacked opportunity to rise in the social scale, we may now expect it to do so, opportunity being offered. But if it is inherently a feeble stock, it will not replace the old New England stock in supplying our cities with the bright youths whom they require but are unable to produce in sufficient numbers. A time of storm and stress like that which now distracts the world may at some future day decide our fitness to survive as a race.

In England a genuine alarm is felt as regards the character of its future citizens, for there as here the cities draw from the country. But the country population there is not only not regenerated by immigration but is further depleted of its best elements by foreign emigration. The consequence is that a eugenics movement has there been started, which seeks to remove the indifference on the part of the best elements in the population to marriage and the rearing of children. Just how this can be done, or whether it can be done at all is uncertain. But the British eugenists are very much in earnest and they base their appeal on both patriotic and religious grounds. Professor and Mrs. Whetham (who have written several books devoted to this subject) discuss primarily conditions in Great Britain. Their point of view is to some extent an aristocratic one. They recognize in the hereditary aristocracy of England a genuinely and germinally superior element of the population. The younger sons of the titled families who inherit (it is supposed) the superior germ-plasm but not the aristocratic titles, have frequently married into successful families of the middle class, and are believed thus to have improved the standard of the entire nation. This theory sounds plausible, but an outsider free from class prejudice might reasonably question its validity.

If the English aristocracy is really a biologically superior race, how are we to account for the historical steady rise in power and influence of the Commons? Opportunity has always favored the aristocratic families; in spite of this we find the great men of the British nation usually coming from the middle class, and not from the younger sons of aristocratic families either. America's experience does not indicate that the English aristocracy is either better or worse than the English yeomanry as a biological human stock. What little of aristocratic blood the colonies received went chiefly to Virginia and previous to the Civil War an aristocracy of first families comparable with that of England ruled Virginia and furnished the nation with presidents and statesmen. Since the war the presidents have come from other sections, and seem not to have been inferior in ability to their predecessors. In some quarters it is the fashion to point to New England as the source of the really superior American stock, viz., its intellectuals, but there is no better ground for thinking the Puritan stock superior than for thinking the Cavalier stock superior. Circumstance has had much to do with the advancement of each in influence. In this connection it is interesting to note the conclusions reached by Professor Cattell (*Popular Science Monthly*, May, 1915) from a study of the families of America's one thousand leading scientists. He says:

"If men of performance could only come from superior family lines, this would be a conclusive argument for a privileged class and for a hereditary aristocracy. If the congenital equipment of an individual should prescribe completely what he will accomplish in life, equality of opportunity, education and social reform would be of no significance. Such an extreme position, though it is approached by men with so much authority as Sir Francis Galton, Professor Karl Pearson, Dr. F. A. Woods, Dr. C. B. Davenport and Professor E. L. Thorndike, is untenable. Equally extreme in the opposite direction is M. Odin's aphorism " Genius is in things not in men," or the not uncommon opinion that almost anything can be done with a child by training and education.

My data show that a boy born in Massachusetts or Connecticut has been fifty times as likely to become a scientific man as a boy born along the southeastern seaboard from Georgia to Louisiana. They further show that a boy is fifty times as likely to do scientific work as a girl. No negro in this country has hitherto accomplished scientific work of consequence. A boy from the professional classes in New England has a million chances to become a scientific leader as compared with one chance for a negro girl from the cotton fields.

"These great differences may properly be attributed in part to natural capacity and in part to opportunity. If the 174 babies born in Massachusetts and Connecticut who became leading scientific men had been exchanged with babies born in the south, it seems probable that few or none of them would have become scientific men. It may also be the case that few or none of the babies from the south transplanted to New England would have become scientific men, but it is probably true that a nearly equal number of scientific men would have been reared in New England. It is certain that there would not have been 174 leading scientific men from the extreme southern states and practically none from Massachusetts and Connecticut. If the stock of the southern states remains undiluted, it may, as social conditions change, produce even more scientific men per thousand of its population than New England has hitherto produced. In the first list [made in 1906] of the thousand leading scientific men, Massachusetts produced 109 and Connecticut 87 per million of their population. Of the younger men added to the list in the second arrangement [made in 1910] under comparable conditions, Massachusetts produced 85 and Connecticut 57. The other North Atlantic states failed in like measure, while the central states show a gain — Michigan from 36 to 74, Minnesota from 23 to 59, etc. These changes must be attributed to an altered environment, not to an altered racial stock. Japan had no scientific men a generation ago and China has none now, but it may be that in a few years their contributions to science will rival ours.

"A Darwin born in China in 1809 could not have become a Darwin, nor could a Lincoln born here on the same day have become a Lincoln had there been no civil war. If the two infants had been exchanged there would have been no Darwin in America and no Lincoln in England. Darwin was a member of a distinguished family line possessing high natural ability and the advantages of opportunity and wealth. Lincoln had no parental inheritance of ability or wealth, but he too had innate capacity and the opportunity of circumstance. If no infants had been born with the peculiar natural constitutions of Darwin and Lincoln, men like them could not have been made by any social institutions, but none the less the work they did might have been accomplished by others and perhaps their fame would have been allotted to others. There may have been in England other family lines equal in natural ability to the Darwins and in this country other individuals as well constituted as Lincoln, but undistinguished from lack of opportunity. It is still more probable that such conditions obtain in Russia and in China, in whose graveyards there may lie innumerable " mute inglorious " Miltons, Lincolns and Darwins.

"The most exceptional ability may be suppressed by circumstances; but it can sometimes deal with them on equal or perhaps superior terms. Thus the writer has pointed out how widely distributed in race, age and performance are the most distinguished men who have lived. When we turn from the most eminent men to those next in rank, we may doubt whether their natural ability has not been equaled by thousands who have not attained distinction. Among the two hundred most eminent men who have lived in the history of the world are: Napoleon III, Nero, Fox, Julian, Fénelon, Clive, Alberoni, Bentley and Gerson. It is quite conceivable that there are at present living in the United States hundreds or thousands of men having as great natural ability as these. There may be a hundred thousand men and women having the natural and specific ability of the thousand in this country who have accomplished the best scientific work.

"President A. Lawrence Lowell has remarked that we have a better chance of rearing eaglets from eagles' eggs placed under a hen than from hen's eggs placed in an eagle's nest. But it is equally true that we have a better chance of raising tame eaglets in a chicken coop than in an eyrie. The difference between a man uninterested in science and a scientific man is not that between a chicken and an eagle, but that between an untrained chicken and a trick cock. Some cockerels can be trained better than others, but there are innumerable cockerels that might be trained and are not.

"The son of a scientific man may on the average have the inherited ability which would make him under equally favorable circumstances twice, or ten times, or a hundred times, as likely to do good scientific work as a boy taken at random from the community. The degree of advantage should be determined. It surely exists, and the children of scientific men should be numerous and well cared for. But we can do even more to increase the number of productive scientific men by proper selection from the whole community and by giving opportunity to those who are fit. Galton finds in the judges of England a notable proof of hereditary genius. It would be found to be much less in the judges of the United States. It could probably be shown by the same methods to be even stronger in the families conducting the leading publishing and banking houses of England and Germany. As I write, the death is announced of Sir William White, the distinguished naval engineer, chief constructor of the British navy, president of the British Association. If his father had been chief constructor of the navy, he would have been included among Galton's noteworthy families of fellows of the Royal Society. The fact that his father-in-law was chief constructor of the British navy throws, if only by way of illustration, a light on the situation in two directions.

On the one hand, the specific character of performance and degree of success are determined by family position and privilege as well as by physical heredity; on the other hand, marriage, chiefly determined by environment, is an important factor in maintaining family lines. The often-quoted cases of the Jukes and Edwards families are more largely due to environment and intermarriage within that environment than to the persistence of the traits of one individual through several generations. The recently published " Kallikak Family " by Dr. H. H. Goddard demonstrates once again the heredity of feeble-mindedness. It would, however, have been a stronger argument for the omnipotence of heredity if the original ancestor had left by a healthy mother illegitimate children who established prosperous lines of descent, and a child by a feeble-minded wife who left degenerate lines of descent. Two experiments have been made on a large scale which seem fairly definite even though quantitative results cannot at present be reached. The mulattoes may be assumed to have a heredity midway between negroes and whites, but their social environment is that of the negroes, and their performance corresponds with their social environment rather than with their heredity. Illegitimate children have perhaps a heredity as good as the average, but their performance falls far below the average. If performance were determined by heredity alone there might be expected to be among our thousand leading scientific men some forty mulattoes and some forty of illegitimate birth, whereas there is probably not one of either class.

"At nearly the same time Agassiz came from abroad to Harvard and Brünnow to Michigan. We all know the list of distinguished naturalists trained under Agassiz — Brooks, Hyatt, Jordan, Lyman, Minot, Morse, Packard, Putnam, Scudder, Shaler, Verrill, Whitman, Wilder, and many more, directly and indirectly. From Michigan have come, as is not so well known, one-fourth of our most distinguished astronomers, including Abbe, Campbell, Comstock, Curtis, Doolittle, Hall, Hussey, Klotz, Leuschner, Payne, Schaeberle, Watson and Woodward. Certainly the coming of Agassiz and Brünnow was the real cause of greatly increased scientific productivity in America. Some, but not all, of those who worked under Agassiz would have become naturalists apart from his influence. The astronomers from Michigan must in the main be attributed to their environment. The men had the necessary ability, but if Brünnow had not gone to Michigan, they would not have become astronomers; if they had gone to the University of Pennsylvania, they would have been more likely to have become physicians than astronomers; if they had not gone to a university they would not have become scientific men.

"It is certainly satisfactory if we can attribute the inferiority of scientific performance in America as compared with

Germany, France and Great Britain to lack of opportunity rather than to lesser racial ability. In Germany scientific research has been made by the university rather than the reverse. In Great Britain also the universities have been potent, and, in addition, its leisure class has contributed greatly. Here prior to 1876 we had no university in which research work was adequately encouraged, and we have had no amateurs comparable to those of Great Britain. Professor Pickering found that of the 87 scientific men who were members of at least two foreign academies, 6 were Americans as compared with 17 from Prussia, 13 from England and 12 from France. In so far as our scientific production is so measured, the reference is to a generation ago, when our universities were only beginning to develop and research work was only beginning to be appreciated. But it is a striking fact that of the six distinguished Americans, three are astronomers; and astronomy is the only science in which thirty years ago the facilities for research work in this country were equal to those of the leading European nations. Of the remaining three, two have not been engaged in teaching, and the third has been practically freed from teaching for his research work. We may hope that when conditions become as favorable for other sciences as they have been for astronomy, the United States will assume leadership in scientific productivity.

"In order to answer questions such as the extent to which the scientific work accomplished in America is due to native endowment, whether such endowment is general or specific, how far it occurs in family lines, what part of those endowed are able to prove their ability, the influence of education and example, the effects of opportunity, encouragement and rewards, it is necessary to make a study of individual cases. A large mass of material is at hand concerning the relatives of scientific men who have shown scientific productivity or have attained distinction, but these data are not in order for publication and should be supplemented by answers to many inquiries. In the meanwhile the writer may say that it is his opinion that while we should welcome and support a eugenic movement tending to limit the birth of feeble-minded and defective children and encouraging the birth of those that are well endowed, it appears that under the existing conditions of knowledge, law and sentiment, we can probably accomplish more for science, civilization and racial advance by selecting from the thirty million children of the country those having superior natural ability and character, by training them and giving them opportunity to do the work for which they are fit. We waste the mineral resources of the country and the fertility of the soil, but our most scandalous waste is of our children, most of all of those who might become men and women of performance and of genius.

"Eugenics may become the most important of all applied sciences, but at present its scientific foundations must be laid by the study of comparative genetics, on the one side, and the study of human conduct, on the other. There is more immediate prospect of improving our civilization than our germplasm. It is easier to decrease or eliminate typhoid fever by hygienic measures than to attain racial immunity, although this is not equally the case for tuberculosis and still less for cancer. We can increase to any desired extent from the existing population by proper selection and training the number of scientific workers in the United States. The number capable of exhibiting genius is limited, but many of them are lost through lack of opportunity. It is our business, it should be our principal business, to improve our civilization by giving opportunity to those who are fit, while at the same time investigating the conditions which will give us a better race."

Writers on sociology have shown that human progress is largely limited and determined by the social environment and that it is even possible for social progress to occur in spite of biological deterioration. If this idea is correct, one argument for control of human matings by the state or some other central agency has been frequently over-emphasized. Racial progress does not require a constantly advancing biological standard in the individual. As individuals, primitive men were probably more than a match for us physically, and at least our equals mentally. As regards the standard of the individual, then, the race has not progressed. Civilization is a matter of collective achievement; it is not a biological inheritance at all, but a cultural one. " We are heirs of all the ages " not biologically, but only culturally. Standing on the shoulders of the last generation we see farther because we are higher up, not because we are taller.

It is of course essential that the racial stock be kept sound and free from taint of disease or racial poison, but granting this, the situation is not so alarming as some persons seem to think. For the normal unperverted instincts of the average man have a distinctly eugenic trend. Cupid is a safer guide in matrimony than a licensing board. The old folks always " make a mess of it " when they interfere in the matchmaking of the young folks. This is as true in real life as in literature. Of course it is possible for young folks to make mistakes as well as for old ones, and it is necessary that those older persons who have been burned by the fire, or have seen others suffer in like fashion, should see that their children do not fall into the fire. For example, civilization has brought into being many perils which did not exist in a simpler and more primitive mode of living. Of these the young must be advised. Implicit trust in the guidance of the instincts will in a civilized community lead to endless trouble. Sexual promiscuity has only disastrous consequences among civilized peoples and for a very simple reason, the certainty of contamination sooner or later with venereal disease, in particular with gonorrhoea or syphilis.

It is probable that Polynesians, before the advent of Europeans, were free from these diseases, and their rather loose sexual relations, as viewed by our standards, had no serious racial consequences. But with the advent of Europeans all this has changed. Continued promiscuity means to them now racial extermination, as it does among Europeans. Sexual purity is necessary with us, not merely because social standards demand it, but because avoidance of loathsome venereal disease is impossible otherwise.

This element of venereal disease has frequently been an important factor in determining the success or failure of race mixtures. European men of loose morals have frequently introduced venereal disease in race mixtures with native populations, and this will account for the poor results observed in many racial crosses. When this element is absent, racial crosses of Europeans with native peoples have been observed to produce offspring of complete vigor and fertility. Racial crossing among men, as among domesticated animals, is biologically beneficial within limits. The English people were originally very mixed racially, and the same is preeminently true of Americans today. This mixture of elements not too dissimilar, provided the *social heritage* is not unduly disturbed, is on the whole beneficial. It results in increase of vigor and energy in the offspring, together with an increase of variability, physical and mental, which favors social progress.

It is certain that human progress depends upon two sets of agencies, one sociological or cultural, the other biological. In this discussion we have dealt chiefly with the biological agencies. Biologically the human race can be improved only by improvement of its germ-plasm. If acquired characters were inherited, we might hope to improve the human race germinally by improving the environment. If as seems more probable acquired characters are not to any considerable extent inherited, then environmental agencies affect man chiefly culturally, not biologically. To change man biologically, to make a different sort of animal of him, it will be necessary to act through heredity, that is through selection of parents for the next generation.

Leaving aside for the present the practical difficulties and supposing that it were possible to manage the human race like a stock farm, the choice of parents would necessarily be limited by the material available. We could select parents only for such characteristics as the human race today possesses. We could not, for example, breed a human race with wings, however desirable such a characteristic might seem. We are limited definitely for all time to the hand type of appendage. But there are different types and sizes of hands among human beings among which a selection might be made if this were considered desirable, as for example *normal* hands, *short-fingered* hands (*i. e.*, brachydactyl), hands with a *reduced number of fingers* (*i. e.*, syndactyl), and hands with an *increased number of fingers* (*i. e.*, polydactyl). These several types of hand are known to be hereditary. If the unusual types were superior to the normal, we might through heredity make them replace the normal in the race. But in reality, the normal type of hand seems on the whole to be the best type, and so we have no desire to change it. The same is true as regards most human traits known to be inherited, whether physical or intellectual. Our ideal is in general the *normal*. There are certain types of abnormality which we should be glad to see become less frequent in occurrence, as for example albinism, night blindness, color-blindness, and haemophilia. A complete control of heredity would render their elimination from the race possible, but it is doubtful if they are serious enough to call for such elimination, even if human matings were wholly controllable by a single central agency, which of course they are not. For in discriminating against persons possessing such minor defects as these we should be in danger of rejecting some of our human stock which is best in regard to characteristics of much greater consequence. The independent inheritance of traits must ever be kept in mind in deciding who are desirable and who undesirable parents, weakness in one particular being frequently offset by unusual strength in another. Those undesirable traits which are inherited in the simplest way, as Mendelian characters, are not likely to become very common in a freely intermarrying population. It is only when society becomes stratified, and class distinctions arise with castes or families closely intermarrying, that heredity is likely to bring Mendelian recessive defects repeatedly to the surface. Democracy is as safe a remedy against such evils as state controlled marriages would be, if they were obtainable.

The most important inherited traits are probably those which are quantitatively variable, which occur in a graded series, like bodily size and strength, mental power, and power of resisting disease. In regard to these, excellence is a matter of degree and is relative. Further no particular grade breeds true. Regression toward the normal is the universal rule. If society could be managed like a stock farm, then it would be possible to change the normal toward which regression occurs, very slowly and gradually, as for example in mental power. The average grade of intelligence could be raised by rigid selection long continued. Possibly this has occurred in the evolution of existing races of men. If so, it has occurred unconsciously and through natural selection and probably more from the struggle of one cultural group with another than from the struggle of one individual with another. But the modern eugenic ideal is to make a conscious selection of parents within the group with a view to elevating the normal within the group, a thing that has not hitherto been attempted, unless in Sparta for the breeding of soldiers.

If there were a central directing agency which had the power as well as the wisdom to control matings within the group, something could undoubtedly be done slowly to elevate the general average of bodily vigor or innate mental power within the group. This could be done most rapidly by polygamy which would permit of a relatively rigid selection of sires; less rapidly under monogamy by a selection of parents among both sexes, the offspring to be cared for largely by the rest of the community. But the social consequences of either of these methods are so tremendous, so subversive are they of individual liberty, that no modern civilized community has been willing to contemplate either of them. The whole movement of modern times is in an opposite direction. Practically therefore, we are limited to such eugenic measures as the individual will voluntarily take in the light of present knowledge of heredity. It will do no good, but only harm, to magnify such knowledge unduly, or to conceal its present limitations. We should extend such knowledge as rapidly as possible, but not legislate until we are very sure of our ground.

Every young person of sound and healthy stock should look forward to marriage and family life as the completion of a normal career and incidentally as fulfilling an obligation which he owes to his country and his race. Any young person who for any reason finds himself debarred from this part in life should fulfill the racial obligation vicariously by helping to care for and to educate the children of his more fortunate fellows.

APPENDIX

APPENDIX

EXPERIMENTS IN PLANT-HYBRIDISATION[1]

By Gregor Mendel

(Read at the Meetings of the 8th February and 8th March, 1865.)

INTRODUCTORY REMARKS

Experience of artificial fertilisation, such as is effected with ornamental plants in order to obtain new variations in colour, has led to the experiments which will here be discussed. The striking regularity with which the same hybrid forms always reappeared whenever fertilisation took place between the same species induced further experiments to be undertaken, the object of which was to follow up the developments of the hybrids in their progeny.

To this object numerous careful observers, such as Kölreuter, Gärtner, Herbert, Lecoq, Wichura and others, have devoted a part of their lives with inexhaustible perseverance. Gärtner especially, in his work "Die Bastarderzeugung im Pflanzenreiche" (The Production of Hybrids in the Vegetable Kingdom), has recorded very valuable observations; and quite recently Wichura published the results of some profound investigations into the hybrids of the Willow. That, so far, no generally applicable law governing the formation and development of hybrids has been successfully formulated can hardly be wondered at by anyone who is acquainted with the extent of the task, and can appreciate the difficulties with which experiments of this class have to contend. A final decision can only be arrived at when we shall have before us the results of detailed experiments made on plants belonging to the most diverse orders.

Those who survey the work done in this department will arrive at the conviction that among all the numerous experiments made, not one has been carried out to such an extent and in such a way as

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[1] This translation was made by the Royal Horticultural Society of London, and is reprinted, by permission of the Council of the Society, with footnotes added and minor changes suggested by Professor W. Bateson, enclosed within [ ]. The original paper was published in the *Verh. naturf. Ver. in Brunn, Abhandlungen*, iv. 1865, which appeared in 1866.

to make it possible to determine the number of different forms under which the offspring of hybrids appear, or to arrange these forms with certainty according to their separate generations, or definitely to ascertain their statistical relations.[1]

It requires indeed some courage to undertake a labour of such far-reaching extent; this appears, however, to be the only right way by which we can finally reach the solution of a question the importance of which cannot be overestimated in connection with the history of the evolution of organic forms.

The paper now presented records the results of such a detailed experiment. This experiment was practically confined to a small plant group, and is now, after eight years' pursuit, concluded in all essentials. Whether the plan upon which the separate experiments were conducted and carried out was the best suited to attain the desired end is left to the friendly decision of the reader.

Selection of the Experimental Plants

The value and utility of any experiment are determined by the fitness of the material to the purpose for which it is used, and thus in the case before us it cannot be immaterial what plants are subjected to experiment and in what manner such experiments are conducted.

The selection of the plant group which shall serve for experiments of this kind must be made with all possible care if it be desired to avoid from the outset every risk of questionable results.

The experimental plants must necessarily —

1. Possess constant differentiating characters.
2. The hybrids of such plants must, during the flowering period, be protected from the influence of all foreign pollen, or be easily capable of such protection.

The hybrids and their offspring should suffer no marked disturbance in their fertility in the successive generations.

Accidental impregnation by foreign pollen, if it occurred during the experiments and were not recognized, would lead to entirely erroneous conclusions. Reduced fertility or entire sterility of certain forms, such as occurs in the offspring of many hybrids, would render the experiments very difficult or entirely frustrate them. In

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[1] [It is to the clear conception of these three primary necessities that the whole success of Mendel's work is due. So far as I know this conception was absolutely new in his day.]

order to discover the relations in which the hybrid forms stand towards each other and also towards their progenitors it appears to be necessary that all members of the series developed in each successive generation should be, *without exception*, subjected to observation.

At the very outset special attention was devoted to the *Leguminosae* on account of their peculiar floral structure. Experiments which were made with several members of this family led to the result that the genus *Pisum* was found to possess the necessary qualifications.

Some thoroughly distinct forms of this genus possess characters which are constant, and easily and certainly recognizable, and when their hybrids are mutually crossed they yield perfectly fertile progeny. Furthermore, a disturbance through foreign pollen cannot easily occur, since the fertilising organs are closely packed inside the keel and the anther bursts within the bud, so that the stigma becomes covered with pollen even before the flower opens. This circumstance is of especial importance. As additional advantages worth mentioning, there may be cited the easy culture of these plants in the open ground and in pots, and also their relatively short period of growth. Artificial fertilisation is certainly a somewhat elaborate process, but nearly always succeeds. For this purpose the bud is opened before it is perfectly developed, the keel is removed, and each stamen carefully extracted by means of forceps, after which the stigma can at once be dusted over with the foreign pollen.

In all, thirty-four more or less distinct varieties of Peas were obtained from several seedsmen and subjected to a two years' trial. In the case of one variety there were noticed, among a larger number of plants all alike, a few forms which were markedly different. These, however, did not vary in the following year, and agreed entirely with another variety obtained from the same seedsman; the seeds were therefore doubtless merely accidentally mixed. All the other varieties yielded perfectly constant and similar offspring; at any rate, no essential difference was observed during two trial years. For fertilisation twenty-two of these were selected and cultivated during the whole period of the experiments. They remained constant without any exception.

Their systematic classification is difficult and uncertain. If we adopt the strictest definition of a species, according to which only those individuals belong to a species which under precisely the same circumstances display precisely similar characters, no two of these varieties could be referred to one species. According to the opinion of experts, however, the majority belong to the species *Pisum sativum;* while the rest are regarded and classed, some as sub-species of *P. sativum*, and some as independent species, such as *P. quadratum*, *P. saccharatum*, and *P. umbellatum*. The positions, however, which may be assigned to them in a classificatory system are quite immaterial for the purposes of the experiments in question. It has so far been found to be just as impossible to draw a sharp line between the hybrids of species and varieties as between species and varieties themselves.

Division and Arrangement of the Experiments

If two plants which differ constantly in one or several characters be crossed, numerous experiments have demonstrated that the common characters are transmitted unchanged to the hybrids and their progeny; but each pair of differentiating characters, on the other hand, unite in the hybrid to form a new character, which in the progeny of the hybrid is usually variable. The object of the experiment was to observe these variations in the case of each pair of differentiating characters, and to deduce the law according to which they appear in the successive generations. The experiment resolves itself therefore into just as many separate experiments as there are constantly differentiating characters presented in the experimental plants.

The various forms of Peas selected for crossing showed differences in the length and colour of the stem; in the size and form of the leaves; in the position, colour, and size of the flowers; in the length of the flower stalk; in the colour, form, and size of the pods; in the form and size of the seeds; and in the colour of the seed-coats and of the albumen [cotyledons]. Some of the characters noted do not permit of a sharp and certain separation, since the difference is of a " more or less " nature, which is often difficult to define. Such characters could not be utilised for the separate experiments; these could only be applied to characters which stand out clearly and definitely in the plants. Lastly, the result must show whether they, in their entirety, observe a regular behaviour in their hybrid unions, and whether from these facts any conclusion can be come to regarding those characters which possess a subordinate significance in the type.

The characters which were selected for experiment relate:

1. To the *difference in the form of the ripe seeds.* These are either round or roundish, the depressions, if any, occur on the surface, being always only shallow; or they are irregularly angular and deeply wrinkled (*P. quadratum*).

2. To the *difference in the colour of the seed albumen* (endosperm).[1] The albumen of the ripe seeds is either pale yellow, bright yellow and orange coloured, or it possesses a more or less intense green tint. This difference of colour is easily seen in the seeds as [= if] their coats are transparent.

3. To the *difference in the colour of the seed-coat.* This is either white, with which character white flowers are constantly correlated; or it is grey, grey-brown, leather-brown, with or without violet spotting, in which case the colour of the standards is violet, that of the wings purple, and the stem in the axils of the leaves is of a reddish tint. The grey seed-coats become dark brown in boiling water.

4. To the *difference in the form of the ripe pods.* These are either simply inflated, not contracted in places; or they are deeply constricted between the seeds and more or less wrinkled (*P. saccharatum*).

5. To the *difference in the colour of the unripe pods.* They are either light to dark green, or vividly yellow, in which colouring the stalks, leaf-veins, and calyx participate.[2]

6. To the *difference in the position of the flowers.* They are either axial, that is, distributed along the main stem; or they are terminal, that is, bunched at the top of the stem and arranged almost in a false umbel; in this case the upper part of the stem is more or less widened in section (*P. umbellatum*).[3]

7. To the *difference in the length of the stem.* The length of the stem[4] is very various in some forms; it is, however, a constant

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[1] [Mendel uses the terms "albumen" and "endosperm" somewhat loosely to denote the cotyledons, containing food-material, within the seed.]

[2] One species possesses a beautifully brownish-red coloured pod, which when ripening turns to violet and blue. Trials with this character were only begun last year. [Of these further experiments it seems no account was published. Correns has since worked with such a variety.]

[3] [This is often called the Mummy Pea. It shows slight fasciation. The form I know has white standard and salmon-red wings.]

[4] [In my account of these experiments (*R.H.S. Journal*, vol. xxv. p. 54) I misunderstood this paragraph and took "axis" to mean the *floral* axis, instead of the

character for each, in so far that healthy plants, grown in the same soil, are only subject to unimportant variations in this character.

In experiments with this character, in order to be able to discriminate with certainty, the long axis of 6 to 7 ft. was always crossed with the short one of $\frac{3}{4}$ ft. to $1\frac{1}{2}$ ft.

Each two of the differentiating characters enumerated above were united by cross-fertilisation. There were made for the

1st trial 60 fertilisations on 15 plants.
2nd “ 58 “ “ 10 “
3rd “ 35 “ “ 10 “
4th “ 40 “ “ 10 “
5th “ 23 “ “ 5 “
6th “ 34 “ “ 10 “
7th “ 37 “ “ 10 “

From a larger number of plants of the same variety only the most vigorous were chosen for fertilisation. Weakly plants always afford uncertain results, because even in the first generation of hybrids, and still more so in the subsequent ones, many of the offspring either entirely fail to flower or only form a few and inferior seeds.

Furthermore, in all the experiments reciprocal crossings were effected in such a way that each of the two varieties which in one set of fertilisation served as seed-bearer in the other set was used as the pollen plant.

The plants were grown in garden beds, a few also in pots, and were maintained in their naturally upright position by means of sticks, branches of trees, and strings stretched between. For each experiment a number of pot plants were placed during the blooming period in a greenhouse, to serve as control plants for the main experiment in the open as regards possible disturbance by insects. Among the insects [1] which visit Peas the beetle *Bruchus pisi* might be detrimental to the experiments should it appear in numbers. The female of this species is known to lay the eggs in the flower, and in so doing opens the keel; upon the tarsi of one specimen, which was caught in a flower, some pollen grains could clearly be seen under a lens. Mention must also be made of a circumstance

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main axis of the plant. The unit of measurement, being indicated in the original by a dash (′), I carelessly took to have been an *inch*, but the translation here given is evidently correct.]

[1] [It is somewhat surprising that no mention is made of Thrips, which swarm in Pea flowers. I had come to the conclusion that this is a real source of error and I see Laxton held the same opinion.]

which possibly might lead to the introduction of foreign pollen. It occurs, for instance, in some rare cases that certain parts of an otherwise quite normally developed flower wither, resulting in a partial exposure of the fertilising organs. A defective development of the keel has also been observed, owing to which the stigma and anthers remained partially uncovered.[1] It also sometimes happens that the pollen does not reach full perfection. In this event there occurs a gradual lengthening of the pistil during the blooming period, until the stigmatic tip protrudes at the point of the keel. This remarkable appearance has also been observed in hybrids of *Phaseolus* and *Lathyrus*.

The risk of false impregnation by foreign pollen is, however, a very slight one with *Pisum*, and is quite incapable of disturbing the general result. Among more than 10,000 plants which were carefully examined there were only a very few cases where an indubitable false impregnation had occurred. Since in the greenhouse such a case was never remarked, it may well be supposed that *Bruchus pisi*, and possibly also the described abnormalities in the floral structure, were to blame.

[F_1] THE FORMS OF THE HYBRIDS[2]

Experiments which in previous years were made with ornamental plants have already afforded evidence that the hybrids, as a rule, are not exactly intermediate between the parental species. With some of the more striking characters, those, for instance, which relate to the form and size of the leaves, the pubescence of the several parts, &c., the intermediate, indeed, is nearly always to be seen; in other cases, however, one of the two parental characters is so preponderant that it is difficult, or quite impossible, to detect the other in the hybrid.

This is precisely the case with the Pea hybrids. In the case of each of the seven crosses the hybrid-character resembles[3] that of one of the parental forms so closely that the other either escapes

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[1] [This also happens in Sweet Peas.]

[2] [Mendel throughout speaks of his cross-bred Peas as "hybrids," a term which many restrict to the offspring of two distinct *species*. He, as he explains, held this to be only a question of degree.]

[3] [Note that Mendel, with true penetration, avoids speaking of the hybrid-character as "transmitted" by either parent, thus escaping the error pervading the older views of heredity.]

observation completely or cannot be detected with certainty. This circumstance is of great importance in the determination and classification of the forms under which the offspring of the hybrids appear. Henceforth in this paper those characters which are transmitted entire, or almost unchanged in the hybridisation, and therefore in themselves constitute the characters of the hybrid, are termed the *dominant*, and those which become latent in the process *recessive*. The expression " recessive " has been chosen because the characters thereby designated withdraw or entirely disappear in the hybrids, but nevertheless reappear unchanged in their progeny, as will be demonstrated later on.

It was furthermore shown by the whole of the experiments that it is perfectly immaterial whether the dominant character belongs to the seed-bearer or to the pollen-parent; the form of the hybrid remains identical in both cases. This interesting fact was also emphasised by Gärtner, with the remark that even the most practised expert is not in a position to determine in a hybrid which of the two parental species was the seed or the pollen plant.[1]

Of the differentiating characters which were used in the experiments the following are dominant:

1. The round or roundish form of the seed with or without shallow depressions.
2. The yellow colouring of the seed albumen [cotyledons].
3. The grey, grey-brown, or leather-brown colour of the seed-coat, in association with violet-red blossoms and reddish spots in the leaf axils.
4. The simply inflated form of the pod.
5. The green colouring of the unripe pod in association with the same colour in the stems, the leaf-veins and the calyx.
6. The distribution of the flowers along the stem.
7. The greater length of stem.

With regard to this last character it must be stated that the longer of the two parental stems is usually exceeded by the hybrid, a fact which is possibly only attributable to the greater luxuriance which appears in all parts of plants when stems of very different length are crossed. Thus, for instance, in repeated experiments, stems of 1 ft. and 6 ft. in length yielded without exception hybrids which varied in length between 6 ft. and $7\frac{1}{2}$ ft.

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[1] [Gärtner, p. 223.]

The hybrid seeds in the experiments with seed-coat are often more spotted, and the spots sometimes coalesce into small bluish-violet patches. The spotting also frequently appears even when it is absent as a parental character.[1]

The hybrid forms of the seed-shape and of the albumen [colour] are developed immediately after the artificial fertilisation by the mere influence of the foreign pollen. They can, therefore, be observed even in the first year of experiment, whilst all the other characters naturally only appear in the following year in such plants as have been raised from the crossed seed.

[F_2] The Generation [bred] from the Hybrids

In this generation there reappear, together with the dominant characters, also the recessive ones with their peculiarities fully developed, and this occurs in the definitely expressed average proportion of three to one, so that among each four plants of this generation three display the dominant character and one the recessive. This relates without exception to all the characters which were investigated in the experiments. The angular wrinkled form of the seed, the green colour of the albumen, the white colour of the seed-coats and the flowers, the constrictions of the pods, the yellow colour of the unripe pod, of the stalk, of the calyx, and of the leaf venation, the umbel-like form of the inflorescence, and the dwarfed stem, all reappear in the numerical proportion given, without any essential alteration. *Transitional forms were not observed in any experiment.*

Since the hybrids resulting from reciprocal crosses are formed alike and present no appreciable difference in their subsequent development, consequently the results [of the reciprocal crosses] can be reckoned together in each experiment. The relative numbers which were obtained for each pair of differentiating characters are as follows:

Expt. 1. Form of seed. — From 253 hybrids 7,324 seeds were obtained in the second trial year. Among them were 5,474 round or roundish ones and 1,850 angular wrinkled ones. Therefrom the ratio 2.96 to 1 is deduced.

Expt. 2. Colour of albumen. — 258 plants yielded 8,023 seeds, 6,022 yellow, and 2,001 green; their ratio, therefore, is as 3.01 to 1.

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[1] [This refers to the coats of the seeds borne by F_1 plants.]

In these two experiments each pod yielded usually both kinds of seeds. In well-developed pods which contained on the average six to nine seeds, it often happened that all the seeds were round (Expt. 1) or all yellow (Expt. 2); on the other hand there were never observed more than five wrinkled or five green ones in one pod. It appears to make no difference whether the pods are developed early or later in the hybrid or whether they spring from the main axis or from a lateral one. In some few plants only a few seeds developed in the first formed pods, and these possessed exclusively one of the two characters, but in the subsequently developed pods the normal proportions were maintained nevertheless.

As in separate pods, so did the distribution of the characters vary in separate plants. By way of illustration the first ten individuals from both series of experiments may serve.

	Experiment 1. Form of Seed.		Experiment 2. Color of Albumen.	
Plants	Round	Angular	Yellow	Green
1	45	12	25	11
2	27	8	32	7
3	24	7	14	5
4	19	16	70	27
5	32	11	24	13
6	26	6	20	6
7	88	24	32	13
8	22	10	44	9
9	28	6	50	14
10	25	7	44	18

As extremes in the distribution of the two seed characters in one plant, there were observed in Expt. 1 an instance of 43 round and only 2 angular, and another of 14 round and 15 angular seeds. In Expt. 2 there was a case of 32 yellow and only 1 green seed, but also one of 20 yellow and 19 green.

These two experiments are important for the determination of the average ratios, because with a smaller number of experimental plants they show that very considerable fluctuations may occur. In counting the seeds, also, especially in Expt. 2, some care is requisite, since in some of the seeds of many plants the green colour of the albumen is less developed, and at first may be easily overlooked. The cause of this partial disappearance of the green colouring has no connection with the hybrid-character of the plants, as it likewise occurs in the parental variety. This peculiarity [bleaching] is also confined to the individual and is not inherited by the offspring. In luxuriant plants this appearance was frequently noted. Seeds which are damaged by insects during their development often vary in colour and form, but, with a little practice in sorting, errors are easily avoided. It is almost superfluous to mention that the pods must remain on the plants until they are thoroughly ripened and have become dried, since it is only then that the shape and colour of the seed are fully developed.

Expt. 3. Colour of the seed-coats. — Among 929 plants 705 bore violet-red flowers and grey-brown seed-coats; 224 had white flowers and white seed-coats, giving the proportion 3.15 to 1.

Expt. 4. Form of pods. — Of 1,181 plants 882 had them simply inflated, and in 299 they were constricted. Resulting ratio, 2.95 to 1.

Expt. 5. Colour of the unripe pods. — The number of trial plants was 580, of which 428 had green pods and 152 yellow ones. Consequently these stand in the ratio 2.82 to 1.

Expt. 6. Position of flowers. — Among 858 cases 651 had inflorescences axial and 207 terminal. Ratio, 3.14 to 1.

Expt. 7. Length of stem. — Out of 1,064 plants, in 787 cases the stem was long, and in 277 short. Hence a mutual ratio of 2.84 to 1. In this experiment the dwarfed plants were carefully lifted and transferred to a special bed. This precaution was necessary, as otherwise they would have perished through being overgrown by their tall relatives. Even in their quite young state they can be easily picked out by their compact growth and thick dark-green foliage.[1]

If now the results of the whole of the experiments be brought together, there is found, as between the number of forms with the dominant and recessive characters, an average ratio of 2.98 to 1, or 3 to 1.

The dominant character can have here a *double signification* — viz. that of a parental character, or a hybrid-character.[2] In which of the two significations it appears in each separate case can only be determined by the following generation. As a parental character it must pass over unchanged to the whole of the offspring; as

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[1] [This is true also of the dwarf or "Cupid" Sweet Peas.]

[2] [This paragraph presents the view of the hybrid-character as something incidental to the hybrid, and not "transmitted" to it — a true and fundamental conception here expressed probably for the first time.]

a hybrid-character, on the other hand, it must maintain the same behaviour as in the first generation [F_2].

[F_3] THE SECOND GENERATION [BRED] FROM THE HYBRIDS

Those forms which in the first generation [F_2] exhibit the recessive character do not further vary in the second generation [F_3] as regards this character; they remain constant in their offspring.

It is otherwise with those which possess the dominant character in the first generation [bred from the hybrids]. Of these *two*-thirds yield offspring which display the dominant and recessive characters in the proportion of 3 to 1, and thereby show exactly the same ratio as the hybrid forms, while only *one*-third remains with the dominant character constant.

The separate experiments yielded the following results:

Expt. 1. Among 565 plants which were raised from round seeds of the first generation, 193 yielded round seeds only, and remained therefore constant in this character; 372, however, gave both round and wrinkled seeds, in the proportion of 3 to 1. The number of the hybrids, therefore, as compared with the constants is 1.93 to 1.

Expt. 2. Of 519 plants which were raised from seeds whose albumen was of yellow colour in the first generation, 166 yielded exclusively yellow, while 353 yielded yellow and green seeds in the proportion of 3 to 1. There resulted, therefore, a division into hybrid and constant forms in the proportion of 2.13 to 1.

For each separate trial in the following experiments 100 plants were selected which displayed the dominant character in the first generation, and in order to ascertain the significance of this, ten seeds of each were cultivated.

Expt. 3. The offspring of 36 plants yielded exclusively grey-brown seed-coats, while of the offspring of 64 plants some had grey-brown and some had white.

Expt. 4. The offspring of 29 plants had only simply inflated pods; of the offspring of 71, on the other hand, some had inflated and some constricted.

Expt. 5. The offspring of 40 plants had only green pods; of the offspring of 60 plants some had green, some yellow ones.

Expt. 6. The offspring of 33 plants had only axial flowers; of the offspring of 67, on the other hand, some had axial and some terminal flowers.

Expt. 7. The offspring of 28 plants inherited the long axis, and those of 72 plants some the long and some the short axis.

In each of these experiments a certain number of the plants came constant with the dominant character. For the determination of the proportion in which the separation of the forms with the constantly persistent character results, the two first experiments are of especial importance, since in these a larger number of plants can be compared. The ratios 1.93 to 1 and 2.13 to 1 gave together almost exactly the average ratio of 2 to 1. The sixth experiment gave a quite concordant result; in the others the ratio varies more or less, as was only to be expected in view of the smaller number of 100 trial plants. Experiment 5, which shows the greatest departure, was repeated, and then, in lieu of the ratio of 60 and 40, that of 65 and 35 resulted. *The average ratio of 2 to 1 appears, therefore, as fixed with certainty.* It is therefore demonstrated that, of those forms which possess the dominant character in the first generation, two-thirds have the hybrid-character, while one-third remains constant with the dominant character.

The ratio of 3 to 1, in accordance with which the distribution of the dominant and recessive characters results in the first generation, resolves itself therefore in all experiments into the ratio of 2:1:1 if the dominant character be differentiated according to its significance as a hybrid-character or as a parental one. Since the members of the first generation [F_2] spring directly from the seed of the hybrids [F_1], *it is now clear that the hybrids form seeds having one or other of the two differentiating characters, and of these one-half develop again the hybrid form, while the other half yield plants which remain constant and receive the dominant or the recessive characters [respectively] in equal numbers.*

The Subsequent Generations [bred] from the Hybrids

The proportions in which the descendants of the hybrids develop and split up in the first and second generations presumably hold good for all subsequent progeny. Experiments 1 and 2 have already been carried through six generations, 3 and 7 through five, and 4, 5, and 6 through four, these experiments being continued from the third generation with a small number of plants, and no departure from the rule has been perceptible. The offspring of the hybrids separated in each generation in the ratio of 2:1:1 into hybrids and constant forms.

If A be taken as denoting one of the two constant characters, for instance the dominant, a, the recessive, and Aa the hybrid form in which both are conjoined, the expression

$$A + 2Aa + a$$

shows the terms in the series for the progeny of the hybrids of two differentiating characters.

The observation made by Gärtner, Kölreuter, and others, that hybrids are inclined to revert to the parental forms, is also confirmed by the experiments described. It is seen that the number of the hybrids which arise from one fertilisation, as compared with the number of forms which become constant, and their progeny from generation to generation, is continually diminishing, but that nevertheless they could not entirely disappear. If an average equality of fertility in all plants in all generations be assumed, and if, furthermore, each hybrid forms seed of which one-half yields hybrids again, while the other half is constant to both characters in equal proportions, the ratio of numbers for the offspring in each generation is seen by the following summary, in which A and a denote again the two parental characters, and Aa the hybrid forms. For brevity's sake it may be assumed that each plant in each generation furnishes only 4 seeds.

				RATIOS
Generation	A	Aa	a	$A : Aa : a$
1	1	2	1	$1 : 2 : 1$
2	6	4	6	$3 : 2 : 3$
3	28	8	28	$7 : 2 : 7$
4	120	16	120	$15 : 2 : 15$
5	496	32	496	$31 : 2 : 31$
n				$2^n—1 : 2 : 2^n—1$

In the tenth generation, for instance, $2^n - 1 = 1023$. There result, therefore, in each 2,084 plants which arise in this generation 1,023 with the constant dominant character, 1,023 with the recessive character, and only two hybrids.

The Offspring of Hybrids in which several Differentiating Characters are Associated

In the experiments above described plants were used which differed only in one essential character.[1] The next task consisted

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[1] [This statement of Mendel's in the light of present knowledge is open to some misconception. Though his work makes it evident that such varieties may exist,

in ascertaining whether the law of development discovered in these applied to each pair of differentiating characters when several diverse characters are united in the hybrid by crossing. As regards the form of the hybrids in these cases, the experiments showed throughout that this invariably more nearly approaches to that one of the two parental plants which possesses the greater number of dominant characters. If, for instance, the seed plant has a short stem, terminal white flowers, and simply inflated pods; the pollen plant, on the other hand, a long stem, violet-red flowers distributed along the stem, and constricted pods; the hybrid resembles the seed parent only in the form of the pod; in the other characters it agrees with the pollen parent. Should one of the two parental types possess only dominant characters, then the hybrid is scarcely or not at all distinguishable from it.

Two experiments were made with a considerable number of plants. In the first experiment the parental plants differed in the form of the seed and in the colour of the albumen; in the second in the form of the seed, in the colour of the albumen, and in the colour of the seed-coats. Experiments with seed characters give the result in the simplest and most certain way.

In order to facilitate study of the data in these experiments, the different characters of the seed plant will be indicated by A, B, C, those of the pollen plant by a, b, c, and the hybrid forms of the characters by Aa, Bb, and Cc.

Expt. 1. —	AB, seed parents;	ab, pollen parents;
	A, form round;	a, form wrinkled;
	B, albumen yellow.	b, albumen green.

The fertilised seeds appeared round and yellow like those of the seed parents. The plants raised therefrom yielded seeds of four sorts, which frequently presented themselves in one pod. In all, 556 seeds were yielded by 15 plants, and of these there were:

315	round and yellow,
101	wrinkled and yellow,
108	round and green,
32	wrinkled and green.

it is very unlikely that Mendel could have had seven pairs of varieties such that the members of each pair differed from each other in *only* one considerable character (*wesentliches Merkmal*). The point is probably of little theoretical or practical consequence, but a rather heavy stress is thrown on "*wesentlich.*"]

All were sown the following year. Eleven of the round yellow seeds did not yield plants, and three plants did not form seeds. Among the rest:

38 had round yellow seeds	*AB*
65 round yellow and green seeds	*ABb*
60 round yellow and wrinkled yellow seeds	*AaB*
138 round yellow and green, wrinkled yellow and green seeds	*AaBb*

From the wrinkled yellow seeds 96 resulting plants bore seed, of which:

28 had only wrinkled yellow seeds	*aB*
68 wrinkled yellow and green seeds	*aBb.*

From 108 round green seeds 102 resulting plants fruited, of which:

35 had only round green seeds	*Ab*
67 round and wrinkled green seeds	*Aab.*

The wrinkled green seeds yielded 30 plants which bore seeds all of like character; they remained constant *ab.*

The offspring of the hybrids appeared therefore under nine different forms, some of them in very unequal numbers. When these are collected and co-ordinated we find:

38 plants with the sign *AB*
35 " " " " *Ab*
28 " " " " *aB*
30 " " " " *ab*
65 " " " " *ABb*
68 " " " " *aBb*
60 " " " " *AaB*
67 " " " " *Aab*
138 " " " " *AaBb.*

The whole of the forms may be classed into three essentially different groups. The first includes those with the signs *AB*, *Ab*, *aB*, and *ab*: they possess only constant characters and do not vary again in the next generation. Each of these forms is represented on the average thirty-three times. The second group includes the signs *ABb*, *aBb*, *AaB*, *Aab:* these are constant in one character and hybrid in another, and vary in the next generation only as regards the hybrid-character. Each of these appears on an average sixty-five times. The form *AaBb* occurs 138 times: it is hybrid in both characters, and behaves exactly as do the hybrids from which it is derived.

If the numbers in which the forms belonging to these classes appear be compared, the ratios of 1, 2, 4 are unmistakably evident. The numbers 32, 65, 138 present very fair approximations to the ratio numbers of 33, 66, 132.

The developmental series consists, therefore, of nine classes, of which four appear therein always once and are constant in both characters; the forms AB, ab, resemble the parental forms, the two other present combinations between the conjoined characters A, a, B, b, which combinations are likewise possibly constant. Four classes appear always twice, and are constant in one character and hybrid in the other. One class appears four times, and is hybrid in both characters. Consequently the offspring of the hybrids, if two kinds of differentiating characters are combined therein, are represented by the expression

$$AB + Ab + aB + ab + 2ABb + 2aBb + 2AaB + 2Aab + 4AaBb.$$

This expression is indisputably a combination series in which the two expressions for the characters A and a, B and b are combined. We arrive at the full number of the classes of the series by the combination of the expressions:

$$A + 2Aa + a$$
$$B + 2Bb + b.$$

Expt. 2.

ABC, seed parents;	abc, pollen parents;
A, form round;	a, form wrinkled;
B, albumen yellow;	b, albumen green;
C, seed-coat grey-brown.	c, seed-coat white.

This experiment was made in precisely the same way as the previous one. Among all the experiments it demanded the most time and trouble. From 24 hybrids 687 seeds were obtained in all: these were all either spotted, grey-brown or grey-green, round or wrinkled.[1] From these in the following year 639 plants fruited, and, as further investigation showed, there were among them:

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[1] [Note that Mendel does not state the cotyledon-colour of the first crosses in this case; for as the coats were thick, it could not have been seen without opening or peeling the seeds.]

8	plants	*ABC*	22	plants	*ABCc*	45	plants	*ABbCc*
14	"	*ABc*	17	"	*AbCc*	36	"	*aBbCc*
9	"	*AbC*	25	"	*aBCc*	38	"	*AaBCc*
11	"	*Abc*	20	"	*abCc*	40	"	*AabCc*
8	"	*aBC*	15	"	*ABbC*	49	"	*AaBbC*
10	"	*aBc*	18	"	*ABbc*	48	"	*AaBbc*
10	"	*abC*	19	"	*aBbC*			
7	"	*abc*	24	"	*aBbc*			
			14	"	*AaBC*	78	"	*AaBbCc*
			18	"	*AaBc*			
			20	"	*AabC*			
			16	"	*Aabc*			

The whole expression contains 27 terms. Of these 8 are constant in all characters, and each appears on the average 10 times; 12 are constant in two characters, and hybrid in the third; each appears on the average 19 times; 6 are constant in one character and hybrid in the other two; each appears on the average 43 times. One form appears 78 times and is hybrid in all of the characters. The ratios 10, 19, 43, 78 agree so closely with the ratios 10, 20, 40, 80, or 1, 2, 4, 8, that this last undoubtedly represents the true value.

The development of the hybrids when the original parents differ in three characters results therefore according to the following expression:

$$\begin{aligned} &ABC + ABc + AbC + Abc + aBC + aBc + abC + abc \\ &+ 2\,ABCc + 2\,AbCc + 2\,aBCc + 2\,abCc + 2\,ABbC \\ &+ 2\,ABbc + 2\,aBbC + 2\,aBbc + 2\,AaBC + 2\,AaBc \\ &+ 2\,AabC + 2\,Aabc + 4\,ABbCc + 4\,aBbCc + 4\,AaBCc \\ &+ 4\,AabCc + 4\,AaBbC + 4\,AaBbc + 8\,AaBbCc. \end{aligned}$$

Here also is involved a combination series in which the expressions for the characters A and a, B and b, C and c, are united. The expressions

$$\begin{gathered} A + 2Aa + a \\ B + 2Bb + b \\ C + 2Cc + c \end{gathered}$$

give all the classes of the series. The constant combinations which occur therein agree with all combinations which are possible between the characters A, B, C, a, b, c; two thereof, ABC and abc, resemble the two original parental stocks.

In addition, further experiments were made with a smaller number of experimental plants in which the remaining characters by twos and threes were united as hybrids: all yielded approximately the same results. There is therefore no doubt that for the whole of the characters involved in the experiments the principle applies that *the offspring of the hybrids in which several essentially different characters are combined exhibit the terms of a series of combinations, in which the developmental series for each pair of differentiating characters are united.* It is demonstrated at the same time that *the relation of each pair of different characters in hybrid union is independent of the other differences in the two original parental stocks.*

If n represents the number of the differentiating characters in the two original stocks, 3^n gives the number of terms of the combination series, 4^n the number of individuals which belong to the series, and 2^n the number of unions which remain constant. The series therefore contains, if the original stocks differ in four characters, $3^4 = 81$ classes, $4^4 = 256$ individuals, and $2^4 = 16$ constant forms; or, which is the same, among each 256 offspring of the hybrids there are 81 different combinations, 16 of which are constant.

All constant combinations which in Peas are possible by the combination of the said seven differentiating characters were actually obtained by repeated crossing. Their number is given by $2^7 = 128$. Thereby is simultaneously given the practical proof *that the constant characters which appear in the several varieties of a group of plants may be obtained in all the associations which are possible according to the* [*mathematical*] *laws of combination, by means of repeated artificial fertilisation.*

As regards the flowering time of the hybrids, the experiments are not yet concluded. It can, however, already be stated that the time stands almost exactly between those of the seed and pollen parents, and that the constitution of the hybrids with respect to this character probably follows the rule ascertained in the case of the other characters. The forms which are selected for experiments of this class must have a difference of at least twenty days from the middle flowering period of one to that of the other; furthermore, the seeds when sown must all be placed at the same depth in the earth, so that they may germinate simultaneously. Also, during the whole flowering period, the more important variations in temperature must be taken into account, and the partial hastening or delaying of the flowering which may result therefrom. It is clear that this experiment presents many difficulties to be overcome and necessitates great attention.

If we endeavour to collate in a brief form the results arrived at, we find that those differentiating characters, which admit of easy and certain recognition in the experimental plants, all behave exactly alike in their hybrid associations. The offspring of the hybrids of each pair of differentiating characters are, one-half, hybrid again, while the other half are constant in equal proportions having the characters of the seed and pollen parents respectively. If several differentiating characters are combined by cross-fertilisation in a hybrid, the resulting offspring form the terms of a combination series in which the combination series for each pair of differentiating characters are united.

The uniformity of behaviour shown by the whole of the characters submitted to experiment permits, and fully justifies, the acceptance of the principle that a similar relation exists in the other characters which appear less sharply defined in plants, and therefore could not be included in the separate experiments. An experiment with peduncles of different lengths gave on the whole a fairly satisfactory result, although the differentiation and serial arrangement of the forms could not be effected with that certainty which is indispensable for correct experiment.

The Reproductive Cells of the Hybrids

The results of the previously described experiments led to further experiments, the results of which appear fitted to afford some conclusions as regards the composition of the egg and pollen cells of hybrids. An important clue is afforded in *Pisum* by the circumstance that among the progeny of the hybrids constant forms appear, and that this occurs, too, in respect of all combinations of the associated characters. So far as experience goes, we find it in every case confirmed that constant progeny can only be formed when the egg cells and the fertilising pollen are of like character, so that both are provided with the material for creating quite similar individuals, as is the case with the normal fertilisation of pure species. We must therefore regard it as certain that exactly similar factors must be at work also in the production of the constant forms in the hybrid plants. Since the various constant forms are produced in *one* plant, or even in *one* flower of a plant, the conclusion appears logical that in the ovaries of the hybrids there are formed as many sorts of egg cells, and in the anthers as many sorts of pollen cells, as there are possible constant combination forms, and that these egg and pollen cells agree in their internal composition with those of the separate forms.

In point of fact it is possible to demonstrate theoretically that this hypothesis would fully suffice to account for the development of the hybrids in the separate generations, if we might at the same time assume that the various kinds of egg and pollen cells were formed in the hybrids on the average in equal numbers.[1]

In order to bring these assumptions to an experimental proof, the following experiments were designed. Two forms which were constantly different in the form of the seed and the colour of the albumen were united by fertilisation.

If the differentiating characters are again indicated as *A*, *B*, *a*, *b*, we have:

AB, seed parent;	*ab*, pollen parent;
A, form round;	*a*, form wrinkled;
B, albumen yellow.	*b*, albumen green.

The artificially fertilised seeds were sown together with several seeds of both original stocks, and the most vigorous examples were chosen for the reciprocal crossing. There were fertilised:

1. The hybrids with the pollen of *AB*.
2. The hybrids " " " " *ab*.
3. *AB* " " " " the hybrids.
4. *ab* " " " " the hybrids.

For each of these four experiments the whole of the flowers on three plants were fertilised. If the above theory be correct, there must be developed on the hybrids egg and pollen cells of the forms *AB*, *Ab*, *aB*, *ab*, and there would be combined:

1. The egg cells *AB*, *Ab*, *aB*, *ab* with the pollen cells *AB*.
2. The egg cells *AB*, *Ab*, *aB*, *ab* with the pollen cells *ab*.
3. The egg cells *AB* with the pollen cells *AB*, *Ab*, *aB*, *ab*.
4. The egg cells *ab* with the pollen cells *AB*, *Ab*, *aB*, *ab*.

From each of these experiments there could then result only the following forms:

1. *AB*, *ABb*, *AaB*, *AaBb*.
2. *AaBb*, *Aab*, *aBb*, *ab*.
3. *AB*, *ABb*, *AaB*, *AaBb*.
4. *AaBb*, *Aab*, *aBb*, *ab*.

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[1] [This and the preceding paragraph contain the essence of the Mendelian principles of heredity.]

If, furthermore, the several forms of the egg and pollen cells of the hybrids were produced on an average in equal numbers, then in each experiment the said four combinations should stand in the same ratio to each other. A perfect agreement in the numerical relations was, however, not to be expected, since in each fertilisation, even in normal cases, some egg cells remain undeveloped or subsequently die, and many even of the well-formed seeds fail to germinate when sown. The above assumption is also limited in so far that, while it demands the formation of an equal number of the various sorts of egg and pollen cells, it does not require that this should apply to each separate hybrid with mathematical exactness.

The first and second experiments had primarily the object of proving the composition of the hybrid egg cells, while the third and fourth experiments were to decide that of the pollen cells.[1] As is shown by the above demonstration the first and third experiments and the second and fourth experiments should produce precisely the same combinations, and even in the second year the result should be partially visible in the form and colour of the artificially fertilised seed. In the first and third experiments the dominant characters of form and colour, A and B, appear in each union, and are also partly constant and partly in hybrid union with the recessive characters a and b, for which reason they must impress their peculiarity upon the whole of the seeds. All seeds should therefore appear round and yellow, if the theory be justified. In the second and fourth experiments, on the other hand, one union is hybrid in form and in colour, and consequently the seeds are round and yellow; another is hybrid in form, but constant in the recessive character of colour, whence the seeds are round and green; the third is constant in the recessive character of form but hybrid in colour, consequently the seeds are wrinkled and yellow; the fourth is constant in both recessive characters, so that the seeds are wrinkled and green. In both these experiments there were consequently four sorts of seed to be expected—viz. round and yellow, round and green, wrinkled and yellow, wrinkled and green.

The crop fulfilled these expectations perfectly. There were obtained in the

1st Experiment, 98 exclusively round yellow seeds;
3rd " 94 " " " "

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[1] [To prove, namely, that both were similarly differentiated, and not one or other only.]

In the 2d Experiment, 31 round and yellow, 26 round and green, 27 wrinkled and yellow, 26 wrinkled and green seeds.

In the 4th Experiment, 24 round and yellow, 25 round and green, 22 wrinkled and yellow, 26 wrinkled and green seeds.

There could scarcely be now any doubt of the success of the experiment; the next generation must afford the final proof. From the seed sown there resulted for the first experiment 90 plants, and for the third 87 plants which fruited: these yielded for the

1st Exp.	3rd Exp.		
20	25	round yellow seeds	*AB*
23	19	round yellow and green seeds	*ABb*
25	22	round and wrinkled yellow seeds	*AaB*
22	21	round and wrinkled green and yellow seeds	*AaBb*

In the second and fourth experiments the round and yellow seeds yielded plants with round and wrinkled yellow and green seeds, *AaBb*.

From the round green seeds, plants resulted with round and wrinkled green seeds, *Aab*.

The wrinkled yellow seeds gave plants with wrinkled yellow and green seeds, *aBb*.

From the wrinkled green seeds plants were raised which yielded again only wrinkled and green seeds, *ab*.

Although in these two experiments likewise some seeds did not germinate, the figures arrived at already in the previous year were not affected thereby, since each kind of seed gave plants which, as regards their seed, were like each other and different from the others. There resulted therefore from the

2d Exp.	4th Exp.	
31	24	plants of the form *AaBb*
26	25	" " " " *Aab*
27	22	" " " " *aBb*
26	27	" " " " *ab*

In all the experiments, therefore, there appeared all the forms which the proposed theory demands, and they came in nearly equal numbers.

In a further experiment the characters of flower-colour and length of stem were experimented upon, and selection was so made that in the third year of the experiment each character ought to appear in half of all the plants if the above theory were correct. *A*, *B*, *a*, *b* serve again as indicating the various characters.

A, violet-red flowers. a, white flowers.
B, axis long. b, axis short.

The form Ab was fertilised with ab, which produced the hybrid Aab. Furthermore, aB was also fertilised with ab, whence the hybrid aBb. In the second year, for further fertilisation, the hybrid Aab was used as seed parent, and hybrid aBb as pollen parent.

Seed parent, Aab. Pollen parent, aBb.
Possible egg cells, Ab,ab. Pollen cells, aB,ab.

From the fertilisation between the possible egg and pollen cells four combinations should result, viz.,

$$AaBb + aBb + Aab + ab.$$

From this it is perceived that, according to the above theory, in the third year of the experiment out of all the plants

Half should have violet-red flowers (Aa), Classes 1, 3
" " " white flowers (a) " 2, 4
" " " a long axis (Bb) " 1, 2
" " " a short axis (b) " 3, 4

From 45 fertilisations of the second year 187 seeds resulted, of which only 166 reached the flowering stage in the third year. Among these the separate classes appeared in the numbers following:

Class	Color of flower	Stem	
1	violet-red	long	47 times
2	white	long	40 "
3	violet-red	short	38 "
4	white	short	41 "

There subsequently appeared

The violet-red flower-colour (Aa) in 85 plants.
" white " " (a) in 81 "
" long stem (Bb) in 87 "
" short " (b) in 79 "

The theory adduced is therefore satisfactorily confirmed in this experiment also.

For the characters of form of pod, colour of pod, and position of flowers, experiments were also made on a small scale, and results obtained in perfect agreement. All combinations which were possible through the union of the differentiating characters duly appeared, and in nearly equal numbers.

Experimentally, therefore, the theory is confirmed that *the pea hybrids form egg and pollen cells which, in their constitution, represent in equal numbers all constant forms which result from the combination of the characters united in fertilisation.*

The difference of the forms among the progeny of the hybrids, as well as the respective ratios of the numbers in which they are observed, find a sufficient explanation in the principle above deduced. The simplest case is afforded by the developmental series of each pair of differentiating characters. This series is represented by the expression $A + 2Aa + a$, in which A and a signify the forms with constant differentiating characters, and Aa the hybrid form of both. It includes in three different classes four individuals. In the formation of these, pollen and egg cells of the form A and a take part on the average equally in the fertilisation; hence each form [occurs] twice, since four individuals are formed. There participate consequently in the fertilisation

The pollen cells $A + A + a + a$
The egg cells $A + A + a + a$.

It remains, therefore, purely a matter of chance which of the two sorts of pollen will become united with each separate egg cell. According, however, to the law of probability, it will always happen, on the average of many cases, that each pollen form, A and a, will unite equally often with each egg cell form, A and a, consequently one of the two pollen cells A in the fertilisation will meet with the egg cell A and the other with an egg cell a, and so likewise one pollen cell a will unite with an egg cell A, and the other with egg cell a.

$$\begin{tikzcd}
\text{Pollen cells} & A \arrow[d] & A \arrow[dr] & a \arrow[dl] & a \arrow[d] \\
\text{Egg cells} & A & A & a & a
\end{tikzcd}$$

The result of the fertilisation may be made clear by putting the signs for the conjoined egg and pollen cells in the form of fractions, those for the pollen cells above and those for the egg cells below the line. We then have

$$\frac{A}{A}+\frac{A}{a}+\frac{a}{A}+\frac{a}{a}.$$

In the first and fourth term the egg and pollen cells are of like kind, consequently the product of their union must be constant, viz. A

and a; in the second and third, on the other hand, there again results a union of the two differentiating characters of the stocks, consequently the forms resulting from these fertilisations are identical with those of the hybrid from which they sprang. *There occurs accordingly a repeated hybridisation.* This explains the striking fact that the hybrids are able to produce, besides the two parental forms, offspring which are like themselves; $\frac{A}{a}$ and $\frac{a}{A}$ both give the same union Aa, since, as already remarked above, it makes no difference in the result of fertilisation to which of the two characters the pollen or egg cells belong. We may write then

$$\frac{A}{A} + \frac{A}{a} + \frac{a}{A} + \frac{a}{a} = A + 2Aa + a.$$

This represents the average result of the self-fertilisation of the hybrids when two differentiating characters are united in them. In individual flowers and in individual plants, however, the ratios in which the forms of the series are produced may suffer not inconsiderable fluctuations.[1] Apart from the fact that the numbers in which both sorts of egg cells occur in the seed vessels can only be regarded as equal on the average, it remains purely a matter of chance which of the two sorts of pollen may fertilise each separate egg cell. For this reason the separate values must necessarily be subject to fluctuations, and there are even extreme cases possible, as were described earlier in connection with the experiments on the form of the seed and the colour of the albumen. The true ratios of the numbers can only be ascertained by an average deduced from the sum of as many single values as possible; the greater the number, the more are merely chance effects eliminated.

The developmental series for hybrids in which two kinds of differentiating characters are united contains, among sixteen individuals, nine different forms, viz.,

$$AB + Ab + aB + ab + 2ABb + 2aBb + 2AaB + 2Aab + 4AaBb.$$

Between the differentiating characters of the original stocks, Aa and Bb, four constant combinations are possible, and consequently the hybrids produce the corresponding four forms of egg and pollen cells AB, Ab, aB, ab, and each of these will on the average figure

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[1] [Whether segregation by such units is more than purely fortuitous may perhaps be determined by seriation.]

four times in the fertilisation, since sixteen individuals are included in the series. Therefore the participators in the fertilisation are

$$\text{Pollen cells } AB + AB + AB + AB + Ab + Ab + Ab + Ab + aB + aB + aB + aB + ab + ab + ab + ab.$$

$$\text{Egg cells } AB + AB + AB + AB + Ab + Ab + Ab + Ab + aB + aB + aB + aB + ab + ab + ab + ab.$$

In the process of fertilisation each pollen form unites on an average equally often with each egg cell form, so that each of the four pollen cells *AB* unites once with one of the forms of egg cell *AB*, *Ab*, *aB*, *ab*. In precisely the same way the rest of the pollen cells of the forms *Ab*, *aB*, *ab* unite with all the other egg cells. We obtain therefore

$$\frac{AB}{AB} + \frac{AB}{Ab} + \frac{AB}{aB} + \frac{AB}{ab} + \frac{Ab}{AB} + \frac{Ab}{Ab} + \frac{Ab}{aB} + \frac{Ab}{ab} + \frac{aB}{AB} + \frac{aB}{Ab} + \frac{aB}{aB} + \frac{aB}{ab} + \frac{ab}{AB} + \frac{ab}{Ab} + \frac{ab}{aB} + \frac{ab}{ab},$$

or

$$AB + ABb + AaB + AaBb + ABb + Ab + AaBb + Aab + AaB + AaBb + aB + aBb + AaBb + Aab + aBb + ab = AB + Ab + aB + ab + 2ABb + 2aBb + 2AaB + 2Aab + 4AaBb.^{1}$$

In precisely similar fashion is the developmental series of hybrids exhibited when three kinds of differentiating characters are conjoined in them. The hybrids form eight various kinds of egg and pollen cells — *ABC*, *ABc*, *AbC*, *Abc*, *aBC*, *aBc*, *abC*, *abc* — and each pollen form unites itself again on the average once with each form of egg cell.

The law of combination of different characters, which governs the development of the hybrids, finds therefore its foundation and explanation in the principle enunciated, that the hybrids produce egg cells and pollen cells which in equal numbers represent all constant forms which result from the combinations of the characters brought together in fertilisation.

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[1] [In the original the sign of equality (=) is here represented by +, evidently a misprint.]

EXPERIMENTS WITH HYBRIDS OF OTHER SPECIES OF PLANTS

It must be the object of further experiments to ascertain whether the law of development discovered for *Pisum* applies also to the hybrids of other plants. To this end several experiments were recently commenced. Two minor experiments with species of *Phaseolus* have been completed, and may be here mentioned.

An experiment with *Phaseolus vulgaris* and *Phaseolus nanus* gave results in perfect agreement. *Ph. nanus* had, together with the dwarf axis, simply inflated, green pods. *Ph. vulgaris* had, on the other hand, an axis 10 feet to 12 feet high, and yellow-coloured pods, constricted when ripe. The ratios of the numbers in which the different forms appeared in the separate generations were the same as with *Pisum*. Also the development of the constant combinations resulted according to the law of simple combination of characters, exactly as in the case of *Pisum*. There were obtained

Constant combinations	Axis	Colour of the unripe pods	Form of the ripe pods
1	long	green	inflated
2	"	"	constricted
3	"	yellow	inflated
4	"	"	constricted
5	short	green	inflated
6	"	"	constricted
7	"	yellow	inflated
8	"	"	constricted

The green colour of the pod, the inflated forms, and the long axis were, as in *Pisum*, dominant characters.

Another experiment with two very different species of *Phaseolus* had only a partial result. *Phaseolus nanus*, L., served as seed parent, a perfectly constant species, with white flowers in short racemes and small white seeds in straight, inflated, smooth pods; as pollen parent was used *Ph. multiflorus*, W., with tall winding stem, purple-red flowers in very long racemes, rough, sickle-shaped crooked pods, and large seeds which bore black flecks and splashes on a peach-blood-red ground.

The hybrids had the greatest similarity to the pollen parent, but the flowers appeared less intensely coloured. Their fertility was very limited; from seventeen plants, which together developed many hundreds of flowers, only forty-nine seeds in all were obtained. These were of medium size, and were flecked and splashed similarly to those of *Ph. multiflorus*, while the ground colour was not materially different. The next year forty-four plants were raised from these seeds, of which only thirty-one reached the flowering stage. The characters of *Ph. nanus*, which had been altogether latent in the hybrids, reappeared in various combinations; their ratio, however, with relation to the dominant plants was necessarily very fluctuating owing to the small number of trial plants. With certain characters, as in those of the axis and the form of pod it was, however, as in the case of *Pisum*, almost exactly 1:3.

Insignificant as the results of this experiment may be as regards the determination of the relative numbers in which the various forms appeared, it presents, on the other hand, the phenomenon of a remarkable change of colour in the flowers and seed of the hybrids. In *Pisum* it is known that the characters of the flower- and seed-colour present themselves unchanged in the first and further generations, and that the offspring of the hybrids display exclusively the one or the other of the characters of the original stocks. It is otherwise in the experiment we are considering. The white flowers and the seed-colour of *Ph. nanus* appeared, it is true, at once in the first generation [*from* the hybrids] in one fairly fertile example, but the remaining thirty plants developed flower-colours which were of various grades of purple-red to pale violet. The colouring of the seed-coat was no less varied than that of the flowers. No plant could rank as fully fertile; many produced no fruit at all; others only yielded fruits from the flowers last produced, which did not ripen. From fifteen plants only were well-developed seeds obtained. The greatest disposition to infertility was seen in the forms with preponderantly red flowers, since out of sixteen of these only four yielded ripe seed. Three of these had a similar seed pattern to *Ph. multiflorus*, but with a more or less pale ground colour; the fourth plant yielded only one seed of plain brown tint. The forms with preponderantly violet-coloured flowers had dark brown, black-brown, and quite black seeds.

The experiment was continued through two more generations under similar unfavorable circumstances, since even among the offspring of fairly fertile plants there came again some which were less fertile or even quite sterile. Other flower- and seed-colours than those cited did not subsequently present themselves. The forms which in the first generation [bred from the hybrids] contained one or more of the recessive characters remained, as regards these, constant without exception. Also of those plants which possessed violet flowers and brown or black seed, some did not vary again in these respects in the next generation; the majority, however, yielded, together with offspring exactly like themselves, some which displayed white flowers and white seed-coats. The red flowering plants remained so slightly fertile that nothing can be said with certainty as regards their further development.

Despite the many disturbing factors with which the observations had to contend, it is nevertheless seen by this experiment that the development of the hybrids, with regard to those characters which concern the form of the plants, follows the same laws as in *Pisum*. With regard to the colour characters, it certainly appears difficult to perceive a substantial agreement. Apart from the fact that from the union of a white and a purple-red colouring a whole series of colours results [in F_2], from purple to pale violet and white, the circumstance is a striking one that among thirty-one flowering plants only one received the recessive character of the white colour, while in *Pisum* this occurs on the average in every fourth plant.

Even these enigmatical results, however, might probably be explained by the law governing *Pisum* if we might assume that the colour of the flowers and seeds of *Ph. multiflorus* is a combination of two or more entirely independent colours, which individually act like any other constant character in the plant. If the flower-colour A were a combination of the individual characters $A_1 + A_2 + \ldots$ which produce the total impression of a purple coloration, then by fertilisation with the differentiating character, white colour, a, there would be produced the hybrid unions $A_1a + A_2a + \ldots$ and so would it be with the corresponding colouring of the seed-coats.[1] According to the above assumption, each of these hybrid colour unions would be independent, and would consequently develop quite independently from the others. It is then easily seen that from the combination of the separate developmental series a complete colour-series must result. If, for instance, $A = A_1 + A_2$, then the hybrids A_1a and A_2a form the developmental series —

$$A_1 + 2A_1a + a, \qquad A_2 + 2A_2a + a.$$

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[1] [As it fails to take account of factors introduced by the albino this representation is imperfect. It is however interesting to know that Mendel realized the fact of the existence of compound characters, and that the rarity of the white recessives was a consequence of this resolution.]

The members of this series can enter into nine different combinations, and each of these denotes another colour —

1 A_1A_2	2 A_1aA_2	1 A_2a
2 A_1A_2a	4 A_1aA_2a	2 A_2aa
1 A_1a	2 A_1aa	1 aa.

The figures prescribed for the separate combinations also indicate how many plants with the corresponding colouring belong to the series. Since the total is sixteen, the whole of the colours are on the average distributed over each sixteen plants, but, as the series itself indicates, in unequal proportions.

Should the colour development really happen in this way, we could offer an explanation of the case above described, viz. that the white flowers and seed-coat colour only appeared once among thirty-one plants of the first generation. This colouring appears only once in the series, and could therefore also only be developed once in the average in each sixteen, and with three colour characters only once even in sixty-four plants.

It must, nevertheless, not be forgotten that the explanation here attempted is based on a mere hypothesis, only supported by the very imperfect result of the experiment just described. It would, however, be well worth while to follow up the development of colour in hybrids by similar experiments, since it is probable that in this way we might learn the significance of the extraordinary variety in the colouring of our ornamental flowers.

So far, little at present is known with certainty beyond the fact that the colour of the flowers in most ornamental plants is an extremely variable character. The opinion has often been expressed that the stability of the species is greatly disturbed or entirely upset by cultivation, and consequently there is an inclination to regard the development of cultivated forms as a matter of chance devoid of rules; the colouring of ornamental plants is indeed usually cited as an example of great instability. It is, however, not clear why the simple transference into garden soil should result in such a thorough and persistent revolution in the plant organism. No one will seriously maintain that in the open country the development of plants is ruled by other laws than in the garden bed. Here, as there, changes of type must take place if the conditions of life be altered, and the species possesses the capacity of fitting itself to its new environment. It is willingly granted that by cultivation the origination of new varieties is favoured, and that by man's labour many varieties are acquired which, under natural conditions, would be lost; but nothing justifies the assumption that the tendency to the formation of varieties is so extraordinarily increased that the species speedily lose all stability, and their offspring diverge into an endless series of extremely variable forms. Were the change in the conditions the sole cause of variability we might expect that those cultivated plants which are grown for centuries under almost identical conditions would again attain constancy. That, as is well known, is not the case, since it is precisely under such circumstances that not only the most varied but also the most variable forms are found. It is only the *Leguminosae*, like *Pisum*, *Phaseolus*,[1] *Lens*, whose organs of fertilisation are protected by the keel, which constitute a noteworthy exception. Even here there have arisen numerous varieties during a cultural period of more than 1000 years under most various conditions; these maintain, however, under unchanging environments a stability as great as that of species growing wild.

It is more than probable that as regards the variability of cultivated plants there exists a factor which so far has received little attention. Various experiments force us to the conclusion that our cultivated plants, with few exceptions, are *members of various hybrid series*, whose further development in conformity with law is varied and interrupted by frequent crossings *inter se*. The circumstance must not be overlooked that cultivated plants are mostly grown in great numbers and close together, affording the most favourable conditions for reciprocal fertilisation between the varieties present and the species itself. The probability of this is supported by the fact that among the great array of variable forms solitary examples are always found, which in one character or another remain constant, if only foreign influence be carefully excluded. These forms behave precisely as do those which are known to be members of the compound hybrid series. Also with the most susceptible of all characters, that of colour, it cannot escape the careful observer that in the separate forms the inclination to vary is displayed in very different degrees. Among plants which arise from *one* spontaneous fertilisation there are often some whose offspring vary widely in the constitution and arrangement of the colours, while that of others shows little deviation, and

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[1] [*Phaseolus* nevertheless is insect-fertilised.]

among a greater number solitary examples occur which transmit the colour of the flowers unchanged to their offspring. The cultivated species of *Dianthus* afford an instructive example of this. A white-flowered example of *Dianthus caryophyllus*, which itself was derived from a white-flowered variety, was shut up during its blooming period in a greenhouse; the numerous seeds obtained therefrom yielded plants entirely white-flowered like itself. A similar result was obtained from a sub-species, with red flowers somewhat flushed with violet, and one with flowers white, striped with red. Many others, on the other hand, which were similarly protected, yielded progeny which were more or less variously coloured and marked.

Whoever studies the coloration which results, in ornamental plants, from similar fertilisation, can hardly escape the conviction that here also the development follows a definite law, which possibly finds its expression *in the combination of several independent colour characters.*

CONCLUDING REMARKS

It can hardly fail to be of interest to compare the observations made regarding *Pisum* with the results arrived at by the two authorities in this branch of knowledge, Kölreuter and Gärtner, in their investigations. According to the opinion of both, the hybrids in outward appearance present either a form intermediate between the original species, or they closely resemble either the one or the other type, and sometimes can hardly be discriminated from it. From their seeds usually arise, if the fertilisation was effected by their own pollen, various forms which differ from the normal type. As a rule, the majority of individuals obtained by one fertilisation maintain the hybrid form, while some few others come more like the seed parent, and one or other individual approaches the pollen parent. This, however, is not the case with all hybrids without exception. Sometimes the offspring have more nearly approached, some the one and some the other of the two original stocks, or they all incline more to one or the other side; while in other cases *they remain perfectly like the hybrid* and continue constant in their offspring. The hybrids of varieties behave like hybrids of species, but they possess greater variability of form and a more pronounced tendency to revert to the original types.

With regard to the form of the hybrids and their development, as a rule an agreement with the observations made in *Pisum* is unmistakable. It is otherwise with the exceptional cases cited. Gärtner confesses even that the exact determination whether a form bears a greater resemblance to one or to the other of the two original species often involved great difficulty, so much depending upon the subjective point of view of the observer. Another circumstance could, however, contribute to render the results fluctuating and uncertain, despite the most careful observation and differentiation. For the experiments, plants were mostly used which rank as good species and are differentiated by a large number of characters. In addition to the sharply defined characters, where it is a question of greater or less similarity, those characters must also be taken into account which are often difficult to define in words, but yet suffice, as every plant specialist knows, to give the forms a peculiar appearance. If it be accepted that the development of hybrids follows the law which is valid for *Pisum,* the series in each separate experiment must contain very many forms, since the number of the terms, as is known, increases, with the number of the differentiating characters, as the powers of three. With a relatively small number of experimental plants the result therefore could only be approximately right, and in single cases might fluctuate considerably. If, for instance, the two original stocks differ in seven characters, and 100 or 200 plants were raised from the seeds of their hybrids to determine the grade of relationship of the offspring, we can easily see how uncertain the decision must become, since for seven differentiating characters the combination series contain 16,384 individuals under 2187 various forms; now one and then another relationship could assert its predominance, just according as chance presented this or that form to the observer in a majority of cases.

If, furthermore, there appear among the differentiating characters at the same time *dominant* characters, which are transmitted entire or nearly unchanged to the hybrids, then in the terms of the developmental series that one of the two original parents which possesses the majority of dominant characters must always be predominant. In the experiment described relative to *Pisum*, in which three kinds of differentiating characters were concerned, all the dominant characters belonged to the seed parent. Although the terms of the series in their internal composition approach both original parents equally, yet in this experiment the type of the seed parent obtained so great a preponderance that out of each sixty-four plants of the first generation fifty-four exactly resembled it, or only differed in one character. It is seen how rash it must be under such circumstances to draw from the external resemblances of hybrids conclusions as to their internal nature.

Gärtner mentions that in those cases where the development was regular, among the offspring of the hybrids, the two original species were not reproduced, but only a few individuals which approached them. With very extended developmental series it could not in fact be otherwise. For seven differentiating characters, for instance, among more than 16,000 individuals — offspring of the hybrids — each of the two original species would occur only once. It is therefore hardly possible that these should appear at all among a small number of experimental plants; with some probability, however, we might reckon upon the appearance in the series of a few forms which approach them.

We meet with an *essential difference* in those hybrids which remain constant in their progeny and propagate themselves as truly as the pure species. According to Gärtner, to this class belong the *remarkably fertile hybrids*, *Aquilegia atropurpurea canadensis*, *Lavatera pseudolbia thuringiaca*, *Geum urbano-rivale*, and some *Dianthus* hybrids; and, according to Wichura, the hybrids of the Willow family. For the history of the evolution of plants this circumstance is of special importance, since constant hybrids acquire the status of new species. The correctness of the facts is guaranteed by eminent observers, and cannot be doubted. Gärtner had an opportunity of following up *Dianthus Armeria deltoides* to the tenth generation, since it regularly propagated itself in the garden.

With *Pisum* it was shown by experiment that the hybrids form egg and pollen cells of *different* kinds, and that herein lies the reason of the variability of their offspring. In other hybrids, likewise, whose offspring behave similarly we may assume a like cause; for those, on the other hand, which remain constant, the assumption appears justifiable that their reproductive cells are all alike and agree with the foundation-cell [fertilised ovum] of the hybrid. In the opinion of renowned physiologists, for the purpose of propagation one pollen cell and one egg cell unite in Phanerogams [1] into a

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[1] In *Pisum* it is placed beyond doubt that for the formation of the new embryo a perfect union of the elements of both reproductive cells must take place. How

single cell, which is capable by assimilation and formation of new cells to become an independent organism. This development follows a constant law, which is founded on the material composition and arrangement of the elements which meet in the cell in a vivifying union. If the reproductive cells be of the same kind and agree with the foundation cell [fertilised ovum] of the mother plant, then the development of the new individual will follow the same law which rules the mother plant. If it chance that an egg cell unites with a *dissimilar* pollen cell, we must then assume that between those elements of both cells, which determine opposite characters, some sort of compromise is effected. The resulting compound cell becomes the foundation of the hybrid organism, the development of which necessarily follows a different scheme from that obtaining in each of the two original species. If the compromise be taken to be a complete one, in the sense, namely, that the hybrid embryo is formed from two similar cells, in which the differences are *entirely and permanently accommodated* together, the further result follows that the hybrids, like any other stable plant species, reproduce themselves truly in their offspring. The reproductive cells which are formed in their seed vessels and anthers are of one kind, and agree with the fundamental compound cell [fertilised ovum].

With regard to those hybrids whose progeny is *variable* we may perhaps assume that between the differentiating elements of the egg and pollen cells there also occurs a compromise, in so far that the formation of a cell as foundation of the hybrid becomes possible; but, nevertheless, the arrangement between the conflicting elements is only temporary and does not endure throughout the life of the hybrid plant. Since, in the habit of the plant, no changes are perceptible during the whole period of vegetation, we must further assume that it is only possible for the differentiating elements to liberate themselves from the enforced union when the fertilising cells are developed. In the formation of these cells all existing

could we otherwise explain that among the offspring of the hybrids both original types reappear in equal numbers and with all their peculiarities? If the influence of the egg cell upon the pollen cell were only external, if it fulfilled the *rôle* of a nurse only, then the result of each artificial fertilisation could be no other than that the developed hybrid should exactly resemble the pollen parent, or at any rate do so very closely. This the experiments so far have in no wise confirmed. An evident proof of the complete union of the contents of both cells is afforded by the experience gained on all sides that it is immaterial, as regards the form of the hybrid, which of the original species is the seed parent or which the pollen parent.

elements participate, in an entirely free and equal arrangement, by which it is only the differentiating ones which mutually separate themselves. In this way the production would be rendered possible of as many sorts of egg and pollen cells as there are combinations possible of the formative elements.

The attribution attempted here of the essential difference in the development of hybrids to *a permanent or temporary union* of the differing cell elements can, of course, only claim the value of an hypothesis for which the lack of definite data offers a wide scope. Some justification of the opinion expressed lies in the evidence afforded by *Pisum* that the behaviour of each pair of differentiating characters in hybrid union is independent of the other differences between the two original plants, and, further, that the hybrid produces just so many kinds of egg and pollen cells as there are possible constant combination forms. The differentiating characters of two plants can finally, however, only depend upon differences in the composition and grouping of the elements which exist in the foundation-cells [fertilised ova] of the same in vital interaction.[1]

Even the validity of the law formulated for *Pisum* requires still to be confirmed, and a repetition of the more important experiments is consequently much to be desired, that, for instance, relating to the composition of the hybrid fertilising cells. A differential [element] may easily escape the single observer,[2] which although at the outset may appear to be unimportant, may yet accumulate to such an extent that it must not be ignored in the total result. Whether the variable hybrids of other plant species observe an entire agreement must also be first decided experimentally. In the meantime we may assume that in material points an essential difference can scarcely occur, since the unity in the developmental plan of organic life is beyond question.

In conclusion, the experiments carried out by Kölreuter, Gärtner, and others with respect to *the transformation of one species into another by artificial fertilisation* merit special mention. Particular importance has been attached to these experiments and Gärtner reckons them among " the most difficult of all in hybridisation."

If a species *A* is to be transformed into a species *B*, both must be united by fertilisation and the resulting hybrids then be fertilised

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[1] "*Welche in den Grundzellen derselben in lebendiger Wechselwirkung stehen.*"

[2] "*Dem einzelnen Beobachter kann leicht ein Differenziale entgehen.*"

with the pollen of B; then, out of the various offspring resulting, that form would be selected which stood in nearest relation to B and once more be fertilised with B pollen, and so continuously until finally a form is arrived at which is like B and constant in its progeny. By this process the species A would change into the species B. Gärtner alone has effected thirty such experiments with plants of genera *Aquilegia*, *Dianthus*, *Geum*, *Lavatera*, *Lychnis*, *Malva*, *Nicotiana*, and *Oenothera*. The period of transformation was not alike for all species. While with some a triple fertilisation sufficed, with others this had to be repeated five or six times, and even in the same species fluctuations were observed in various experiments. Gärtner ascribes this difference to the circumstance that " the specific [*typische*] power by which a species, during reproduction, effects the change and transformation of the maternal type varies considerably in different plants, and that, consequently, the periods within which the one species is changed into the other must also vary, as also the number of generations, so that the transformation in some species is perfected in more, and in others in fewer generations." Further, the same observer remarks " that in these transformation experiments a good deal depends upon which type and which individual be chosen for further transformation."

If it may be assumed that in these experiments the constitution of the forms resulted in a similar way to that of *Pisum*, the entire process of transformation would find a fairly simple explanation. The hybrid forms as many kinds of egg cells as there are constant combinations possible of the characters conjoined therein, and one of these is always of the same kind as that of the fertilising pollen cells. Consequently there always exists the possibility with all such experiments that even from the second fertilisation there may result a constant form identical with that of the pollen parent. Whether this really be obtained depends in each separate case upon the number of the experimental plants, as well as upon the number of differentiating characters which are united by the fertilisation. Let us, for instance, assume that the plants selected for experiment differed in three characters, and the species ABC is to be transformed into the other species abc by repeated fertilisation with the pollen of the latter; the hybrids resulting from the first cross form eight different kinds of egg cells, viz.,

$$ABC,\ ABc,\ AbC,\ aBC,\ Abc,\ aBc,\ abC,\ abc.$$

These in the second year of experiment are united again with the pollen cells *abc*, and we obtain the series

$$AaBbCc + AaBbc + AabCc + aBbCc + Aabc + aBbc + abCc + abc.$$

Since the form *abc* occurs once in the series of eight terms, it is consequently little likely that it would be missing among the experimental plants, even were these raised in a smaller number, and the transformation would be perfected already by a second fertilisation. If by chance it did not appear, then the fertilisation must be repeated with one of those forms nearest akin, *Aabc*, *aBbc*, *abCc*. It is perceived that such an experiment must extend the farther *the smaller the number of experimental plants and the larger the number of differentiating characters* in the two original species; and that, furthermore, in the same species there can easily occur a delay of one or even of two generations such as Gärtner observed. The transformation of widely divergent species could generally only be completed in five or six years of experiment, since the number of different egg cells which are formed in the hybrid increases, as the powers of two, with the number of differentiating characters.

Gärtner found by repeated experiments that the respective period of transformation varies in many species, so that frequently a species *A* can be transformed into a species *B* a generation sooner than can species *B* into species *A*. He deduces therefrom that Kölreuter's opinion can hardly be maintained that "the two natures in hybrids are perfectly in equilibrium." It appears, however, that Kölreuter does not merit this criticism, but that Gärtner rather has overlooked a material point, to which he himself elsewhere draws attention, viz. that "it depends which individual is chosen for further transformation." Experiments which in this connection were carried out with two species of *Pisum* demonstrated that as regards the choice of the fittest individuals for the purpose of further fertilisation it may make a great difference which of two species is transformed into the other. The two experimental plants differed in five characters, while at the same time those of species *A* were all dominant and those of species *B* all recessive. For mutual transformation *A* was fertilised with pollen of *B*, and *B* with pollen of *A*, and this was repeated with both hybrids the following year. With the first experiment $\frac{B}{A}$ there were eighty-seven plants available in the third year of experiment for selection of the individuals for further crossing, and these were of the possible thirty-two forms; with the second experiment $\frac{A}{B}$ seventy-three plants resulted, which *agreed throughout perfectly in habit with the pollen parent;* in their internal composition, however, they must have been just as varied as the forms in the other experiment. A definite selection was consequently only possible with the first experiment; with the second the selection had to be made at random, merely. Of the latter only a portion of the flowers were crossed with the *A* pollen, the others were left to fertilise themselves. Among each five plants which were selected in both experiments for fertilisation there agreed, as the following year's culture showed, with the pollen parent:

1st Experiment	2nd Experiment	
2 plants	—	in all characters
3 "	—	" 4 "
—	2 plants	" 3 "
—	2 "	" 2 "
—	1 plant	" 1 character

In the first experiment, therefore, the transformation was completed; in the second, which was not continued further, two or more fertilisations would probably have been required.

Although the case may not frequently occur in which the dominant characters belong exclusively to one or the other of the original parent plants, it will always make a difference which of the two possesses the majority of dominants. If the pollen parent has the majority, then the selection of forms for further crossing will afford a less degree of certainty than in the reverse case, which must imply a delay in the period of transformation, provided that the experiment is only considered as completed when a form is arrived at which not only exactly resembles the pollen plant in form, but also remains as constant in its progeny.

Gärtner, by the results of these transformation experiments, was led to oppose the opinion of those naturalists who dispute the stability of plant species and believe in a continuous evolution of vegetation. He perceives [1] in the complete transformation of one species into another an indubitable proof that species are fixed within limits beyond which they cannot change. Although this

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[1] [" Es sieht " in the original is clearly a misprint for " Er sieht."]

opinion cannot be unconditionally accepted, we find on the other hand in Gärtner's experiments a noteworthy confirmation of that supposition regarding variability of cultivated plants which has already been expressed.

Among the experimental species there were cultivated plants, such as *Aquilegia atropurpurea* and *canadensis, Dianthus caryophyllus, chinensis,* and *japonicus, Nicotiana rustica* and *paniculata,* and hybrids between these species lost none of their stability after four or five generations.

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