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GENETICS
IN
RELATION TO AGRICULTURE

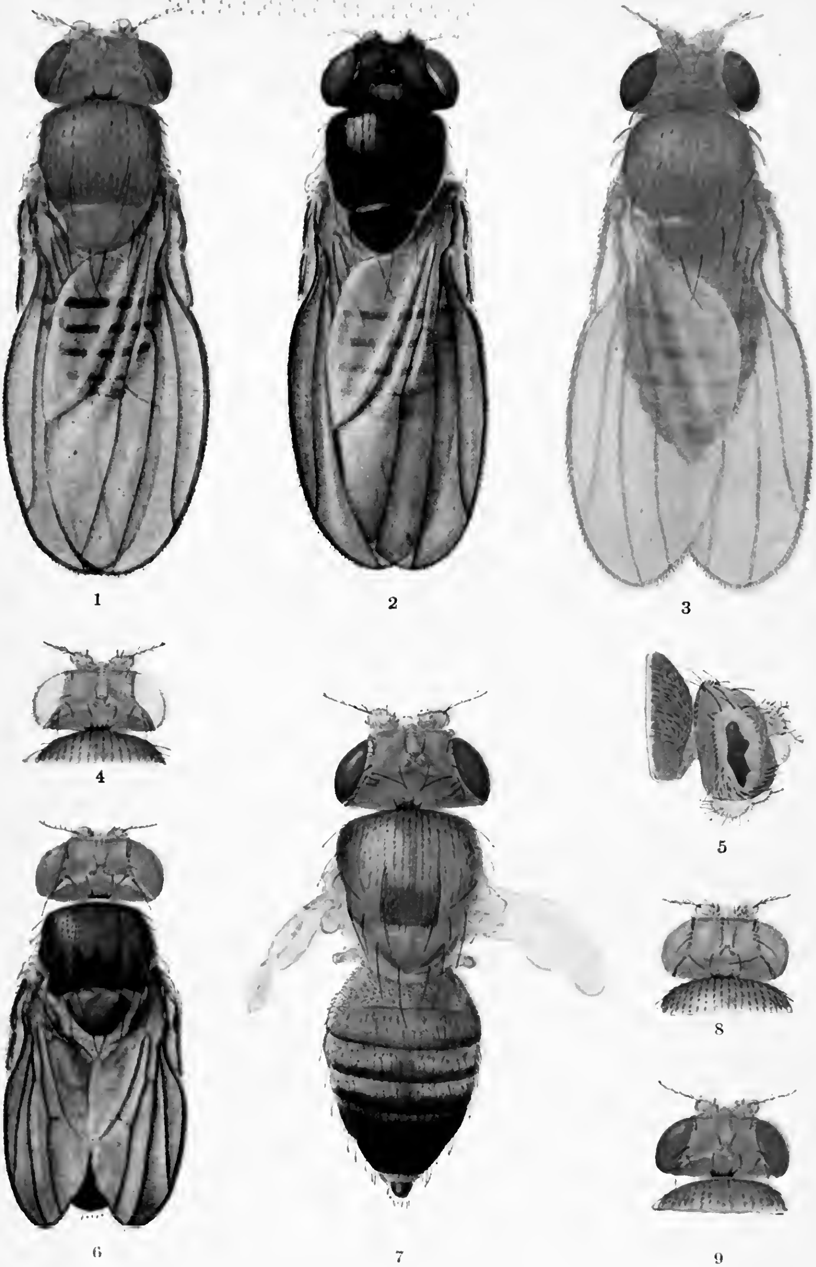

Plate I.—**Mutant Forms of Drosophila Melanogaster** (*Ampelophila*).

1. Wild Type. 2. Ebony. 3. Yellow. 4. White Eye. 5. Bar Eye. 6. Eosin Miniature Black. 7. Vestigial. 8. Buff Eye. 9. Cherry Eye.

(From Drawing by E. M. Wallace.)

GENETICS
IN
RELATION TO AGRICULTURE

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To
THOMAS HUNT MORGAN

[redacted]

PREFACE

Of all the sciences that contribute to the great, tertiary composite which is known as agriculture none is more important economically than genetics. One may not overlook the fundamental relation borne by the primary sciences, mathematics, physics and chemistry, and by the secondary sciences, botany, zoology, geology, meteorology and economics, to the production and distribution of raw materials. But we confidently assert that the science which underlies the improvement of plants and animals for agricultural purposes is destined to receive increasing attention in agricultural education and in agricultural practice. Without doubt vast possibilities await realization through the more thorough and systematic development of our living economic resources. Such development is directly dependent upon the successful utilization of genetic principles in plant and animal breeding. The science of genetics is still very young, but it is firmly established and is developing rapidly. It claims the attention of the producer of today and invites the most serious study of the agriculturist of tomorrow. It lays claim also to the interest of the eugenist, the sociologist and the philanthropist and all students of biology.

This text has been prepared in response to a real and widely recognized need. The experience of the authors in teaching the principles of breeding to undergraduate students has forced home the conviction that an adequate presentation in a single text of the facts and principles of genetics and their practical applications is a prime necessity. Those familiar with the literature of the subject will appreciate the magnitude of the task and, we trust, will be lenient in criticizing our choice of subject matter. It is impossible to include many things of mutual interest to genetics and agriculture if the work be limited to a single volume. We are keenly aware of many deficiencies and it is our desire to prepare a revised edition of the book in the near future. With this in view the suggestions of others are earnestly solicited.

We take this opportunity to express gratitude to all who have rendered assistance, especially to those who have read portions of the manuscript or assisted in proof-reading and to all who donated or loaned photographs or who assisted otherwise with the illustrations. The onus of the work has been lessened in no small degree by the interest and encouragement of our colleagues.

THE AUTHORS.

BERKELEY, CALIFORNIA,
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GENETICS
IN
RELATION TO AGRICULTURE

PART I—FUNDAMENTALS

CHAPTER I

THE METHODS AND SCOPE OF GENETICS

Soon after Mendel's report of investigations in heredity had been rediscovered, it became evident to most biological investigators that a flood of light had been thrown upon the problem of heredity, and the related subjects of variation, development, and evolution. The need for a new term, therefore, to designate this interrelated portion of biological science led Bateson to coin the word, genetics, from the Greek root, ΓEN, "become." The derivation does not indicate, it must be admitted, very clearly the portion of biology to which the term genetics applies, but this vagueness has in it an element of desirability, for it is extremely difficult to define accurately the boundaries which delimit the province of genetics. Bateson himself has stated that genetics deals with the physiology of heredity and variation; and a favorite statement of authors has been that genetics is the science of the origin of individuals. But these statements—they can hardly be called definitions—must be qualified carefully in order that they may be understood. Accordingly it has seemed desirable to construct a definition of genetics in purely objective terms. The following definition is, therefore, proposed to fulfill this need; it, too, will require some qualification:

Genetics is the science which seeks to account for the resemblances and the differences which are exhibited among organisms related by descent.

The Content of Genetics.—If genetics be defined in the above manner, it may be stated roughly that variation is that portion of genetics having to do with the differences beween organisms, whereas heredity has to do with the resemblances which they exhibit. But this statement does not define very accurately the exact meanings of the two terms; to do this it is necessary to consider certain fundamental facts.

Organisms exhibit various degrees of difference and resemblance, and classification is made possible first, by resemblances between individuals and, second, by differences between groups of individuals. Further, the orderly interrelations which are exhibited by living beings in general has made it possible to group them into orders, families, genera, and species according to the degree of resemblance which exists among groups of individuals. But this is merely a view *en masse* of the differences between organisms, for it is universally true that no two individuals are exactly alike. There are, therefore, for all practical purposes, two orders of difference between individuals; first, racial differences, those which separate groups of individuals, and second, individual differences, those which distinguish the individuals of a group from one another. Strictly, of course, there are all possible gradations from the one degree of difference to the other, but conveniently it may be said that the former, the racial differences, are those which characterize different lines of descent, whereas the latter, the individual differences, distinguish individuals within a given line of descent. The problem as to the origin of racial differences is a problem of evolution; the problem of the origin of individual differences is a problem of genetics, and we accordingly shall construct our definition of variation to apply to differences exhibited by individuals related by descent.

Now all multicellular organisms which reproduce by sex exhibit the common characteristic of two distinct cycles of cellular development; gametogenesis, or development of the germ cells, and somatogenesis or development of the body. The resemblances which make it possible to group individuals into orders, families, genera, and species are the result of the fundamental relation which exists between these two cycles, for it is a commonplace fact that the germ cells of any species can reproduce individuals of the same and no other species. This relation of germinal constitution to the development of the soma is specific for all classes and grades of characters, but the order of specificity may be either racial or individual, just as the order of difference between individuals is racial or individual.

The term variation carries with it the idea of deviation from type, and obviously the above statements, brief as they are, of the cycles in individual development leave room for several possibilities of deviation from type. Thus, if we look at the matter from one point of view, the guiding hand in determining the characters of the individual is the specificity of the germinal substance. But every individual develops under a certain set of conditions, the environment, which is independent of the germinal substance; and these conditions have a certain, usually merely modifying, influence in the development of the individual. There is, therefore, a possibility for differences to arise in individuals independently of differences in the germinal substance, differences which are specifically attributable to diversities in the environment, and which may have no effect on the germinal substance itself, just as the degree of heat, for example, may cause a variation in the end products which a given chemical system yields. Differences in development may, also, occur because of actual diversities in the germinal substance, and these may arise from the intermingling of different kinds of germinal substance, such as obviously takes place in sexual reproduction, a cause of variation which has been ably advocated by Weismann and styled by him amphimixis; or they may arise from actual changes in the germinal substance, distinct from the intermingling of germinal elements which already exist, a form of variation which has been proposed and elaborated by de Vries under the name of the mutation theory. Accordingly the term variation in genetics is so defined that it includes differences in individuals related by descent, although many authors do not include within the term those differences which are due to environmental conditions of all categories. The following definition is framed in conformity to that already given for genetics.

Variation is difference, whether in the expression of somatic characters or in the elements of germinal substance, among organisms related by descent.

Heredity is commonly defined as the tendency of offspring to develop characters like unto those of their parents; according to Castle it is resemblance based upon descent. Thomson presents a very able discussion of the concept, heredity, together with criticism of definitions which have been offered from time to time for the term. According to his definition, by heredity is meant nothing more nor less than organic or genetic relation between successive generations.

The universal tendency of organisms to produce similar organisms is the cause of the maintenance of organic groups and group relations. But experimental research has demonstrated that sometimes new combinations of germinal substance produce characters which have not been exhibited by parents. It is necessary, therefore, to define heredity in such general terms that it will include those exceptional characters which have never been exhibited by any ancestor. Now regardless of any external difference which may be exhibited by an individual, its germinal constitution bears a perfectly definite relation to those of its parents. For that reason the following definition is stated in terms of elements of the germinal substance, rather than in terms of somatic characters.

Heredity is germinal resemblance among organisms related by descent.

Finally, with respect to the content of genetics, emphasis should be laid upon the importance of a consideration of the various phases of development. In development are included all those changes and cycles through which the individual passes in attaining the adult condition. Obviously there is much in development which cannot be treated at all in an elementary text-book of genetics, for particular cycles or phases of development are treated as separate sub-divisions of biology, such as embryology, cytology, experimental morphology, and like subjects. While obviously there is much in all of these subjects which is irrelevant to a treatment of genetics, nevertheless, rightly interpreted, there is little which is essential to any one of them which does not bear some more or less intimate relations to those phenomena which belong more strictly in the province of genetics. The reason for this is very apparent, the development of the individual is a consequence of the elaboration of the hereditary material, it is the fulfillment of the possibilities wrapped up in the germ cell; how then can it fail to possess much that is of very great significance to genetics? Assuredly the further advancement of the science of genetics will focus more and more attention upon the problems of growth and differentiation in the individual; for that reason these emphatic statements are made.

The Problems of Genetics.—Obviously the problems of genetics are those which grow out of a study of resemblances and differences in individuals related by descent. Wilson has reduced the statement of the problems of inheritance and development to that oft-quoted question: "How do the adult characteristics lie latent in the egg; and how do they become patent as development proceeds?" Pearl has voiced very much the same thought in his statement that the critical problem of inheritance is the problem of the cause; the material basis; and the maintenance of the somatogenic specificity of germinal substance.

There are four general methods of attacking the problems of heredity; namely, the methods of observation, experimental breeding, cytology, and experimental morphology. Each of these methods has its specific advantage and particular value as well as its definite limitations. In the following discussion each method is considered briefly with respect to its relation to the development of the science of genetics.

The Method of Observation.—The method of observation, or description as it is often called, requires special treatment because it employs the inductive mode of reasoning. Briefly the essential steps involved in the application of inductive reasoning to the problems of genetics may be stated as follows. The first step is the observation of the resemblances and differences between representative individuals of a given line of descent or, if problems of evolution are under consideration, of different lines of descent. The next step is a comparison of the observations which have been made for the purpose of determining whether they show orderliness with respect to each other; in other words to determine whether they probably have a common causal basis. If they do show such orderliness, an attempt is made to formulate the principles or laws which govern them. Finally, the principles or laws thus formulated are applied to other instances not included in the original set of observations in order to test their general validity. The weakness of the method in biology lies in the lack of rigid experimental control over the phenomena which are under observation, and also in the fact that often it is either very difficult or impossible to subject to experimental verification the principles or laws which have been thus formulated. For this reason, the method of observation as a means of formulating principles and laws must constantly be subjected to rigid scrutiny, lest undetected fallacies lead to the acceptance of conclusions which actually have no significance from a biological standpoint.

But although the observational method has very definite limitations in the determination of genetic principles, nevertheless it has been the chief method of investigation in the formulation of some of the most stimulating theories of biological science. The marshalling of evidence by Darwin in support of the evolution theory depended almost entirely on an application of this mode of research to a vast array of more or less isolated cases. The mass of evidence, which he accumulated in order to demonstrate that natural selection by favoring the "survival of the fittest," to use Spencer's phrase, results in evolutionary progress in succeeding generations, will ever stand as a monument to his masterly skill in observation and interpretation.

In addition to its utilization in the development of the evolution theory, the observational method has been employed widely in the field more strictly included in genetics. Sir Francis Galton employed a refined type of the observational method in his study of heredity. His object was to establish a law of organic resemblance within a single species, distinctly a problem of genetics. In order to do this he employed a system of more exact observation based upon accurate determinations in a large number of instances and mathematical reduction of the data thus collected. This system has since undergone notable development, particularly at the hands of Karl Pearson, and, as biometry, it is often accorded recognition as a distinct branch of biology. As one of the results of his studies, Galton announced the law of ancestral inheritance which states that on an average each parent contributes one-quarter or 0.5^2, each grandparent one-sixteenth or 0.5^3, and so on to the total heritage of the individual, which equals 1.0. The other notable result of these studies, the law of filial regression states essentially that on the average any deviation from racial type is transmitted to the offspring in a lessened degree, so that, in general, offspring differ less from the type of the race than their parents; specifically they exhibit a deviation from the racial mean only two-thirds as great as the parents.

Mere observation, be it ever so precise, is subject to very decided limitations when employed as a method of analyzing the general problems of evolution and heredity. To be convinced of this, one need only consider the opinions which have been entertained by those who have employed this method in the solution of biological problems. Thus Darwin believed that minute continuous variations are transmitted and form a basis for evolution and that the more striking discontinuous variations are of little moment in the origin of species. These are beliefs which rigid experimental investigation has failed to establish, and which are, therefore, highly improbable. In fact it has been clearly demonstrated that minute differences between individuals are for the most part not transmitted, and that distinct new characters which appear suddenly are often heritable. Similarly, the inheritance of acquired characters, so readily accepted by men with minds as keen as those of Darwin and Spencer, has failed to receive confirmation when subjected to rigid experimental enquiry. Definite knowledge on points such as these is of tremendous importance in making for progress toward the solution of the general problems of genetics, but such progress is slow and uncertain by the employment of the observational method of attack alone. It is for this reason that the favor of geneticists has swung so strongly toward a more rigid method of experimentation.

However, the observational method is not unique in possessing limitations. No single method is known invariably to give correct results. It is necessary to combine all available methods in order to insure the most certain and rapid approximation to the truth. But the difficulty with the observational method, particularly that part of it known as biometry, has been in the manner of its employment in the elucidation of genetic phenomena. It has been employed, as Pearl points out, both as a method of research and as a method of stating the results of experience. The former manner of utilization is unquestionably of great value in genetic research, its particular value residing in the fact that it has substituted exact methods of expression for vague and indefinite statements. It has performed a service of tremendous value to biology in the introduction of the probable error concept as an index of the degree of reliance to be placed in the results of determinations arrived at by other methods. The latter manner of utilization, however, as a method of stating the results of experience, the employment of which is characteristic of the biometrical school, is subject to serious objections. However, it is worthy of note that the method of observation will ever remain a valuable aid to the extension of knowledge, particularly in directions in which, by their very nature, it is impossible to employ experimental methods of research. It is difficult to imagine, for instance, any notable advance in our knowledge of human heredity save by a proper employment of this method of investigation.

The Method of Experimental Breeding.—The essential feature of all experimental breeding is the raising of pedigreed cultures of plants and animals, for which reason it is sometimes called the pedigree method. The notable progress which has been made in genetics during the past few decades has come from the application of this mode of enquiry. It is the analytic method of the geneticist and it is often and not unjustly compared, both with respect to its utility and its limitations, to the test-tube method of analytical chemistry. From it have come many stimulating ideas of heredity and variation; the Mendelian theory of heredity; the closely related pure line theory of Johannsen; and the mutation theory of de Vries: few methods of research can boast a more honorable array of achievements.

Of these achievements, the Mendelian theory is the accepted foundation of present ideas of heredity. For the application of Mendelian methods of analysis three essential breeding operations are necessary; first, the raising of pedigreed strains of plants and animals to determine their behavior under controlled conditions; second, the hybridization of diverse races; and third, the intensive study of the hybrid progeny through successive generations. From this outline of the breeding methods which are employed, it may be concluded rightly that the Mendelian method, like the Galtonian, is essentially statistical. It differs radically, however, from the Galtonian method in that it substitutes the observation of controlled progenies for that of ancestral generations. Its particular advantage lies in the fact that it is strictly verifiable. Moreover, it has had a different and more specific purpose in view, namely to state in definite terms how the particular individual will behave in heredity, rather than to arrive at a determination of average behavior in this respect. The important result of this method of analysis has been to demonstrate that the germinal material is made up of definite units or factors which stand in close relationship to particular characters of the soma, and to demonstrate how these elements of the germinal substance are transmitted from generation to generation.

The two remaining products of the pedigree culture method, the pure line theory and the mutation theory, stand in close relationship to the Mendelian theory of heredity; because they may be interpreted in terms of the elements which constitute the germinal substance. Of these the pure line theory may be said to add another conception to those of the Mendelian theory, namely that elements of the germinal substance possess a high degree of stability. If this conception be accepted, it follows—and this is the central postulate of the pure line theory—that variation among individuals of like germinal constitution is a response to external or internal conditions which are not reflected in the germinal substance. Such variations, therefore, are of no consequence for the establishment of new hereditary characters. A large number of plants, among them barley, oats, rice, wheat, and practically all the legumes, are almost invariably self-fertilized. They consequently give rise automatically to populations which are composed entirely of pure lines. The pure line theory, therefore, has tremendous practical significance.

The mutation theory adds yet another conception to those which have already been stated, namely that of occasional mutability of germinal elements. It is, therefore, directly contradictory to the pure line theory in its fundamental postulate; but the very great infrequency with which changes occur in germinal elements saves the pure line theory from inutility. Here the important result has been to establish firmly the occurrence of occasional, definite, discontinuous changes in germinal substance in consequence of which new characters are added to the heritage of the race. Much of the variability in individual characters which is exhibited by plants and animals appears to have had its beginning in mutational changes in the germinal substance. The mutation theory, therefore, is another consequence of genetic investigations which has far-reaching practical consequences.

Fruitful as have been the results of the method of experimental breeding in prosecuting genetic research, students and investigators should not delude themselves as to the nature of the knowledge which it has yielded. It cannot stand alone as a mode of investigation, for even the present illuminating conception as to the structure and operation of the hereditary mechanism has been almost as much the result of cytological as of breeding investigation. But taking this conception in its present form, tremendous as has been the advance of recent years, this sort of knowledge cannot represent the ultimate goal of genetic research. Mendelism has given us the plan of heredity—the more intimate and fundamental knowledge of the material which is employed in the elaboration of that plan remain the task of some other mode of research.

The Method of Cytology.—The method of cytology in genetic research is concerned primarily with questions of cell mechanism. It may be said to be directed toward the solution of two distinct problems, first the behavior of the hereditary elements in somatogenesis, the building up of the body, and secondly in the determination of the nature and operation of the mechanism which distributes hereditary elements from parent to offspring. These are matters of fundamental importance in genetic enquiry; it is unfortunate that the methods of dealing with the problems here presented are necessarily static and so little under the control of the investigator. Nevertheless even with these handicaps, the contributions of cytology to genetic interpretation are by no means inconsiderable. The determination of the equivalent distribution of the hereditary elements in the cell divisions of somatogenesis and the probable fact that every ultimate cell in the body normally possesses all the hereditary elements of the initial fertilized egg-cell have been established as nearly as may be by cytological research. Moreover, the separation of homologous contributions of the parents in the formation of germ cells and the union of two homologous sets of hereditary elements for the production of new individuals represent another phase of the problems which have been solved by cytological research.

Although obviously the dangers of misinterpretation in dealing with fixed and stained preparations of cells or sections of cells are very great, a fact which is disclosed by the diverse interpretations which different investigators have given of the same phenomena and structures, nevertheless the importance of this field of research should not be underestimated on that account. There are several reasons for reposing confidence in the results of cell investigations, and these come from two sources; from the confirmations of the growing field of what may be called experimental cytology, the observation of cell phenomena directly in living cells, and from the broad general result of cytological research that the mechanism which has been discovered is by nature such an one as might be expected from *a priori* consideration of the results of Mendelian investigations. The close correspondence which exists between cell behavior as it is believed to exist from cell investigations and hereditary phenomena as they are known to exist from Mendelian investigations has given renewed confidence to students of heredity in the validity of their interpretive conclusions.

The most important progress which has been made within the last decade in genetic science has been that of interpreting Mendelian phenomena of inheritance in terms of the behavior of the cell mechanism. Thus far this work has been carried to any degree of completeness in only one species, the common fruitfly, *Drosophila ampelophila*. In the extensive investigations which have been made with this species, Morgan and his associates have demonstrated how close a correlation exists all along the line between cell behavior and hereditary distribution of characters. Certain characters are distributed independently of each other, the pairs of chromosomes separate independently of each other in the formation of gametes; certain characters display irregularities in distribution and expression associated with differences in sex, the chromosome content of the two sexes is demonstrably different; four sets of characters exist the members of which tend to remain together in transmission in the combinations in which they occurred originally, the entire chromatin material is contained in four pairs of chromosomes; and finally irregularities in character distribution have been discovered, the chromosome constitution and distribution in such cases are correspondingly irregular. These facts the student will be better fitted to appreciate later on; they are given here to show how the results of one method of investigation are supported and strengthened by those of other methods.

The Method of Experimental Morphology.—Under the heading morphology, we include those particular phases of development which are designated by the terms, ontogeny and embryology. The method of experimental morphology has for its task the solution of the problem of the development of the individual as it is related to problems of variation and heredity. The aim of this method is to determine how the characters of the adult become patent as development proceeds, the broad question of the origin of complexities within organisms.

In the Mendelian method, the formal relations which exist between hereditary elements are dealt with, particularly their relations in distribution and recombination. The characters of the adult organism are for the most part the basis of judgment. In spite of the general truth of this statement, however, Mendelian analysis has in many cases extended into the field of the physiological relations which exist between hereditary elements, not merely with regard to contrasted homologous hereditary determiners, but with regard to the physiological relations existing in development between entire sets of hereditary elements, and at times even between these and definite factors of environment. But for the most part the solution of such problems depends upon thorough experimental study of development in individuals of known genetic constitution. This portion of the problem remains almost untouched. If development be thought of as a series of successive physico-chemical reactions, the complexity of the problem may easily be judged. Certain of the simpler features of it, however, have been attacked and the results of these preliminary studies have indicated still other modes of approach, so that we may expect that when geneticists come to appreciate the light which may be thrown upon heredity by the experimental investigation of development, research in this field will be greatly stimulated. Already as Jennings has pointed out the main features of the process of development are clearly indicated; the hereditary elements of the chromosomes remain the same in each cell, the reactions and functions of any cell depend upon this chromatin system working in conjunction with the cytoplasmic matrix in which it is located. From this fact may be drawn the broad conclusion that differentiation within the individual depends upon cytoplasm differentiation. The difficulty of the question of how and why should not deter investigation.

Prerequisites for Genetics.—The foregoing discussion of modes of research in genetics should indicate something as to the nature of the working equipment necessary for a study of the science. Since genetics is a biological science, intelligent study of it presupposes a thorough grounding in general biology such as is given in foundation courses in botany and in zoology. Inasmuch as practically all domesticated plants and animals belong to the higher orders, particular attention should be given to the cycles of developments in these organisms, especially those phases which are comprised in development and reproduction. Of particular importance is a general knowledge of physiology, not so much on account of the direct utility which it has in the study of genetics as for the attitude toward life phenomena which it awakens in the student. Genetics, indeed, is essentially a sub-division of physiology in the broader sense. A knowledge of mathematics is a valuable asset because it is often necessary to subject the data of heredity and variation to mathematical treatment in order to interpret them properly. For the elementary study of genetics, a knowledge of the methods of dealing with simpler algebraic problems is sufficient; for advanced study a knowledge of the differential and integral calculus is highly advantageous. Finally it may not be out of place to mention the fact that investigation in genetics is not confined to those who employ the English language. A reading knowledge of French and German is practically necessary for those who desire to pursue the subject very far.

The Applications of Genetics.—Genetics has both scientific and practical applications. As an example of its scientific applications, the part which it has played in shaping doctrines of evolution instantly comes to mind, for of necessity such doctrines must conform to the fundamental principles of genetics. The science of genetics and that of evolution are by their very natures constantly encroaching each upon the fields of research of the other. Thus experimental investigations of evolution are of vital interest to genetics, because they deal with the mode of origin of hereditary characters. Genetics, also, has its applications in branches of biology other than that of evolution, indeed throughout the entire realm of biology its influence is felt in shaping thought and directing interpretation. There are few other sciences which possess so much of general interest as that of genetics.

The practical applications of genetics are found in agriculture and in human affairs. Here genetics involves many things which are extra-biological. Thus in agriculture emphasis is placed upon the employment of the principles of genetics for the amelioration of plants and animals for man's use. Breeding, then, may be defined as the art of improving plants and animals by hybridization and selection. To make effective progress along this line methods of testing given individuals or races, both with respect to fixity of type and comparative value, have been devised. The methods of attack are very much the same as those which are employed in the experimental study of heredity and evolution, the primary aim of which is merely to discover underlying principles. Eugenics is concerned with the principles of genetics in so far as they may be applied in the improvement of the human race; but it includes much that is sociological, rather than biological. The applications of the principles of genetics, therefore, are always subject to such modifications as may be determined by practical considerations.

Genetics in Agriculture.—Modern agriculturists, for the most part, appreciate fully the importance of producing only the best types of plants and animals; for in spite of the strange anomalies of economic conditions which at times appear to give actually a greater return for smaller total yields, the fact must remain that the larger view of the agriculturist's place in society requires of him as of all its other members the fullest possible returns compatible with economic principles and the requirements for a permanent agriculture. But although the desirability of high production and quality is very generally recognized, it is a fact that very often this ideal cannot be attained except by the most careful and intelligent efforts. This is more often the case with plants than with animals, for plants are on the whole less independent of environmental conditions and therefore more susceptible to differences in them. Producers of crops are always in need of varieties which are better adapted to local conditions, but except in rare cases they are not fitted to develop such varieties. Here genetics comes very definitely to the aid of the plant breeder for its principles provide a safe guide for him in attaining his ideal. Already breeders of plants have realized a great saving of time and expense as a result of the application of principles derived from scientific investigations in their work.

The animal breeder on the other hand has faced a somewhat different problem. The far greater comparative value of the individual in livestock operations has led in animal breeding to the establishment of pure breeds of domesticated animals of remarkable excellence. Long application of the method of trial and error has developed a body of empirical knowledge which has achieved results nothing short of the marvelous. But while the old empirical methods have served their purposes well, nevertheless they cannot from their very nature give complete satisfaction. Knowledge is only secure when it rests upon a firm foundation of principle, and however excellent have been the results of empirical breeding from a utilitarian standpoint, they have not led to the discovery of fundamental principles. The principles of genetics provide a consistent interpretation of the results of breeding methods. To the novice a knowledge of such principles is an abundant aid in interpreting and organizing details of experience; by its help he can progress more safely and more surely in determining the methods of procedure which are essential to the fullest success in his breeding operations. The real service of genetics to animal breeding lies in the promotion of clarity of thought, and that is a thing of no little value.

Although genetics thus far has contributed but little toward improvement of the existing methods of animal breeding, it is not a dream impossible of realization that in the future its contributions in this direction will be of considerable importance. The science of genetics is still in its infancy, it is still in the formative period of its existence. It has not yet been possible with any degree of satisfaction to analyze the hereditary constitution of any farm animal, even to the incomplete extent which has been accomplished in some plants and in some of the smaller animals. Obviously we cannot apply even the general principles of genetics intelligently in animal breeding until we are more thoroughly conversant with the facts of character behavior and factor relationship. Such facts can only be determined by means of carefully planned experimental investigations. A few investigations have already resulted in important extensions of our knowledge in this respect, others now under way promise to extend this knowledge considerably further. Systematic crossbreeding of cattle and sheep for definite commercial purposes is of proven value. The method of breeding for high winter egg production in fowls has been determined. Investigation of the inheritance of high milk production in cattle is under way. Geneticists are also seeking to analyze the extensive data with respect to certain characters such as color, fecundity, and speed which have been recorded in herd books. Progress in such work with the larger domestic animals is necessarily exceedingly slow, but this should not deter investigators from organizing carefully planned experiments to extend knowledge in this direction. It is only in this way that genetics can take its proper place in practical animal breeding. The progressive agriculturist can well afford to encourage every proper effort having as its aim the collection of genetic data.

CHAPTER II

VARIATION

Organic differences, their nature and causes, have furnished abundant material for speculative enquiry since time immemorial. The great significance of the fact of organic individuality was not fully grasped until Lamarck founded his theory of evolution which postulated the progressive, imperceptible change of one species into another. It remained for Darwin to scrutinize all phases of organic life, past and present, wild and domesticated, in his search for a guiding principle which should explain the course of evolution. Darwin's hypothesis of natural selection assumes variability without enquiring into its causes, but this does not mean that Darwin was not concerned with the problem of causes. In both his "Origin of Species" and "Variation in Animals and Plants under Domestication" the causes of variability are often referred to and he suggested among others, the kind and amount of food, climatic changes and hybridization. Our respect for the great naturalist's keen perception deepens when we realize that very little has been added as yet to our knowledge of the causes of variation.

The Universality of Variation.—Individuality is common to all organisms. No two trees, no two leaves, no two cells in a leaf are identical in every respect. Individuals sometimes appear exactly alike but even identical twins will be found to differ in some features. The shepherd knows his sheep individually and the orchardist his trees. Were there no differences in individuals there would be no changes in species and there could be no improvement of cultivated plants. "Variation is at once the hope and despair of the breeder," the hope because without it no improvement would be possible, the despair because very often, when improvement has been made, variation results in a tendency to fall below the standard previously reached. In the sugar beet, for example, a high percentage of sugar has been maintained by continually testing and selecting the "mother" beets for the next crop of seed. However, this necessity for continual selection does not exist in respect to all important field crops although they are subject to the general law of variation. That this must be so is clear when we realize that many natural species as well as cultivated varieties of plants are really mixtures of sub-species, varieties, or races and that upon being isolated these distinct forms reproduce their own particular type. This is most easily demonstrated in plants normally self-fertilized, yet in all naturally cross-fertilized plants and in higher animals this same endless diversity among individuals is even more marked.

The Variation Concept.—As we have implied in the above remarks the term, variation, may be used in very different senses in referring to different phenomena. Thus variation within a species or variety means that the group in question is heterogeneous. Among individuals variation may consist of differences between members of the same generation or between parents and offspring. Even when thus restricted, however, the term is apt to prove ambiguous. Hence it is necessary to give some thought to the sources, nature and causes of these individual differences in order that we may use clear cut expressions which shall always convey to one another a concept of the same particular sort of organic difference.

Classification of Variations.—1. *Heritability.*—Character differences either represent something specific in the germ or they are merely the effect of external stimuli upon the individual soma. In the first case they are inherited, although they will not reappear necessarily in all later generations or in all the progeny. In the second case they will not be inherited. This is a fundamental distinction and may well serve as our primary basis of classification. According to *heritability* variations are either *germinal* or *somatic.* Under germinal variations we recognize two sub-classes, combinations and mutations. Purely somatic variations will be referred to hereafter as modifications.

Modifications are non-heritable differences between the individuals of a race caused by the unequal influence of different environmental factors. Such variations frequently approximate continuity and, when studied statistically, display the normal variability curve, which will be explained in the next chapter.

Combinations are heritable differences between the individuals of a race or between the offspring of a pair of parents caused by segregation and recombination of hereditary units. They also frequently display the normal variability curve.

Mutations are heritable differences between parents and offspring which do not depend upon segregation and recombination.

These three categories, as Baur has shown, are not to be recognized and separated merely according to appearances. The cause of any individual differences can usually be established only by careful breeding experiments; but by this means the separation of the three categories is always possible as the boundaries between them are quite sharp. Modifications are somatic effects of environmental differences and should not be confused with germinal changes which are sometimes induced by natural or artificial means and which result in the production of mutations. Within this first category must be included all place-effects in plants and somatic environmental effects in animals. Modifications comprise a large portion of what are commonly spoken of as fluctuations due to environment, *but all cases of fluctuating variation are not modifications* inasmuch as variations due to combinations frequently display the normal variability curve also. Modifications are not heritable. The second category, variation by combination of hereditary units is often confused with modification, as already stated, because of the fact that variations caused by segregation and recombination when studied statistically often display the normal variability curve. This is especially apt to be the case in quantitative characters (those of size or weight) and segregation and recombination may be the cause of gradations in color intensity. In autogamous (self-fertilized) organisms hybridization between races is sufficiently rare to be negligible in this connection, *i.e.*, in such species the fluctuating variations are caused by the environment. But in allogamous organisms (those in which two individuals are necessary to accomplish sexual reproduction) fluctuating variations may be caused either by the environment, by segregation and recombination of factors, or by both causes acting together. We shall take up the third category, mutations, in a later chapter. For the present it is sufficient to remember that mutations are no doubt the least frequent of the three classes, that easily distinguishable mutations are comparatively rare, but that there may also occur true mutations of such moderate extent, as compared with the population, that their existence would only be detected by breeding tests, since their progeny would exhibit a different range of fluctuation from that of the population.

2. *Nature.* We may next enquire into the nature of variation as it affects the organism. Upon this basis we may distinguish between four classes: morphological, physiological, psychological and ecological.

Morphological variations are differences in size and form (Fig. 1). In general morphological variations have more significance for the biologist than for the agriculturist. However in many products of the farm, size and conformation are of decided importance. Two sub-classes under morphological variations are *meristic* and *homeotic* variations. Meristic variations are differences in number of repeated parts such as the petals in a flower, the leaflets in a compound leaf or number of phalanges. Homeotic variations are differences caused by the replacement of one part by another, as the production of an antenna in place of an eye in an insect.

Physiological variations are differences in quality and performance. Examples of qualitative variations are difference in degree of hardness of bone, flavor of meat, richness of milk, difference in normal color (Fig. 2), resistance to drouth, frost or alkali. Variations in performance constitute the most important group for the producer. Differences in performance are sometimes, though not necessarily, associated with certain details of structure. For example, note the prominent milk veins on the udder of Tilly Alcartra as shown in Fig. 231.

Psychological variations are differences in mental traits. That mental and nervous conditions have very definite effects upon physical conditions is well known, but the problem of distinguishing between purposeful action and automatic response, between manifestations of reason and manifestations of instinct, is set for the students of animal behavior. While variations in mental characteristics have an important place in eugenics and merit the attention of livestock breeders, yet the inheritance

Fig. 1.—Morphological variation in number, form and size of leaflets in the blue elderberry, *Sambucus glauca*.

of pyschological characters must be more extensively investigated before the subject can be considered with profit in a fundamental study of genetics.

Ecological variations are those differences between individuals that result from their fixed relation to the environment. These differences are especially noticeable in plants and are known as place-effects or place variations. This category includes some of the phenomena of variation in crop yield and hence is of immediate significance to agriculture. Fig. 3 illustrates place-effects in a common weed.

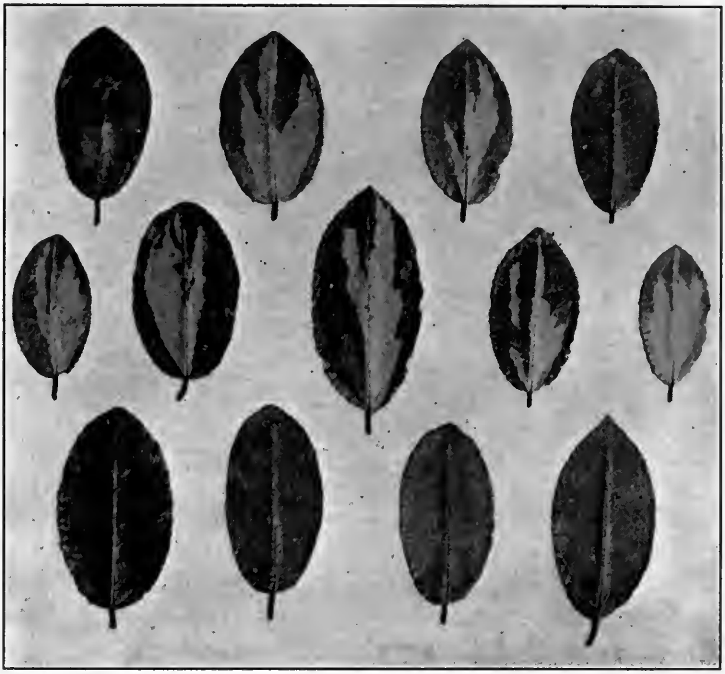


Fig. 2.—**Substantive variation due to chlorophyll reduction in certain areas of the leaves of *Elæagnus pungens*.**

3. According to *differences between them* there are two general classes of variations: first, the slight differences in every character which are always to be observed even among individuals of identical heredity; second, unusual, striking differences commonly known as sports. The first class are called normal, indefinite fluctuating or *continuous* variations and the second, abnormal, definite and *discontinuous* variations. It should be noted, however, that all discontinuous variations are not necessarily definite or even distinguishable. Continuous variations when examined statistically are found to conform to the law of statistical regularity.

That is, if measured and plotted the graph will approximate the normal curve of variability (Chapter III). Continuous variations are either heritable (combinations) or non-heritable (modifications) and, as was stated above, the only certain method of determining the class in which a given case may fall is the breeding test. Discontinuous variations are essentially discrete differences whether they be large or small. They are also either heritable or non-heritable and there is no correlation between size and heritability. Thus the extremely large and small

FIG. 3.—Place-effects in common mustard (*Brassica campestris*) due to soil differences (herbarium specimens).

mustard plants shown in Fig. 3 considered by themselves are discontinuous variations, but they are almost certainly due entirely to environmental differences and seed from the small plant if grown under optimum conditions would produce plants of normal size. On the other hand, it is known that many minute differences in organisms are heritable.

4. According to *direction* variations are classed as orthogenetic and fortuitous. *Orthogenetic* variations are those differences found in individuals related by descent which form progressive series tending in a definite direction. Many remarkable illustrations are found among paleontological records of the evolution of animals. Occasional examples are found among short-lived or vegetatively propagated species. The remarkable series of variations of the Boston fern described in Chapter XVI is a good example. *Fortuitous* variations are chance differences occurring in all directions.

5. According to *cause* variations are either *ectogenetic*, differences arising from conditions acting upon the organism from without; or *autogenetic*, differences resulting from strictly internal relations between germ and soma.

Variation and Development.—Somatogenesis, in sexually produced multicellular organisms, includes the entire history of cellular multiplication and specialization from the first cleavage of the fertilized (or parthenogenetic) egg to the completion of all adult features. From the standpoint of individual development it includes gametogenesis, for the production of sexual glands and of secondary sexual characters are merely phases of differentiation. Cell growth and cell function depend directly upon the activity of the living substance within the cell. The nature and degree of this activity depends upon two sets of determining causes acting simultaneously. First, there are the specific hereditary determiners or genetic factors, which react with the other elements of the protoplasm and, under favorable circumstances, condition normal development. Second, there are all the conditions external to the cell which stimulate or inhibit protoplasmic activity. These "developmental stimuli" are chemical and physical changes wrought by energy from without the organism or caused by its own physiological activities. Chemical stimuli are exerted mainly through the medium of the circulating liquid which surrounds each living cell. Normally this fluid contains the elements essential for maintenance of life as well as various waste products. It may also bear toxic substances that suppress or inhibit the cell functions and in higher animals it contains the secretions of the ductless, sexual and other glands that profoundly affect development. Physical stimuli are exerted chiefly from without and upon the organism as a whole. They include changes in temperature, light and density of medium, the effects of electric and radiant energy, force of gravity, etc. Obviously, so many interrelated causes acting simultaneously, each being independently capable of inducing a change in the end product, may cause an infinite number of differences in substance and in degree of development.

Variation and Environment.—External stimuli affect the development of characters in three ways: (1) they *modify* the development of inherited characters; (2) they actually *condition* the production of characters whose hereditary determiners are present in the germ-plasm; (3) they may *cause* germinal variations which result in the appearance of new heritable characters. The following are illustrations of these effects with reference to particular environmental factors.

FIG. 4.—*Sedum spectabile.* The three shoots (taken from a single plant) were planted in small pots on March 12, 1904, and placed in different greenhouses: *I*, in blue light; *II*, in mixed white light; *III*, in red light. Photographed on Sept. 30, 1914. (*After Klebs.*)

1. Environment Modifies Development of Inherited Characters.—(*a*) *Light and Function.*—Klebs reports the results of growing the Showy Sedum (*Sedum spectabile*) in white, red and blue light. The diverse effects of the three kinds of light are clearly shown in Fig. 4. Although the visible differences between the three plants were very pronounced the experiment was carried much further. During 1905–06 observations were made on the numbers of stamens in the flowers of plants similarly propagated under white, red and blue light and under various conditions of temperature, moisture, and food. About 20,000 flowers were examined and six distinct types were found, according to the variation in number of stamens. These had the following average numbers of stamens: (1) 9.68, (2) 8.45, (3) 6.54, (4) 5.05, (5) 9.47, (6) 7.33. Finally, Klebs subjected similar plants from white, red and blue light to chemical analysis in order to secure further evidence of the physiological effects of light of different wave lengths. Table I shows the composition of the leaves in three plants like those shown in Fig. 4. They were in their respective greenhouses from June 6 to September 7. The percentages shown are per 100 g. of dry substance. In comparing these percentages it should be remembered that the plant in white light produced 1324 flower buds and the plant in red light 405, while the plant in blue light produced none. This explains the higher percentage of ash, nitrogen and protein in the last. On the other hand, the amounts of starch and sugar found in the plant from white light are decidedly larger than the one from blue light. In short, according to Klebs, in comparison with normal white light, the production of organic substances, such as starch and sugar, is diminished under the influence of blue light as microchemical and macrochemical tests distinctly show. In consequence of this diminished assimilation of carbon dioxide the rosettes become purely vegetative. In red light the carbon assimilation is greater than in blue light but less than in white. These experiments prove that the transformation of a plant "ripe to flower" into a vegetative one is possible on the one hand by an increase of temperature and of inorganic salts and on the other hand by a decrease of carbon assimilation.

TABLE I.—CHEMICAL COMPOSITION OF THREE PLANTS OF *Sedum Spectabile* GROWN IN WHITE, RED AND BLUE LIGHT.

Substance	White	Red	Blue
Ash	13.20	13.20	18.60
Sugar	11.04	15.40	2.40
Calcium malate	22.29	18.02	18.10
Free nitrogen	0.16	0.33	0.59
Starch	5.82	3.66	1.20
Crude protein	5.33	6.15	7.64

(*b*) *Temperature and Pigmentation.*—Many experiments in the rearing of moths and butterflies under controlled temperatures prove that degree of pigmentation is profoundly influenced by the temperature at which the pupæ are kept. Some species exhibit seasonal dimorphism in the wild state. By taking pupæ of the common European form of the swallowtail butterfly, *Papilio machaon,* and subjecting them to a temperature of 37° to 38°C., Standfuss obtained the characteristic summer form which occurs in Palestine. Again it has been shown by temperature experiments that many variations found among insects in nature are merely aberrations due to temperature effects. Goldschmidt by artificially controlled temperatures has produced a series of forms of the diurnal peacock butterfly, *Vanessa io,* which show the fading out of the "peacock eye" mark (see Fig. 5).

(*c*) *Food and Structure.*—Woltereck was able to prove that the form (hence the structure) of the fresh water crustacean, Hyalodaphnia, varies directly with the food supply. These minute animals produce many generations during a season and the successive generations from the same water exhibit a morphological cycle, the earlier and later generations having shorter heads and the generations produced from midsummer to autumn having longer ones. Fig. 6 is a reproduction of Woltereck's diagram of the morphological cycle in Hyalodaphnia showing variation

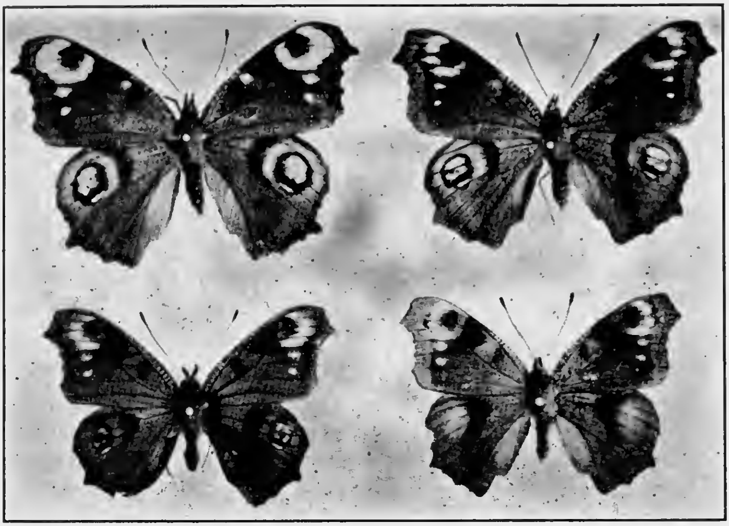


FIG. 5.—The diurnal peacock-butterfly (*Vanessa io*), *above*, and *below*, forms produced by subjecting the pupæ to unusual temperatures. (*After Goldschmidt.*)

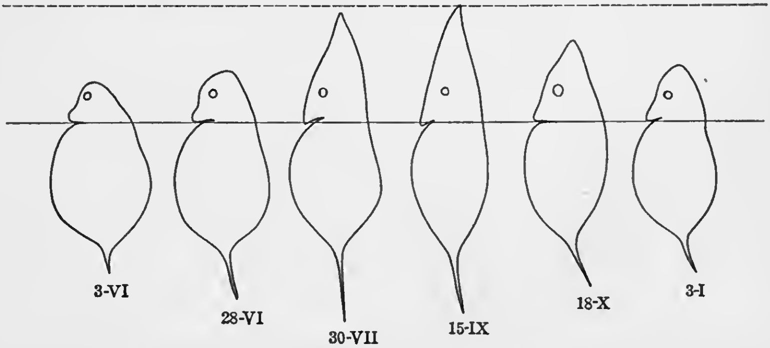


FIG. 6.—Morphological cycle of head-height and shell-length in Hyalodaphnia. Roman numerals designate months. (*After Woltereck, from Goldschmidt.*)

in head and shell length as found on successive dates from June 3 to January 3. By raising these animals under constant temperature conditions and varying the strength of the nutrient solution, Woltereck proved that the relative size of body parts varied with the food. In Fig. 7 the percentages of head height to shell length are plotted as abscissas and the numbers of individuals as ordinates. Animals from three strengths of nutrient media were measured, the curves of those from the weaker, the medium and the richer media being shown at m_1, m_2 and m_3 respectively.

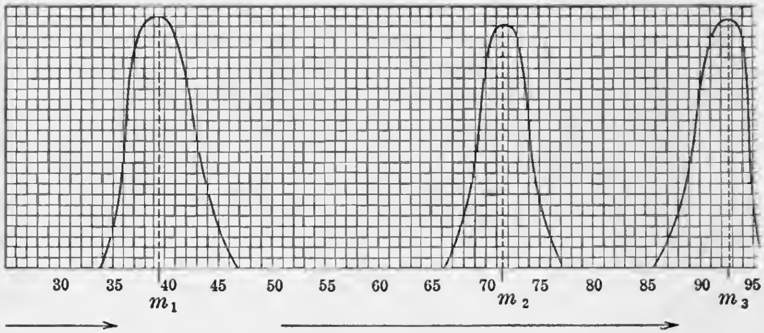


Fig. 7.—Schematic curves of head-height in Hyalodaphnia as grown in media of three different food values. (*After Woltereck from Goldschmidt.*)

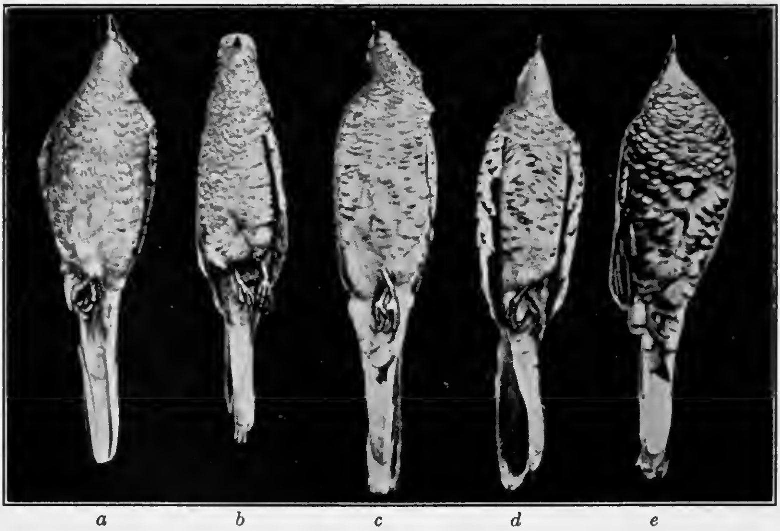


Fig. 8.—*a*, Typical wild pigeon, *Scardafella inca*; *b*; the form *dialeucos; c, braziliensis; d, ridgwayi; e, S. inca* after three moultings in a moist atmosphere. (*After Beebe from Goldschmidt.*)

(*d*) *Moisture and Plumage Color.*—Beebe experimented with the pigeon, *Scardafella inca.* This species, as found in North and Central America, is very constant in color of plumage, but in the moist tropics the following darker colored forms occur: in Honduras, *dialeucos;* in Venezuela, *ridgwayi;* in Brazil, *braziliensis;* and these differ in the amount of pigment in the feathers. By subjecting birds of the northern type to an especially moist atmosphere, Beebe caused them to be so influenced that with each new moulting, whether natural or artificially induced, they always developed darker feathers. Thus a wild bird having pigment in 25.9 per cent. of its area, would have after the second moulting under experimental conditions, 38 per cent. and after the third, 41.6 per cent. Thus during the experiment the typical form assumed the appearance of the three other forms and finally developed plumage markings which have never been seen in nature. Fig. 8 shows the type form, *inca*, the three geographical variants, and the darkest artificially produced form.

Fig. 9.—Plants of Scilla, started alike but the pot on the right was kept in a dark room. (*From Ganong.*)

2. Environment Conditions Development of Inherited Characters.—(*a*) *Light and Metabolism.*—In a general sense light conditions life in all normally green plants. It certainly conditions normal development in such plants. Potatoes sprouted in a dark room develop no chlorophyll in the stems and the rudimentary leaves are abortive. In many bulbous plants, however, the influence of moisture and heat are sufficient to induce leaf growth and even development of the inflorescence, but it is all done at the expense of the food stored up in the bulb as is shown in Fig. 9.

(*b*) *Temperature and Flower Color.*—Baur reports an experiment with a red variety of the Chinese primrose, *Primula sinensis rubra.* If plants of this variety are raised by the usual method until about one week before time to bloom and then some of the plants are put in a warm room under partial shade (temperature from 30° to 35°C.) and the remainder in a cool house (temperature from 15° to 20°C.), when they bloom those in the warm temperature have pure white flowers while those in the cool temperature have the normal red color of the variety. Moreover, if plants are brought from the warm into the cool temperature the flowers which develop later on will be normal red in color. Thus it cannot be said that this primula inherits either red or white flowers. What it really inherits is ability to react in certain ways under the influence of temperature.

(*c*) *Food and Fertility.*—It is well known that the kind of food supplied to the larvæ of bees determines whether the females shall be fertile (queens) or infertile (workers), (Fig. 10). The striking differences in structure and instincts of the two classes of females are all conditioned by the food provided for the larvæ. Each larva inherited the capacity to react in either way according to the stimulus received.

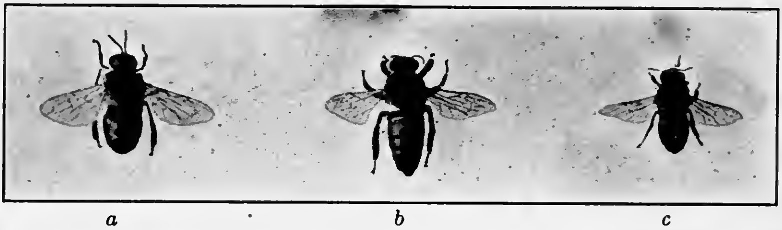


FIG. 10.—The three forms of bees: *a*, drone; *b*, queen; *c*, worker. The two latter develop as the result of difference in the food supplied to the larvæ. (*After Harrison.*)

(*d*) *Moisture and Structure.*—Morgan reports a variety of the pomace fly, *Drosophila ampelophila,* with abnormal abdomen (Fig. 60); "the normal black bands of the abdomen are broken and irregular or even entirely absent. In flies reared on moist food the abnormality is extreme; but even in the same culture the flies that continue to hatch become less and less abnormal as the culture becomes more dry and the food scarce, until finally the flies that emerge later cannot be told from normal flies. If the culture is kept well fed (and moist) the change does not occur but if the flies are reared on dry food they are normal from the beginning."

3. Environment May Cause New Heritable Characters.—As yet there is a dearth of evidence which can be accepted as scientific proof that external stimuli actually cause germinal variations. At the same time there is an abundance of data which falls into the class of circumstantial evidence in favor of such a doctrine. Moreover, there are a few cases in which new heritable characters have been artificially produced by carefully controlled external stimuli. Hence some germinal variations are apparently caused by known environmental conditions and we are justified in recognizing this third category of developmental differences due to environmental effects.

Considerable evidence of permanent changes in both morphological and physiological characters has been secured from experiments with the culture of bacteria and yeast, in unusual culture media, in the presence of toxic solutions, or under extreme temperature conditions. The significant results of four investigators who worked independently, Hansen, Barber, Wolf and Jordan, have been reviewed and discussed in regard to their bearing on genetic theory by Cole and Wright. The four investigators mentioned above used refined methods and three of them began by isolating a single organism from whose progeny they obtained distinct strains or biotypes which remained constant for hundreds of test-tube "generations." It must be admitted that in most of these cases no specific influence can be named as the direct cause of the inherited variation. But there is no longer any doubt that permanent, discontinuous variations do occur spontaneously in these lowest organisms, and it is highly probable that certain incidental, external forces play an important part in inducing such variations.

Fig. 11.—*O*, Portion of leaf of parental Scrophularia showing branching lateral vein; *D*, branching vein replaced by two laterals in leaf of a seedling grown from seed produced by an injected ovary. Also note difference in size and margin of leaves. (*After Mac Dougal.*)

Direct experimental attack upon the germ cells themselves has been made with plants by a number of investigators, notably by MacDougal, who injected very dilute solutions of potassium iodide, zinc sulphate, sugar, etc., directly into the ovaries of various plants immediately before fertilization. Consequently somatic changes have been produced which were inherited throughout several generations. By means of check experiments and observations it was found that these germinal variations were not caused by the wounding of the ovary and it is thought that they must have been induced in some way by the presence of the foreign chemical solution in the ovary. Fig. 11 shows a morphological change which appeared in a seedling of an unnamed species of Scrophularia as a result of ovarial injection. Having tested this species sufficiently to determine that it was a simple one, MacDougal treated several ovaries with potassium iodide, one part in 40,000 and secured seed. No other species of Scrophularia grew near the cultures. From this seed only three plants were raised. "One formed a shoot fairly equivalent to the normal, finally producing flowers in which the anthocyans were of a noticeably deep hue. The two remaining plantlets were characterized by a succulent aspect of the leaves and by a lighter and yellow color of the leaves and stems. The flowers on one of the derivatives, as they may be called, were so completely lacking in color as to be a cream-white, this derivative being designated as *albida,* while the other showed some marginal color and a rusty tinge and was designated as *rufida* . . . . . Seeds of the original two derivatives were sowed in the greenhouse. But one plant of *albida,* the most extreme departure, survived, while four of *rufida* were secured." MacDougal compared these second generation seedlings with seedlings from the original stock of the species, noting differences in size and margin of leaves, length of petioles and number of marginal glands. He found that the differences shown by the first generation appeared again in the second generation. Striking as these results appear it must be admitted that it would be difficult, on account of the small numbers of individuals differing from the parent type, to prove satisfactorily to the biometrician that they were not mutations which would have occurred regardless of the ovarial treatment.

What appear to be germinal variations in the tomato have been induced by intensive feeding. T. H. White tested the effect of dried blood, dissolved phosphate rock, sulphate of potash and iron filings all in excessive amounts, and (with the exception of the iron) in various combinations, on the Red Cherry tomato. The lack of data on control cultures of seedlings from the same parent as the experimental cultures makes it impossible to compare the actual amount of permanent variation produced. T. H. White states that measurements "show that the plants of the sixth generation grown under the influence of the dried blood are one-third larger in height, length of leaf and size of fruit, than those of the second"; (see Fig. 12). The author concludes that "there can be no doubt . . . that, in the case of Red Cherry treated with dried blood, there is permanent variation to the third generation." If these results are corroborated by more carefully planned and rigidly controlled experiments they will add the weight of scientific proof of a principle in plant breeding long since recognized on empirical grounds, to wit, that the introduction of wild plants into intensive cultivation induces variation. Furthermore, it suggests a possible means for rapid permanent improvement of wild forms with which hybridization may be impracticable.

In experiments on lower animals, e.g., the protozoa, the same difficulty is met with as has been encountered in bacteria and yeasts, in that it is manifestly impossible to distinguish between somatic and germinal variations. Moreover, in most of these experiments, as with most of those on higher animals, the necessary conditions for rigid scientific analysis have been lacking. Either the same strain as was subjected to artificial conditions was not grown for comparison under natural conditions or else the conditions themselves were not sufficiently well controlled to permit of certain analysis. It is interesting to note that the pomace fly, *Drosophila ampelophila*, which has produced more mutations so far as we know than any other organism, was subjected to the effects of ether on a grand scale and under controlled conditions by Morgan, but that not a single mutation was observed to result from this treatment. However, mutations have subsequently appeared again and again in cultures of "wild" flies not only of this species but also of other species of Drosophila. Thus it appears that germinal variations frequently occur independently of external stimuli. It also seems that a tendency to produce mutations may be inherited.

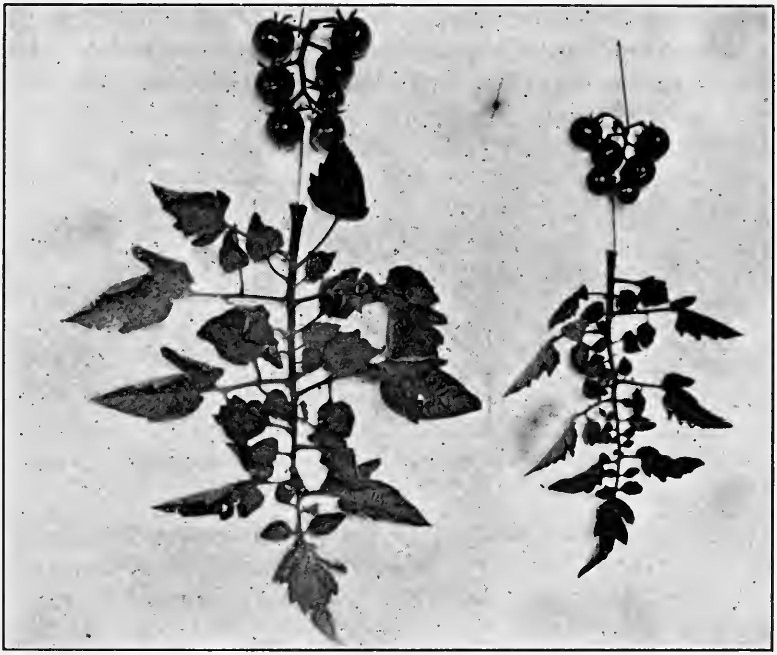


Fig. 12.—Leaf and cluster of fruit of Red Cherry tomato of the second generation (right); same of the sixth generation (left) of continuous treatment with excessive amount of dried blood. (*Photo by T. H. White.*)

With animals the best known experiments on the artificial production of germinal variations are those of Tower who worked with the Colorado potato beetle, *Leptinotarsa decemlineata,* and related species. Like other arthropods these beetles are more directly under the influence of temperature changes at least than are warm-blooded animals. Tower first determined the period in ontogeny when external stimuli will affect the germ cells. He found that in Leptinotarsa the germ cells do not become susceptible to external stimuli until after the time in ontogeny when the color pattern of the individuals subjected to the stimuli can be influenced. He found that eggs were most susceptible just before and during maturation and this observation is in agreement with those of Fischer, Standfuss, Weismann and others who have conducted similar investigations. Tower concluded that certain individuals from the germ cells of a stimulated parent "show intense heritable variations, whereas those not acted upon do not show these changes." Most of the inherited variations involve changes in the pigmentation of the body parts. In certain cases there was an actual change in the color pattern (see Fig. 13). It is to these results that Tower attaches the greatest significance inasmuch as most similar experiments have not succeeded in causing pattern changes. In spite of the elaborateness of Tower's methods considerable skepticism exists regarding the validity of his conclusions, and this has not been lessened by the non-appearance of confirmatory data. In a recent paper he reports the production of very striking germinal modifications in *L. decemlineata* as a result of subjecting a morphologically homogeneous race to an extreme change in environment. However, it is still a question whether the material used may not be heterogeneous as regards the germinal factors that condition certain physiological characters.

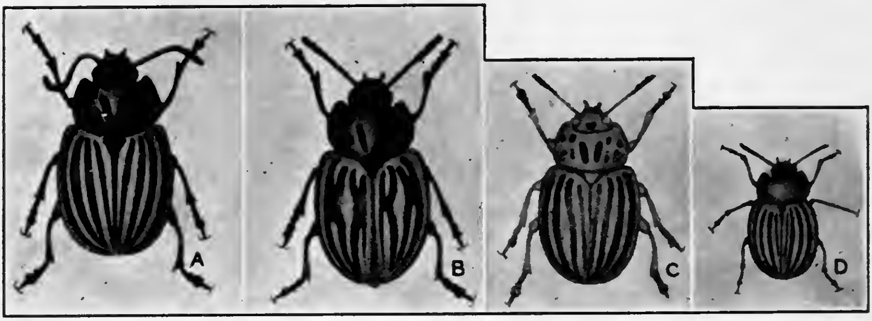


FIG. 13.—*A, Leptinotarsa decemlineata* and three mutants; *B, tortuosa; C, pallida; D, defectopunctata.* (*After Tower.*)

Stockard's investigations on the effect of alcohol on the progeny of guinea pigs have shown that the germ cells as well as the somatic tissues of the alcoholized animals are injured. This case is considered further in Chapter XXX.

On the whole it must be admitted that the experimental induction of heritable variations is still largely an unworked field. The complex conditions to be considered and consequent obstacles to be overcome are appreciated by no one more fully than by those who have attempted such investigations. For, as Tower has said: "It is evident that the problem of germinal change is one of difficulty, and involves more of indirect than of direct methods of investigation. There is little reason to expect that present biochemical methods can give a solution, but they may give valuable suggestions for further indirect investigation. It seems not improbable, however, that this problem like so many others in biology, must await the solution of the larger question of what life is before it will be possible to express in exact terms the nature of germinal changes. Our present status, with several methods of production and much knowledge of the behavior of induced germinal changes available, is a basis from which great advances in knowledge and in operation may reasonably be expected."

CHAPTER III

THE STATISTICAL STUDY OF VARIATION

In the present chapter we shall consider the application of purely statistical methods in the analysis of biological phenomena especially the phenomena of variation. The treatment given here does not pretend to be exhaustive or rigorous, but it presents the commonly used method of recognized biometricians, from several of whom valuable suggestions have been received. We shall have occasion to refer to the utilization of statistics in the study of heredity by the "biometrical school," but the application of statistical methods in the analysis of specific genetic problems will be deferred until later chapters.

Causes of Fluctuations.—Continuous variations, or the slight differences normally found in organisms, are generally referred to as fluctuating variations or fluctuations. It is frequently assumed that "fluctuating variability" is due entirely to differences in environment. But, as was stated in the preceding chapter, either the modifications in development due to environment, or individual differences which are caused by segregation and recombination of genetic factors, may display the normal curve of variation when examined statistically. Hence fluctuations may be due to either of two causes and before conclusions may be drawn from the study of frequency distributions and statistical constants, the causes of the variations studied must be clearly differentiated. The only way to accomplish this is to make one set of conditions or the other as uniform as possible. If the object be to examine modifications, only pedigree material should be used and, on the other hand, if variations due to recombinations are to be considered, the environmental conditions must be as uniform as possible or else due account must be taken of existing irregularities. Certain technical requisites to the biometrical method will be mentioned later. This difference in the nature of fluctuating variations according to their cause is of such fundamental importance that it should be clearly understood at the outset.

Law of Statistical Regularity.—This fundamental principle, which is also known as the law of probability or law of chance, may be most simply introduced by means of an illustration. Suppose two persons, blindfolded, were each to pick about 500 beans from a bag containing a million beans of any standard variety. The average weights of the beans picked out by the two persons would be *almost* identical even though the individual beans varied considerably in size. Furthermore if one were to obtain the average weight of the whole million, it would not differ, essentially, from the average weights of the smaller groups. The principle involved here may be stated in various ways. Weld expresses it

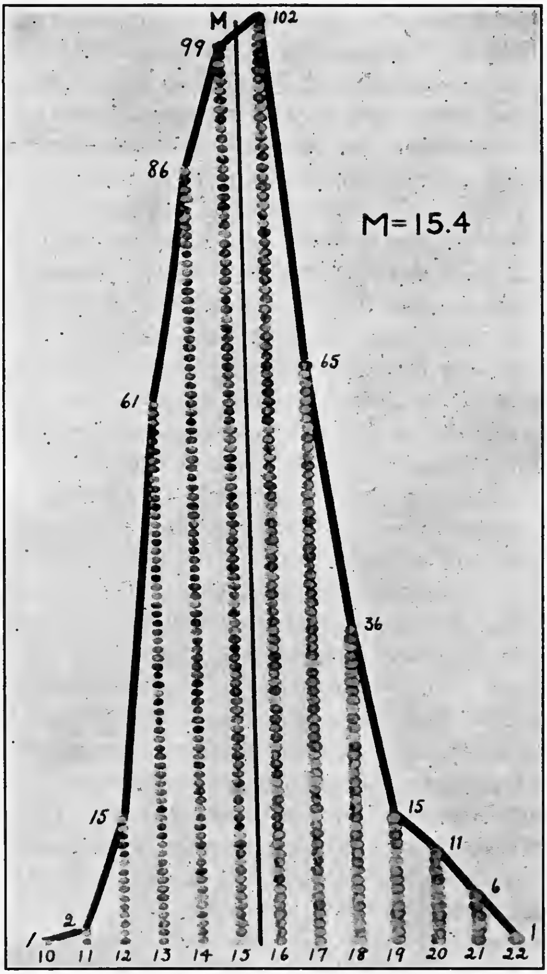


Fig. 14.—Frequency distribution of 500 Broad Beans arranged in classes according to width.

as follows: *"If a number of different events are equally possible as regards constant conditions (that is, if there is no persistent reason why one should occur rather than another), and all are repeatedly given opportunity to occur, they will in the long run occur with equal average frequency."* While this is a satisfactory general statement of the law of probability, the same principle has been expressed by King in terms, which fit well the imaginary case under discussion, as follows: "A moderately large number of items chosen *at random* from among a very large group are almost sure, *on the average*, to have the characteristics of the large group." It must not be inferred that any partial group of individuals no matter how large, will give *exactly* the same results as would be obtained by the use of the entire mass. But the averages will be close and the probability of inaccuracy due to accidental error diminishes as the numbers increase because individual errors tend in the long run to counteract each other.

Law of Deviations from the Average.—If, now, one lot of 500 beans be measured to the nearest millimeter and then arranged in columns from left to right according to width beginning with the narrowest beans, the result will be very similar to Fig. 14. It will be noticed first that the middle classes contain the most beans while the classes on the extreme left and right are very small. The black vertical line *M* indicates the average width or *mean* of all the beans and the column with the most beans in it represents the most frequent width of beans and is called the *mode*. The columns nearest the average value on either side contain the most beans and the further the column is from the average the fewer the beans in it. Thus we see that the majority of the beans show only slight deviations from the average while a few exhibit wide deviations therefrom. Statistical study has proved that it is a general rule with fluctuations that individuals showing extreme deviations in either direction for a given character are comparatively rare, while individuals exhibiting smaller deviations, and hence occupying a position intermediate between the two extremes are especially frequent. In other words, continuous variations usually appear in frequencies such that, if we represent these frequencies graphically, we obtain a polygon which resembles more or less the normal variability curve. Such a polygon is produced by connecting the ends of the columns in Fig. 14.

The Normal Curve and its Significance.—The normal variability curve is a theoretical curve which pictures the result of expanding the binomial $(a + b)^n$ when $a = b = 1$ and n is assumed to be indefinitely great. By the binomial theorem

$$(a + b)^1 = 1 + 1$$
$$(a + b)^2 = 1 + 2 + 1$$
$$(a + b)^3 = 1 + 3 + 3 + 1$$
$$(a + b)^4 = 1 + 4 + 6 + 4 + 1$$
$$(a + b)^5 = 1 + 5 + 10 + 10 + 5 + 1$$
$$(a + b)^6 = 1 + 6 + 15 + 20 + 15 + 6 + 1$$
$$(a + b)^7 = 1 + 7 + 21 + 35 + 35 + 21 + 7 + 1$$
$$(a + b)^8 = 1 + 8 + 28 + 56 + 70 + 56 + 28 + 8 + 1$$
$$(a + b)^9 = 1 + 9 + 36 + 84 + 126 + 126 + 84 + 36 + 9 + 1$$
$$(a + b)^{10} = 1 + 10 + 45 + 120 + 210 + 252 + 210 + 120 + 45 + 10 + 1.$$

From Fig. 15 it is evident that as *n* becomes larger the straight lines of the polygon more closely approximate the normal curve.

The normal curve is perfectly symmetrical because it represents the distribution of an indefinitely large number of items and it assumes all causes to be of equal strength or value. It is assumed that certain biological frequency polygons should simulate this curve for these reasons. It is probable that the environment of any organism is made up of a large number of factors each of which may vary around a mean independently of the others. Now if a frequency polygon is to be made regarding a character of a population composed of individuals alike in zygotic constitution, such as a field of potatoes of the same variety, the differences found in the development of any character are due wholly to these environmental factors. Hence it is likely that the mean of the distribution is made up of observations on individuals upon which an equal number of favorable and unfavorable forces have acted and the deviates are those upon which a greater or less number of favorable or unfavorable forces have acted. But in sexually reproduced allogamous species the individuals are not alike in zygotic constitution. Moreover, the causes affecting a given character may have an unequal mass effect according to ecological conditions. Either of these factors may cause a high degree of asymmetry in a polygon of variation. Graphs in which the mode is rather far removed from the mean are called skew polygons or curves.

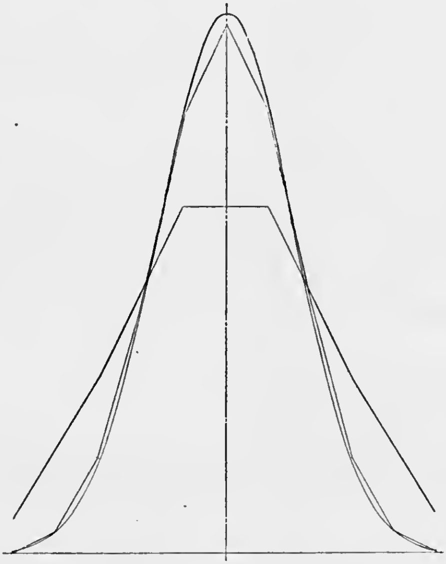


Fig. 15.—Polygons representing expansion of the binomials (a + b)^5 and (a + b)^{10} as compared with the normal curve.

The significance of the normal curve as an index of variation is based on the conception that the area within the curve represents an indefinite number of individuals and that the constants of the curve indicate the distribution of these individuals with respect to a given character. If in any curve (Fig. 16) the perpendicular erected at M divides the area of the curve into two equal parts, this line is the median and the point M represents the average or mean of all the values from which the curve is constructed. The perfect symmetry of the normal curve causes the median to coincide with the mean and the mode; but in actual cases these three values will not coincide because the curve will not be symmetrical. If a perpendicular be erected in either half of the curve at such a distance from M that it divides the area enclosed by the median, the base and half of the curve into two equal parts, the distance of such a perpendicular, Q_1 or Q_3 from M is the quartile, q. Then in the normal curve $q = MQ_1 = MQ_3$. Now the slope of the curve is an index of the amount of variability. The steeper the slope supposing the area (the number of individuals) to remain the same, the nearer to the median will be the position of the quartile and hence the position of the quartile is also an index of variability (Fig. 17). Since curves constructed from actual distributions are never symmetrical, in practice the index taken is $\frac{q_1 + q_3}{2}$. However, the *measure of variation in common use is the standard deviation,* σ, *which in the normal curve represents a distance from the median equal to* $\frac{q}{0.6745}$.

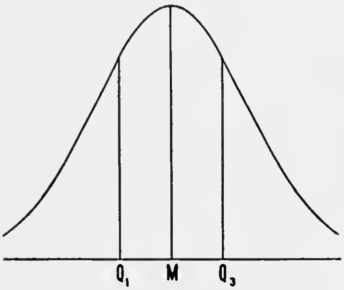


FIG. 16.—A normal curve divided into quartiles by the perpendiculars erected at M, Q_1, Q_3.

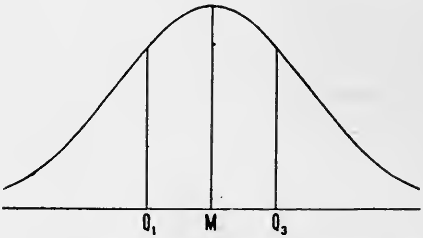


FIG. 17.—A normal curve of exactly the same area as the curve in Fig. 16, but with flatter slope and correspondingly greater breadth. The distribution pictured by this curve presents a greater range of variation than in Fig. 16 as is indicated also by the value of Q.

Requirements of Biometrical Study.—The data for statistical analysis are obtained by counting, by measurement, or by arbitrary graduation of continuous differences like degree of pigmentation. In order that such data may be compared with other similar data some sort of *precise description* must be prepared. Graphical representation is good as far as it goes; a frequency polygon conveys to the eye more knowledge than one would have without it. But in order to secure the best description of organisms with reference to specified characters, some mathematical expression for the degree of variation must be deduced from the data. This process involves two essential steps: (1) To obtain a measure of type for the group under observation; (2) to derive an expression for the amount of variation from the type. There are three measures of type, the median, the mode and the mean, and we have seen that in the theoretical normal curve they always coincide. In actual cases they may be widely separated. There are three commonly used measures of variation from type, viz., the range, or the distance from one extreme to the other, the quartile, and the standard deviation. These expressions and others derived from them are known as the *constants of the normal curve.* In practical work the *mean*, or arithmetical average, is commonly used as the measure of type and the *standard deviation* as the absolute measure of variation. A relative index of degree of variation is derived by dividing the standard deviation by the mean; this is called the *coefficient of variation.* These three constants are the indispensable mathematical tools of the biometrician. Some knowledge of their calculation and significance is necessary for an intelligent appreciation of considerable important biological and agricultural literature. Before proceeding to discuss these constants it will be necessary to present a few technical terms and methods.

Some Biometrical Terms.—An *Individual* may be either an entire organism or only a single part as the leaves of a tree or seeds of a plant. Individuals are also called variables.

A *Sample* is any group of individuals which are measured or compared with a standard. Samples may be divided into sub-samples for definite reasons; for example, corn from different parts of a field.

The *Population* is the general mass or entire group from which samples are taken.

A *Variate* is a single magnitude-determination of a character.

A *Class* includes variates of the same or nearly the same magnitude. The class range gives the limits between which the variates of any class fall.

Requisites to Reliability.—1. *Biological Soundness.*—Three great sources of untrustworthiness in biological work are:

(*a*) Differences due to age; different ages must not be lumped together without taking account of it.

(*b*) Heterogeneity due to conditions of environment; for example, corn from a field in which the soil is definitely heterogeneous.

(*c*) Mixing of distinct varieties, which must never be permitted if known in advance.

2. *Definition of Population.*—The population must be so defined that conclusions reached will not be wrongly applied to other populations.

3. *Typical Sample.*—The sample must be really typical of the species, variety, breed, strain or race. Otherwise the results are not applicable to large populations. Also the sample must be large enough so that conclusions may be drawn fairly.

4. *Sufficient Accuracy.*—Measurements must be made with a sufficient degree of accuracy. It might be thought that a coarse or slightly variable scale of measurement would satisfy since the measurements are to be grouped, but the relative size of the groups is a most critical matter so that the size of scale and degree of accuracy are very important. Yet perfect accuracy is hardly obtainable. Relative not absolute accuracy is the desideratum. As stated by King: *For every statistical problem there should be determined in advance a definite standard of accuracy for each item and every endeavor should be made to bring each recorded instance up to this standard.*

Grouping Variates into Classes.—When the individuals have all been measured the collection of variates must be grouped. The following rules should be observed:

1. Classes should be of equivalent ranges. One must not neglect the extremely large and small variates. Employ a uniform scale throughout all classes.

2. Arrange the classes so there will be no possibility of mistake by the reader. Calculations may be based on the centers of the class intervals or on the upper limits of the intervals for certain purposes.

The Frequency Table.—A list of the classes formed by the grouped variates together with the number of individuals in each class is called a frequency table. For example, Love and Leighty give the data on total yield of plant in grams of Sixty Day oats for the year 1910 at Ithaca, N. Y. These are presented in the form of a frequency table in Table II.

TABLE II.—FREQUENCY TABLE SHOWING VARIATIONS IN YIELD OF SIXTY DAY OATS. (*After Love and Leighty*)

(Class value = V Grams of oats	(Frequency = f) Number of plants	(Class value = V) Grams of oats	(Frequency = f) Number of plants
0–1 = 0.5	3	5–6 = 5.5	42
1–2 = 1.5	50	6–7 = 6.5	7
2–3 = 2.5	106	7–8 = 7.5	2
3–4 = 3.5	109	8–9 = 8.5	1
4–5 = 4.5	80		

Total number of individuals..................400 = n

Frequency Graphs.—To graphically represent the data in the above frequency table, indicate a base line on a sheet of coördinate paper, mark off equidistant points for class intervals and midway between the limits of each class indicate the class center. In this case the class intervals are 0–1, 1–2, 2–3, etc., and the class centers are 0.5, 1.5, 2.5, etc. Counting each space above the base line as one or more individuals (according to the modal number and size of sheet), either construct rectangles of proper altitude to represent the frequency of each class or merely indicate the points of intersection of the frequencies plotted as abscissas and the class centers as ordinates. The latter method is usually employed since it is more rapid and the polygon more truly represents the distribution of classes in a sample showing continuous variation in the character in question. This method is illustrated in Fig. 18. The area within the polygon represents the *actual data* for which purpose a curve should never be employed.

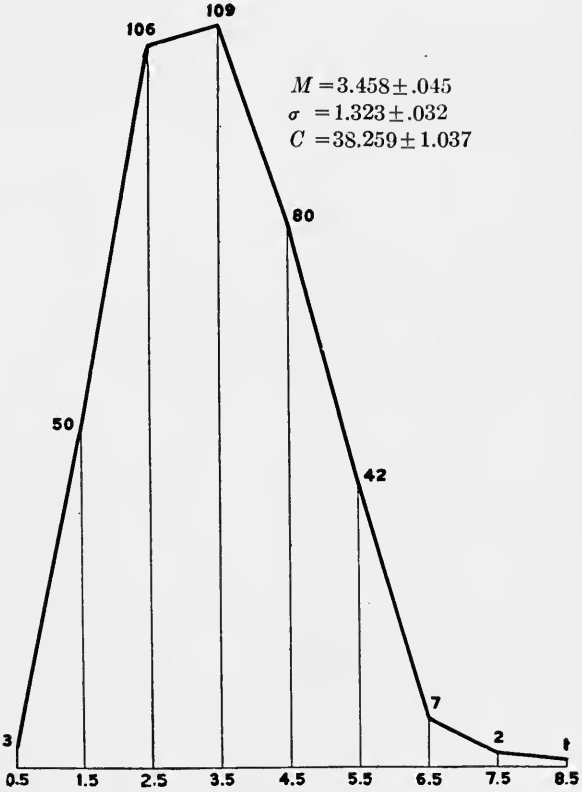


FIG. 18.—Frequency polygon showing variation in total yield per plant in grams of Sixty Day oats at Ithaca, N. Y., 1910. (*Data from Love and Leighty.*)

The Mean, Calculation and Significance.—To compute the mean of a series of single variates summate the variates and divide by the number of variates. Thus if x = any variate and n = the number of variates, then the mean, $M, = \frac{\Sigma\,(x)}{n}$ where Σ indicates summation.

For a series of groups of variates (classes), first multiply each class value (V) by the number of variates in the class or frequency (f) then summate and divide by n. Thus

$$M = \frac{\Sigma\,(f.V)}{n}.$$

In the calculation of this and other constants it is important that the work be indicated in a systematic manner. The form as indicated in Table III is usually preferred. The data are the same as in the frequency table (Table II).

Table III.—To Compute the Mean Total Yield of Plant in Grams

V	f	$f.V$
0.5	3	1.5
1.5	50	75.0
2.5	106	265.0
3.5	109	381.5
4.5	80	360.0
5.5	42	231.0
6.5	7	45.5
7.5	2	15.0
8.5	1	8.5
	$n = 400$	$\Sigma = 1383.0$

$$M = \frac{1383}{400} = 3.458.$$

A valuable short method of computing the mean consists in the use of an *assumed mean* which removes the necessity of multiplying the class values by their frequencies and hence greatly reduces the actual labor in dealing with large numbers. For the same data the short method is shown in Table IV. The rule is as follows: To compute the mean of a series of classes of variates, write the frequency of each class in a column on the right of the class values, then the deviation of each class from an assumed mean, and lastly the product of each deviation by its corresponding frequency. Summate the deviation-by-frequency products, divide by n, and add *algebraically* the correction factor thus obtained to the assumed mean (in this case, 3.5).

$$\text{Correction factor} = w = \frac{-17}{400} = -0.0425$$

$$M = 3.5 + (-\,0.0425) = 3.458.$$

Thus for the computation of the mean by the short method we have the formula

$$M = G + w = G + \frac{\Sigma[f(V-G)]}{n}.$$

The mean is the best measure of type in organisms because it takes into account all the individuals measured. For this reason *the sum of the* *variations from the true mean of all the items in the table equals zero.* Unlike the mode it is affected by every item in the group so that its location can never be due to a single class; moreover it gives weight to extreme deviations. The measure of type used and its value should always be indicated on a graph. For a precise description of the variation within a group it is necessary to have something more than a measure of the type. Knowing the arithmetical average is not sufficient to permit comparison of the variation in different populations. There is needed some measure of variability.

TABLE IV.—TO COMPUTE THE MEAN TOTAL YIELD OF PLANT IN GRAMS. Let G = assumed mean = 3.5

V	f	$V-G$	$f(V-G)$	
0.5	3	−3	− 9	
1.5	50	−2	−100	
2.5	106	−1	−106	−215
3.5	109	0	0	
4.5	80	1	80	
5.5	42	2	84	
6.5	7	3	21	
7.5	2	4	8	
8.5	1	5	5	198
	n = 400			−17

The Standard Deviation, Calculation and Significance.—Examination of the original records of weighings of the total yield of the 400 oat plants would reveal a certain amount of variation in the yield of each plant from the mean yield, 3.458 g. The plants were grouped into classes in computing the mean yield and they can be treated similarly in calculating the average amount of variation from the mean yield for the whole sample. It may be noted that the simplest measure of the absolute variation within the sample is the *average deviation,* which is simply calculated by summating the products of the deviation of each class from the true mean multiplied by its frequency and dividing this sum by n. The standard deviation is universally preferred as an absolute measure of variability. The standard deviation differs from the average deviation in one important feature, viz., that in calculating the standard deviation each individual variation from the mean is squared. This gives additional weight to the extreme variations which is especially desirable in biometrical work.

In calculating the standard deviation (Table V) the regular procedure is as follows: Write the minus and plus deviation (d) of each class from the mean, square each deviation (d^2), multiply each d^2 by the frequency (f), summate the products, divide by n and extract the square root. This is expressed by the formula

$$\sigma = \sqrt{\frac{\Sigma (f.d^2)}{n}}.$$

TABLE V.—TO COMPUTE THE STANDARD DEVIATION IN MEAN TOTAL YIELD OF PLANT IN GRAMS (Complete Process Including Calculation of the Mean)

V	f	$f.V$	d	d^2	$f.d^2$
0.5	3	1.5	−2.958	8.750	26.250
1.5	50	75.0	−1.958	3.834	191.700
2.5	106	265.0	−0.958	0.918	97.308
3.5	109	381.5	0.042	0.002	0.218
4.5	80	360.0	1.042	1.086	86.880
5.5	42	231.0	2.042	4.170	175.140
6.5	7	45.5	3.042	9.254	64.778
7.5	2	15.0	4.042	16.338	32.676
8.5	1	8.5	5.042	25.422	25.422
	$n = 400$	$\Sigma(f.V) = 1383$ $M = 3.458$			$\Sigma(f.d^2) = 700.372$

$$\sigma = \sqrt{\frac{700.372}{400}} = 1.323.$$

TABLE VI.—TO COMPUTE THE STANDARD DEVIATION BY THE SHORT METHOD

Let assumed mean $= G = 3.5$; $V - G = d'$

V	f	d'	$f.d'$	$f.d'^2$	$f(d' + 1)^2$
0.5	3	−3	− 9	27	12
1.5	50	−2	−100	200	50
2.5	106	−1	−106 −215	106	0
3.5	109	0	0	0	109
4.5	80	1	80	80	320
5.5	42	2	84	168	378
6.5	7	3	21	63	112
7.5	2	4	8	32	50
8.5	1	5	5 198	25	36
	$n = 400$		$\frac{-17}{400} = -0.0425$	$\frac{701}{400} = 1.7525$	1067

$$M = G + w \qquad w^2 = 0.0018$$

$$= 3.5 + (-0.0425) \qquad 1.7525 - 0.0018 = 1.7507$$

$$= 3.458 \qquad \sigma = \sqrt{1.7507} = 1.323$$

$$\text{Check: } \Sigma(f) + 2\Sigma(f.d') + \Sigma(f.d'^2) = 1067 = \Sigma[f(d' + 1)^2]$$

The short method for computing the standard deviation is based upon the same principle as the short method for the mean. The rule, therefore, is as follows: Select some number approximating the mean (G); write the minus and plus deviation therefrom (d'); multiply each deviation by the corresponding frequency ($f.d'$); divide the difference between the minus and plus products by n to obtain correction factor (w); then multiply each $f.d'$ by d' to get $f.d'^2$; summate the last products and divide by n; from the quotient subtract w^2 and then extract the square root. The illustration, Table VI, is based upon the same data as the preceding.

The short method of computing the standard deviation is the more accurate because of the elimination of many decimal places. In addition to the complete short method there is shown in the last column on the right a very useful method of checking the computation. Each $f(d' + 1)^2$ is calculated algebraically. Thus in the first case $f = 3$ and $d' = -3$; substituting we have $3(-3 + 1)^2 = 12$. In the same way $\Sigma(f) + 2\Sigma(f.d') + \Sigma(f.d'^2)$ is computed algebraically. Substituting we have $400 + (-34) + 701 = 1067$.

The standard deviation, being a measure of absolute variation, is exceedingly useful in comparing the variability of one variety with another with respect to the same character, or of the same variety in different years with respect to a given character, or of one character with another in the same or different species. For example, Love and Leighty in their memoir on "Variation and Correlation of Oats" give the means and standard deviations for total yield of plant in grams (as well as for eight other characters) for the same pure strain of Sixty Day oats for three years as follows:

$$1909 - M = 4.032,\ \sigma = 2.249$$
$$1910 - M = 3.458,\ \sigma = 1.323$$
$$1912 - M = 7.962,\ \sigma = 3.353.$$

The differences between these values are due mainly to differences in climatic conditions during the three years, the year 1910 having been especially dry and hot. Similar differences appear in the means and standard deviations for height of plant, number of culms and number of grains produced. This particular observation leads to no new conclusion as it is well known that climatic conditions profoundly influence crop yield, but it illustrates the significance of the standard deviation as a measure of variation. Furthermore it is of interest to note that drouth not only reduces plant growth and yield in this variety but the amount of variation as well.

In 1910 the amount of absolute variation was only one-third that of 1912. However, the amount of *relative* variation was not so much affected by drouth as might at first appear. When comparing standard deviations of different varieties or of the same variety under diverse conditions, it should be remembered that the means of the groups under consideration may be widely different in value. It may even happen that the characters to be compared were measured in different units, as inches and grams. Hence it is desirable to have an expression of *variability in relation to the mean.* Such an expression is the *coefficient of variability* which is the ratio of the mean to the standard deviation expressed in per cent. The formula for the coefficient of variability is

$$C = \frac{100\sigma}{M}.$$

In the case of total yield of plant in grams for Sixty Day oats in 1910 substituting the values which have been calculated we have

$$C = \frac{100 \times 1.323}{3.458} = 38.259.$$

The coefficients for the other two years are: 1909, 55.779 and 1912, 42.113. Thus the amount of relative variation in yield was much greater in 1909 than in 1912 and although the standard deviation for 1910 is only a third as large as that for 1912, yet the amount of relative variation is almost as great. A measure of absolute variation is very useful but a relative measure is essential, especially when comparing different kinds of material such as total yield in grams and number of culms or milk production and butter fat production.

The Theory of Error.—It has been said that the frequency curves of many biological measurements follow the curve made by plotting the points given by the expanded binomial $(a + b)^n$ where $a = b = 1$. The reasons why this should be true are not difficult to see. They depend upon the laws of probability or chance that have been generalized into the theory of error. The chance of an event happening in an infinite number of trials is expressed by a fraction of which the numerator is the number of ways it may occur and the denominator is the total number of ways it may occur or fail to occur, if each is equally likely. Thus in tossing a coin a great number of times, the chances that it falls heads is one-half. Further, the probability that all of a set of independent events will occur on a single occasion in which all of them are in question is the product of the probabilities of each event. Hence, the probability that two coins tossed together will fall heads is $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$.

Now suppose four coins are tossed at random; what is the probability that any particular number m of them will be heads and the rest tails? The number m may be 0, 1, 2, 3, and 4, and the probabilities are as follows:

0 head and 4 tails = $1(\frac{1}{2})^4$
1 head and 3 tails = $4(\frac{1}{2})^4$
2 heads and 2 tails = $6(\frac{1}{2})^4$
3 heads and 1 tail = $4(\frac{1}{2})^4$
4 heads and 0 tail = $1(\frac{1}{2})^4$.

The coefficients that appear are what they are because precisely those combinations are possible. There is but one combination in which there are no heads, there are four combinations consisting of 1 head and 3 tails, there are six combinations possible of 2 heads and 2 tails, there are four combinations of 3 heads and 1 tail, and again but 1 with no tails. But this is simply the expansion of the binomial $(1 + 1)^4$. The probability that when n coins are tossed exactly m of them will be heads and the rest tails, therefore, is given by the $m + 1$st term of the binomial expansion $(1 + 1)^n$. When n is small a symmetrical frequency polygon is obtained somewhat similar to that given by plotting the yields of individual oat plants. When n is very large more points are obtained

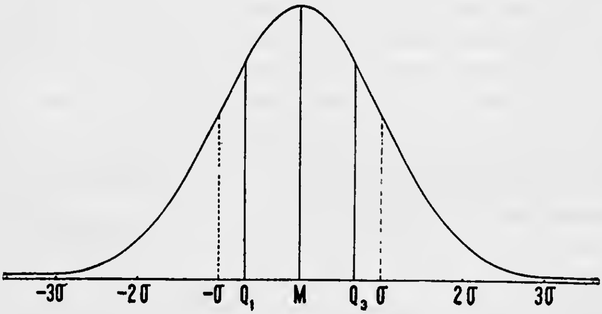


FIG. 19.—A normal curve or curve of error showing the relationship between the quartile, *i.e.*, the probable error of a single variate, and the standard deviation. $Q = .6745\sigma$. In this curve the mode, median and mean are identical. The quartile equals the probable error of a single variate because by definition one-half of the variates lie within its limits; therefore the chances are even that any variate lies within or without it. The proportions of variates within certain areas of the curve are as follows:

within $M \pm Q$, 50 % of the variates,
within $M \pm 2Q$, 82.3 % of the variates,
within $M \pm 3Q$, 95.7 % of the variates,
within $M \pm \sigma$, 68.3 % of the variates,
within $M \pm 2\sigma$, 95.5 % of the variates,
within $M \pm 3\sigma$, 99.7 % of the variates.

and the polygon becomes a regular curve, the normal probability curve or curve of error. It is called the "curve of error" because if a refined set of direct measurements are made and plotted as abscissas, the corresponding ordinates represent the frequencies or probabilities that each will occur. The mean is the most probable value and is assumed to be the true value and the deviations from the mean are errors. Positive errors lie to the right and negative errors lie to the left of the mean. Positive and negative errors are equally likely to occur if they are governed by chance only and as the errors increase in magnitude the frequency with which they occur becomes less and less.

Let us assume that we have a perfectly normal frequency curve such as that represented in Fig. 19, and we shall be able to demonstrate the meaning of some of the constants that we have learned to calculate for it. This curve represents observations on a large number of individuals and its shape represents the general distribution of these individuals. The mean represents the average of the distribution. The standard deviation (plus and minus) represents the ordinates of those points on the curve where the slope changes from convex to concave; it therefore measures the slope of the curve and is a good measure of its variability. Measuring from M to σ on each side of the curve, we find that the space enclosed includes 68.3 per cent. of the total number of individuals; within the limits $\pm 2\sigma$ lie 95.5 per cent. of all individuals and within $\pm 3\sigma$ lie 99.7 per cent. Thus we see that although theoretically the curve never meets the ground line but extends out to infinity, practically all individuals are found within the limits $\pm 3\sigma$.

Similarly we find that the quartile measures the number of individuals within the limits of the curve that it marks off as follows:

$M \pm Q$ includes 50.0 per cent. of the individuals
$M \pm 2Q$ includes 82.3 per cent. of the individuals
$M \pm 3Q$ includes 95.7 per cent. of the individuals
$M \pm 4Q$ includes 99.3 per cent. of the individuals
$M \pm 5Q$ includes 99.9 per cent. of the individuals.

In a normal curve, therefore, the standard deviation and the quartile have a constant relationship such that $Q = 0.6745\sigma$.

From these relationships an idea of the meaning of the term "probable error" which is always calculated for any series of observations may be obtained. The probable error tells us what confidence we may place in our work, if the errors are due to chance only and not to avoidable mistakes of method. The probable error is not the "most probable error." The most probable error is 0 and hence is identical with the mean. Probable error is an arbitrary term used to denote the amount that must be added to or subtracted from the observed value to obtain two limiting figures of which it may be said that there is an even chance that the true value lies within or without these limits.

The probable error, E, of a single variate is the quartile,[1] since the chances are even that any variate lies within or without the value $M + Q$; and since 82.3 per cent. of the variates lie within the value $M + 2Q$, the chances are 4.6 to 1 that the true value of any series of a calculated constant is within these limits. Thus the chances that the true value lies within any multiple of E are

$\pm E$ the chances are even
$\pm 2E$ the chances are 4.6 to 1

[1] The Germans use σ as the measure of error. It is known as the error of mean square and is proportionately larger than the probable error as is shown by the fact that

within $M \pm \sigma$ lie 68.3 per cent. of the variates
within $M \pm 2\sigma$ lie 95.5 per cent. of the variates
within $M \pm 3\sigma$ lie 99.7 per cent. of the variates.

± $3E$ the chances are 21 to 1
± $4E$ the chances are 142 to 1
± $5E$ the chances are 1310 to 1
± $6E$ the chances are 19,200 to 1.

Since biometricians use the standard deviation as the measure of variability, the relation between it and the quartile is utilized in determining all probable errors, even though there is some real error in such a proceeding due to the distribution scarcely ever being exactly normal. The probable error of the mean is found by multiplying the standard deviation by 0.6745 and dividing by the square root of the number of variates, thus $E_m = \frac{\pm 0.6745\sigma}{\sqrt{n}}$. Hence the reliability of the determination of the mean increases not in proportion to the number of variates but in proportion to the increase of their square roots.

The probable errors of the standard deviation and the coefficient of variability are as follows, but it is not necessary here to go into the proof of the determinations.

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

$$E_C = \frac{\pm 0.6745C}{\sqrt{2n}}\left[1 + 2\left(\frac{C}{100}\right)^2\right]^{1/2}$$

$$= \frac{\pm 0.6745C}{\sqrt{2n}}$$

approximately if C is not greater than 10 per cent. because, if the group of variates approximates a normal frequency distribution, the value of C will be less than 10 per cent. and the value of the quantity within the brackets will approximate unity and so can be neglected.

The significance of probable error is most apparent when comparing statistical results; for example, the standard deviations for average total yield of plant in two or more varieties. Concerning the significance of probable errors Rietz and Smith make the following statement:

In the comparison of two statistical results, the difference between the two results compared to its probable error is of great value. *In general, we may take the probable error in a difference to be the square root of the sum of the squares of the probable errors of the two results.* If the difference does not exceed two or three times the probable error thus obtained, the difference may reasonably be attributed to random sampling. If the difference between the two results is as much as five to ten times the probable error, the probability of such differences in random sampling is so small that we are justified in saying that the difference is significant. In fact a difference of ten times its probable error is certainly significant in so far as there is certainty in human affairs.

Multimodal Curves.—Thus far we have considered only homogeneous populations, which, when examined statistically, exhibit a certain degree of approximation to the normal curve of variation. Populations frequently occur, however, both in nature and among domesticated animals and plants, which are found to be heterogeneous for certain characters at least when subjected to statistical analysis. Graphically shown the data for such a character produces a polygon with more than one mode. In general such data indicate either the permanent influence of different causes affecting only certain individuals or of the same cause acting differently upon a portion of the population. Conditions of bimodal curves are more or less familiar to all. Sexual dimorphism and certain differences in development which are contingent upon sex, such as height of comb in fowls, obviously would result in a "notched" graph if the characters were measured and the data plotted. The classic example of dimorphism producing a bimodal curve is found in the length of the pincers of the common earwig (*Forficula auricularia*) as reported by Bateson. Fig. 20 illustrates the two mean types, each sketch being placed directly above its corresponding modal class in the graph. Other conditions commonly causing mixed populations such as would result in bi- or multimodal curves are the following:

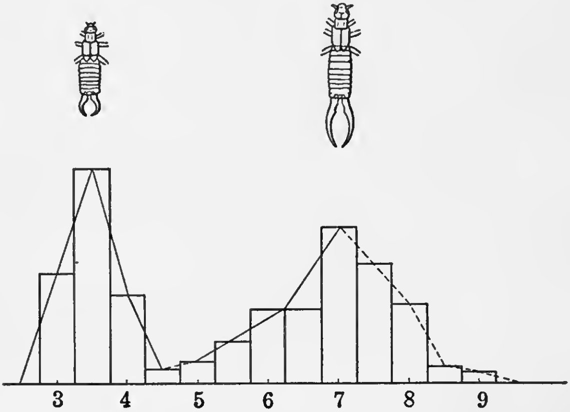


Fig. 20.—Bimodal polygon plotted from data on the earwig. Mean types (× ¾) indicated above corresponding modes. Numbers below the base line indicate length of pincers in mm. (*From Bateson and Johannsen.*)

1. Coexistence of groups of different ages; common in birds at certain times of the year.

2. Overlapping of geographical races of the same species—birds, mammals.

3. Coexistence of different races of the same species, for example, many grasses in the wild state and various cultivated grains contain

several or many different races. Variation in the number and proportion of these races in the population would produce wide differences in statistical data.

4. Germinal diversity among the individuals of a population due to hybrid ancestry.

Analysis of the causes contributing to bi- and multimodal curves is possible by means of experimental breeding. By testing individuals typical of the various groups indicated by the statistical examination and examining their progeny statistically, the elements composing the original population can be differentiated. It should be noted that the close proximity of two different races sometimes causes contamination of material and consequent skewness of the variation polygon but not necessarily a bimodal curve.

Correlation.—All of the biometrical principles considered in the preceding pages pertain to the analysis of variation in a single character. One of the most striking facts of somatogenesis, however, is the physiological interdependence of characters in multicellular organisms. From the earliest stages of embryogeny it is possible to trace associations in the development of various characters. This physiological correlation of characters is one of the most important considerations in the modern study of heredity and it is given due attention in Chapter VI. As regards the statistical study of variation the question to be considered is whether the continuous variations in adult somatic characters are in any cases mutually related or interdependent. It is obvious that, if such a condition be found to exist, it will have an important bearing upon plant and animal breeding inasmuch as selection with reference to a single character would in all likelihood have a definite effect upon certain other characters. The most satisfactory method of investigating this matter is to consider the variation in two characters at a time.

The Correlation Table.—In preparing a correlation table the observed data are transferred directly from the original record by the simple method of tallying. In order to prepare a correlation table either the individuals to be examined must be labelled with permanent numbers or else the observation on the two characters must be made for each individual before passing on to the next. In either case the datum on each character is recorded under the individual number. Next a table is ruled off with a number of horizontal rows corresponding to the total number of class values for one of the characters and a number of columns equal to the total number of class values for the other character. It is understood that a frequency table for each of the two characters has been previously prepared so that the range of class values is known. In Fig. 21 the material examined consists of the same 400 plants of Sixty Day oats that we have studied with reference to total yield of plant.

The character of yield is now to be considered *in relation to* the number of culms per plant. Hence there will be nine rows and seven columns in the correlation table. The class values are indicated in consecutive order beginning usually at the upper left-hand corner. In the present instance, oat plant No. 1 yielded 0.5 g. and had 2 culms, hence this plant is tallied in the upper left-hand square of the table; plant No. 2 yielded 2.5 g. and had 3 culms, it is tallied in row 3 column 2, and so on throughout the list of 400 plants. Then the tallies in each square are counted, recorded and transferred to a new table drawn on a smaller scale for future use, the original table being filed as a permanent record. In this way the tables shown in Figs. 22 and 23 were prepared.

No. of individual	Yield in gm. V_x	No of culms V_y
1	0.5	2
2	2.5	3
3	6.5	5
4	4.5	4
5	1.5	4
6	2.5	7
7	7.5	5
8	0.5	2
9	8.5	6
10	5.5	4
11	1.5	3
12	1.5	4
13	2.5	3
etc.		etc.

	2	3	4	5	6	7	→ x
0.5	11						
1.5		1	11				
2.5		11				1	
3.5							
4.5			1				
5.5				1			
6.5				1			
7.5				1			
8.5					1		
↓ y							

FIG. 21.—To illustrate transference of data from original record to correlation table. V_x indicates class values for total yield of plant, V_y, number of culms per plant.

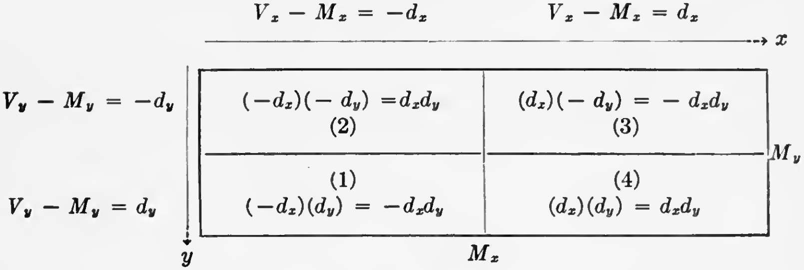
Interpretation of the Correlation Table.—A correlation table is a record of the frequency distributions for two different characters so arranged as to show the tendency, if any exists, for one character to

	2	3	4	5	6	7	
0–1	3						3
1–2	28	19	3				50
2–3	18	66	20	1		1	106
3–4	1	42	58	7	1		109
4–5		7	59	11	3		80
5–6			26	14	2		42
6–7				4	3		7
7–8			1	1			2
8–9					1		1
	50	134	167	38	10	1	400

FIG. 22.—Correlation table for 400 plants of Sixty Day oats. Total yield of plant in grams, subject. Number of culms per plant, relative. 1910. Coefficient of correlation = 0.712 ± 0.017. (*From Love and Leighty*, 1914.)

	2	3	4	5	6	7	
45–50		1	1				2
50–55	2	3	3			1	9
55–60	4	9	4	2	2		21
60–65	6	10	13	4	1		34
65–70	8	40	42	6	1		97
70–75	15	41	53	12	2		123
75–80	10	22	43	11	3		89
80–85	4	8	8	3	1		24
85–90							0
90–95	1						1
	50	134	167	38	10	1	400

FIG. 23.—Correlation table for 400 plants of Sixty Day oats. Average height of plant in centimeters, subject. Number of culms per plant, relative. 1910. Coefficient of correlation = 0.042 ± 0.034. (*From Love and Leighty*, 1914.)



	$V_x - M_x = -d_x$	$V_x - M_x = d_x$
$V_y - M_y = -d_y$	$(-d_x)(-d_y) = d_xd_y$ (2)	$(d_x)(-d_y) = -d_xd_y$ (3)
$V_y - M_y = d_y$	(1) $(-d_x)(d_y) = -d_xd_y$	(4) $(d_x)(d_y) = d_xd_y$

FIG. 24.—Interpretation of the correlation table.

change as the other character changes. The general features of such a table are shown in Fig. 24. The intersection of the two means M_x and M_y, divides the table into quadrants, which are numbered 1, 2, 3, and 4. The signs of the deviations from the mean of x and y are opposite in the 1st and 3d, while they are the same in the 2d and 4th quadrants. Now the deviation from M of every individual in the table is $V_x - M_x$ in terms of x and $V_y - M_y$ in terms of y. As these deviations are to be considered relatively, their products are taken. The products of unlike signs are negative, 1st and 3d, and of like signs, positive, 2d and 4th. After arranging the x and y individuals in arrays, if the larger number fall in the 1st and 3d quadrants, we learn that there is negative correlation or a tendency for one character to diminish as the other increases. If the majority fall in the 2d and 4th quadrants, we conclude that there is positive correlation or a tendency for one character to increase as the other increases. If the individuals are uniformly distributed in the four quadrants we find no evidence of interdependence *i.e.*, zero correlation. These typical distributions are illustrated by the three diagrams in Fig. 25. Comparing the two correlation tables (Figs. 22 and 23) with these diagrams it is evident that the correlation between yield of plant and number of culms is definitely positive, while the nature of correlation (whether positive or negative) between average height of plant and number of culms cannot be inferred from mere observation of the table but that it is very low indeed is clear from the widely scattered distribution.

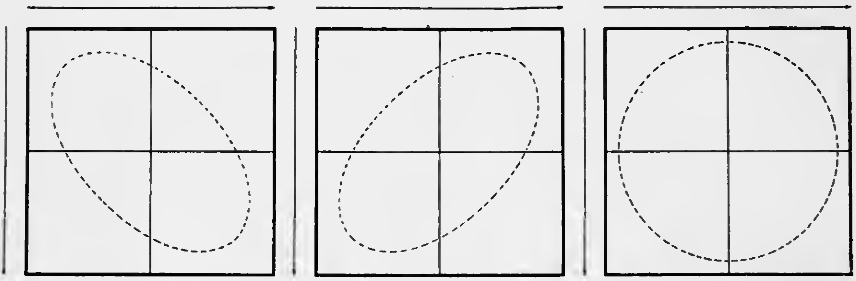


FIG. 25.—Interpretation of the correlation table. Shape of "swarm" indicates nature and amount of correlation.

The Coefficient of Correlation.—The interpretation of a correlation table is based upon the fact that the table shows deviations with respect to *two* characters for each individual or class of individuals. We must remember that the x and y deviations of each class from the mean are *multiplied* in order to understand how the distribution in the table can indicate plus, minus, or zero correlation between the characters. The product of the two deviations for any individual or class is its product-moment, and the summation of all the product-moments divided by n is the average product-moment. This measure of absolute correlation is expressed by the formula

$$\text{Av. prod.-mom.} = \frac{\Sigma(d_x d_y)}{n}.$$

No. of culms per plant ⟶ x

$G_x = 4$

y ⟵ Total yield of plant in grams, $G_y = 3.5$

	2	3	4	5	6	7	f_y	d'_y	$f.d'_y$	$f.d'^2_y$	$\Sigma(d'_x d'_y)$	
0–1	3						3	−3	−9	27	18	−3(−6)
1–2	28	19	3				50	−2	−100	200	150	−2[−56+(−19)]
2–3	18	66	20	1		1	106	−1	−106	106	98	−1[−36+(−66)+1+3]
3–4	1	42	58	7	1		109	0	0	0		
4–5		7	59	11	3		80	1	80	80	10	1(−7+11+6)
5–6			26	14	2		42	2	84	164	36	2(14+4)
6–7				4	3		7	3	21	63	30	3(4+6)
7–8			1	1			2	4	8	32	4	4(1)
8–9					1		1	5	5	25	10	5(2)
f_x	50	134	167	38	10	1	400			697	356	
d'_x	−2	−1	0	1	2	3						
$f.d'_x$	−100	−134	0	38	20	3						
$f.d'^2_x$	200	134	0	38	40	9						

$$w_y = \frac{-17}{400} = -.0425 \qquad w^2_y = .0018$$

$$\frac{697}{400} = 1.7425 \qquad \begin{array}{r} 1.7425 \\ .0018 \\ \hline 1.7407 \end{array} \qquad \sigma_y = 1.323$$

$$\frac{356}{400} = .890 \qquad w_x w_y = .0184 \qquad \begin{array}{r} .890 \\ .0184 \\ \hline .8716 \end{array}$$

$$\frac{-173}{400} = -.4325 = w_x \qquad w^2_x = .1871$$

$$\frac{421}{400} = 1.0525 \qquad \begin{array}{r} 1.0525 \\ .1871 \\ \hline .8654 \end{array} \qquad \sigma_x = .9303$$

$$r_{xy} = \frac{.8716}{(1.323)(.9303)} = .708$$

$$E_r = \pm\frac{.6745(1-r^2)}{\sqrt{n}}$$

$$= \pm\frac{.6745(1-.5013)}{20} = .0168$$

$$r_{xy} = .708 \pm .017.$$

FIG. 26.—Calculation of coefficient of correlation (r) for total yield of plant in grams and number of culms per plant for Sixty Day oats grown at Ithaca, N. Y., in 1910.

But we cannot compare such a number as derived for instance from size of potatoes and starch content with size of beets and sugar content without reducing them to a relative basis. Pearson suggested the product of the two standard deviations as the best index of variability by which to divide the average product-moment so as to reduce it to a relative basis.

His formula is the one now generally used. If the coefficient of correlation equal r,
Then

$$r_{xy} = \left(\frac{\Sigma(d_x d_y)}{n}\right)\left(\frac{1}{\sigma_x \sigma_y}\right).$$

We know the work of computing the standard deviation is lessened by using the short method. Hence this method should be employed in computing the correlation coefficient. On the basis of assumed means from which the deviations are d'_x and d'_y we have

$$r_{xy} = \left(\frac{\Sigma(d'_x d'_y)}{n} - w_x w_y\right)\left(\frac{1}{\sigma_x \sigma_y}\right)$$

from which we read the following rule:

To compute the coefficient of correlation, multiply the x and y deviations from G for each class; summate the products and divide by n; from the quotient subtract the product of the two correction factors; divide this difference by the product of the two standard deviations.

The application of this formula is based upon the correlation table and is illustrated in the case of total yield of plant in grams and number of culms per plant for Sixty Day oats (Fig. 26).

Interpretation of the Coefficient of Correlation.—King gives the following rules for the interpretation of the coefficient of correlation according to its relation to the probable error:

1. If r is less than the probable error, there is no evidence whatever of correlation.

2. If r is more than six times the size of the probable error, the existence of correlation is a practical certainty.

3. In cases where the probable error is relatively small:

(*a*) If r is less than 0.3 the correlation cannot be considered at all marked.

(*b*) If r is above 0.5 there is decided correlation.

Applying these rules to the case of variation in yield as related to number of culms we see that r is over 40 times the probable error and under rule 3, the probable error being relatively small, since $r = 0.7+$, there is very decided correlation. Referring now to relation of number of culms per plant to average height of plant (Fig. 23) we find that $r = 0.042 \pm 0.034$ from which it is clear that there is little if any indication of correlation.

Biometricians consider the correlation coefficient the most powerful tool the agricultural investigator can have since it is a most excellent measure and is applicable to an immense range of variables. Remembering that this constant is an index of the mutual relation that exists between the variations of any two characters, we realize that, if it is high, it indicates they are in some way closely related, and, if it amounts to unity it shows that one is the cause of the other or else both are the result of the same causes. The importance of biological soundness as a requisite to reliability in the correlation coefficient must not be overlooked, *e.g.*, see Harris on physical conformation of cows and milk yield. Pearl reminds us that statistical knowledge of correlation is *precise* only in the same limited sense that similar knowledge of type and deviation from type is precise, viz., as applied to the particular group or groups in the particular instance in time. However, this ability to describe groups in terms of the groups' own attributes is extremely useful in the practical conduct of scientific experiments. Love and Leighty point out that correlations may be classified as *fluctuating* and *stable*, "these divisions being based on the behavior of the relationship of the characters concerned when variation occurs in environmental conditions, such as exist in different years, or in different locations. As the names indicate, the correlations of the first class may be made to vary considerably by changes in conditions, while those of the second class remain of about the same value or are stable in character." The practical value of knowledge of correlation is great, especially when one character is easily seen or readily measured and the other is not. Although it is difficult for the mind to grasp the relation which exists between two groups of data on several hundred or thousand individuals, yet when the relation between those data is expressed in a single number as a correlation coefficient the difficulty disappears.

Regression.—The correlation between parents and offspring when used as a measure of inheritance—Galton thought his measure of somatic resemblance was a measure of inheritance—is usually known as regression. If in an allogamous species parents and offspring be compared with respect to the same character, it is found that *the means of the offspring are nearer the mean of the general population of parents than they are to the mid-value of their own parents.* In other words, extreme parents do not produce progeny as extreme as themselves. Galton believed this regression toward the mean of the general population to be due to "pull" of a mediocre back ancestry. He expressed a mathematical law, good under certain conditions, that is directly opposed to biological facts. It expresses the truth, that, if from a general population of mixed heritage in which there is continual crossing, extremes are selected as parents, there will be regression toward the mean of the general population; and continued selection will be necessary therefore to improve the race. But this regression is not due to the pull of a back ancestry; it is due to the fact that *individuals whose somatic appearance places them in diverse classes in the frequency distribution are themselves gametically different and will breed differently.* Circumstances may come about by which the breeding efficiency is such that the regression will be negative—that is, away from the mean of the general population—as has been proved by Shull, by Emerson and by East in experiments with maize. Furthermore, Johannsen, Jennings and others have shown that when the individuals of a population are alike gametically and their differences are due to external conditions only, these differences are not inherited at all and regression is perfect. This means that if a number of beans are alike gametically, selection of extreme sizes will not shift the mean in either direction.

More recently biometricians have applied the mathematical principle involved in Galtonian regression in order to express in absolute terms the relative interdependence of characters expressed by correlation coefficients. Used in this sense regression is commonly represented by a straight line which approximates the largest possible number of the subject means in a correlation table. The "regression straight line" is extensively used by some authors as a method of representing the relation between the absolute values of characters. For excellent illustrations consult Harris on body pigmentation and egg production in the domestic fowl.

Employment and Value of the Statistical Method.—It may be assumed that biometrical methods are not worth very much if the great biological generalities of the biometricians are misleading. Such an assumption would also be misleading. Statistical methods are a great aid to biologists, but they are only an aid. Trouble has arisen only when biological conclusions have been drawn by mathematicians who ignored certain biological premises. One can only take out of his mathematical mill just what he puts in, but he can take it out in a more comprehendible form. If he has made an accurate biological analysis mathematics are a help; if he has made no biological analysis mathematics are a hindrance. Johannsen sums up the whole situation in the sentence: "We must treat genetic facts with mathematics not as mathematics." If the beginner is careful of his biological premises, if he is certain that the material with which he deals is representative—that he has a *random* sample—if he makes no mathematical deduction unjustified by common sense analysis, he will find that the use of mathematics will remove many a rough place from his road. Biometry will always be an indispensable instrument for the scientific breeder as well as the geneticist. The agronomist and pomologist also have need to resort to statistical methods in order to reach a satisfactory solution of many problems involving variation such as variety testing, seed germination tests, investigation of the value of bud selection, etc. Intelligent employment of the statistical method insures conservative and reliable conclusions regarding many questions which would otherwise remain in the debatable class.

CHAPTER IV

THE PHYSICAL BASIS OF MENDELISM

Recent investigations in heredity have focused attention upon the chromosome mechanism as the physical basis for the segregation and recombination of the units of Mendelian inheritance. The importance of cytological phenomena to students of genetics is admirably summed up by E. B. Wilson in the brief statement that "heredity is a consequence of the genetic continuity of cells by division, and the germ cells form the vehicle of transmission from one generation to another." It is appropriate, therefore, to introduce the subject of Mendelism with a formal and brief treatment of the chromosome mechanism and its mode of operation, on the one hand, in the building up of the body from the single cell with which the individual begins its existence, and, on the other hand, in the production of germ cells when the individual reaches the reproductive period of its life cycle. It is the purpose of this chapter merely to deal with the fundamental facts of cytology which are necessary to an understanding of the connection between cell behavior and Mendelian phenomena. Details unessential to such an understanding, however well established cytologically, will not be dealt with in this treatment to the end that the cardinal points may be presented as simply and as clearly as possible.

The Chromosomes.—With few exceptions the number of chromosomes in the cells of any individual is constant and characteristic of the species to which the individual belongs. Thus it is characteristic of *Drosophila ampelophila* that the cells contain eight chromosomes. In maize the cells contain twenty chromosomes, in wheat sixteen, and in man forty-eight, and so on through the entire plant and animal kingdoms.

Not only is the number of chromosomes in a particular species constant, but the chromosomes themselves possess a definite individuality. Man and tobacco have cells with the same number of chromosomes. It is needless to point out that these chromosomes, however, are qualitatively very different. Similarly within the species the chromosomes are not all alike; on the contrary, especially in certain forms, they exhibit very marked differences in size and shape. This is peculiarly well illustrated in Drosophila as shown in Fig. 27. Here it is possible to recognize in the female two large pairs of curved chromosomes very similar in size and shape. There is also a very small pair of chromosomes, and finally there is a pair of straight ones about two-thirds as long as the large curved chromosomes. In the male the same relations hold except that instead of the pair of straight chromosomes there is a pair consisting of one straight and one somewhat larger hooked chromosome. The significance of this difference in chromosome content in the sexes will be pointed out in a consideration of the inheritance of sex. The pair of straight chromosomes we call the sex or X-chromosomes, the unequal mate of the X-chromosome in the male of this species is called the Y-chromosome. The other chromosomes are called autosomes when it is desired to distinguish them as a class from the sex chromosomes. Drosophila is not unique in possessing chromosomes of such characteristic shapes and sizes; but more and more as cytology advances it is becoming possible to distinguish individual chromosomes, and to recognize them at every cell division.

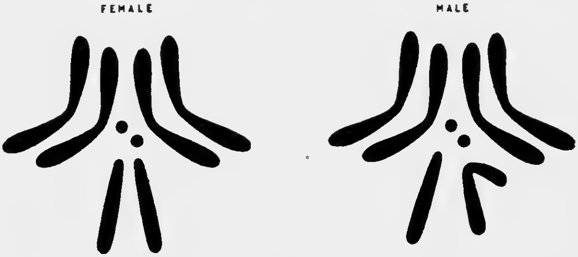


FIG. 27.—Diagram showing the characteristic pairing, size relations, and shapes of the chromosomes of *Drosophila ampelophila*. In the male an X- and a Y-chromosome correspond to the X pair of the female. On the basis of $X = 100$ the length of each long autosome is 159, of each small autosome 12, of the whole Y 112, of the long arm of the Y 71, and of the short arm of the Y 41. (*After Bridges.*)

Moreover, the characteristic paired relations which exist among the chromosomes of Drosophila are of general significance. When mature germ cells are formed in an individual, reduction divisions occur by means of which the chromosome number is reduced in the germ cells to one-half that characteristic of the body cells. Thus the germ cells of Drosophila contain four chromosomes as the result of a reduction which takes place in such a manner that each germ cell contains one member of each pair of chromosomes. As a consequence, the germ cell of Drosophila contains two large curved autosomes, representing the two pairs of these chromosomes, one small autosome, and one X- or one Y-chromosome. The same thing is true for other species of plants and animals—in the reduction divisions the chromosomes are distributed in such a manner that each germ cell receives one member of each pair of chromosomes. It follows from this that in general a definite number of *pairs* of chromosomes is characteristic of the body cells of individuals of a given species, and, taking the chromosomes by pairs, one member of each pair is derived from one parent and the other from the other parent.

From the standpoint of interpretation the chromosomes are aggregates of chromatic material which in itself is definitely and highly organized. Our conceptions of this feature of cell organization are based on appearances of the cytological preparations from certain of the more favorable plants and animals and further interpreted by investigations on heredity. Accordingly the entire chromatin content of the nucleus is regarded as made up of a definite number of individual chromatin elements called chromomeres. The number of chromomeres in a cell of any species must run into the thousands. A certain definite group of these elements make up each chromosome, and at every cell division this chromosome is reformed from the same group of chromomeres. The individuality of the chromosome, therefore, depends on the individuality of the chromatin elements of which it is made up. Not only is each chromosome made up of a definite group of chromomeres, but the chromosome is definitely organized with respect to the position or locus occupied by each chromomere. At certain stages in the history of chromosomes, they are simply lines of chromomeres, very much like single strings of beads with each bead corresponding to a chromomere. Now it appears probable that all the chromomeres in a chromosome are different, as though our string of beads had no duplicates throughout its length. Moreover, each chromomere has a definite place or locus in the particular chromosome in which it belongs and it is always found at that particular locus. The chromomeres of this discussion are identified with the factors of Mendelian heredity, and how closely this conception of the nature of chromatin and its complex organization corresponds to the modern view of Mendelian phenomena will be pointed out as each new phase of Mendelism is taken up.

Somatic Cell Division.—The phenomena of cell division (called mitosis) are represented in outline in Fig. 28, for a species having four chromosomes in its body cell. Bearing in mind the description which has just been given of the organization of the chromatin material we may follow the steps involved in mitosis as they are outlined in this figure. In the "resting" cell at *A* the chromatin is scattered throughout the nucleus in clumps or knots loosely strung together to form an irregular network. As the cell prepares for division the chromatin elements appear in more definite form until at *B* the chromomeres have arranged themselves in a single row in a long, continuous spireme-thread. This spireme-thread may be considered to be made up of the four chromosomes united end to end with the chromomeres arranged in a linear series. As mitosis progresses to the next stage represented at *C*, each chromomere of the spireme-thread divides into two so that a double spireme-thread results from the longitudinal splitting of the original thread. Both parts of the thread are quantitatively and qualitatively equal, for, by the splitting of all the chromomeres both of the threads come to possess all of the individual elements of the original spireme thread. Following the splitting of the chromomeres and the formation of a double spireme, the spireme-thread contracts and segments transversely forming four double chromosomes, the number characteristic of the cells of this individual. This is the stage shown at *C* where also is shown the origin of the spindle, a part of the mechanism in mitosis. The chromosomes now still further contract until they assume their characteristic shapes and sizes. They next appear in an equatorial position on the spindle as shown at *D*, where the two pairs of double chromosomes, one larger and one smaller, are diagrammed and the nucleolus, the large black body of the previous steps, is shown cast out and degenerating. The daughter chromosomes of each pair now separate from each other until at *E* they have moved nearly to the opposite poles of the spindle and are beginning to fray out and seemingly to lose their identity. At this stage actual division of the cell body has begun. Finally at *F*, the chromosomes have completely lost all appearance of their identity, the chromatin material is distributed throughout the nucleus as in the original cell shown at *A*, and the nucleolus has been reformed in each nucleus. Division of the cell-body has resulted in two daughter cells each of which, so far as chromomeres are concerned, contains exactly the same chromatin elements as the original cell.

There are many variations in this process particularly in the order of occurrence of the steps, but these variations in nowise modify the essential fact of mitosis which is that the chromatin material of the cell is converted into a thread which splits throughout its entire length into two halves so that the daughter nuclei receive exactly equivalent portions of chromatin material. This precise division of the chromatin is brought about by a division of each chromomere so that not only do the daughter nuclei receive equivalent portions of chromatin but these portions are also equivalent qualitatively to the entire chromatin content of the mother cell. By this method then each of the cells of the body finally comes to possess not only the whole number of chromosomes contributed by the two parents, but also the entire set of chromatin elements which it received from them. The extreme care with which the cell mechanism partitions the chromatin material in each successive cell division is in itself eloquent testimony of the fundamental importance of this material.

The Production of Germ Cells.—In the production of germ cells a different set of phenomena occur which result in a reduction of this number of chromosomes to one-half that characteristic of the somatic cells.

Preceding the actual reduction division the chromatin material passes through a complex series of steps which may be included under the term synapsis. (This term is sometimes applied in a specific sense to the pairing of homologous chromosomes and sometimes to the contraction of the chromatin threads in the conjugation stage.) The essential steps in the prereduction process are shown in outline in Fig. 29. At *A* is diagrammed a "resting" nucleus at the completion of the multiplication divisions in the germ plasm. As a result of the exact type of mitosis which has been outlined above it contains the full number of chromosomes characteristic of the species. The chromatin of the nucleus next becomes organized into threads of chromomeres which pair as shown at *B*. In this diagram the paired threads are taken to represent homologous chromosomes, and the opposite chromomeres in a pair of threads are considered as the homologous chromomeres of the two chromosomes. The paired threads contract and fuse along their entire length giving the figure diagrammed at *C* in which the two loops represent two pairs of homologous chromosomes in the conjugation stage, the essential step in synapsis. Following this stage the two contracted loops of chromatin split lengthwise and unravel in somewhat the manner shown in *D*. These filaments contract again forming the intertwined pairs of chromosomes shown at *E*, and the nuclear membrane thereupon begins to disappear. Further contraction and the formation of a spindle results in the reduc-

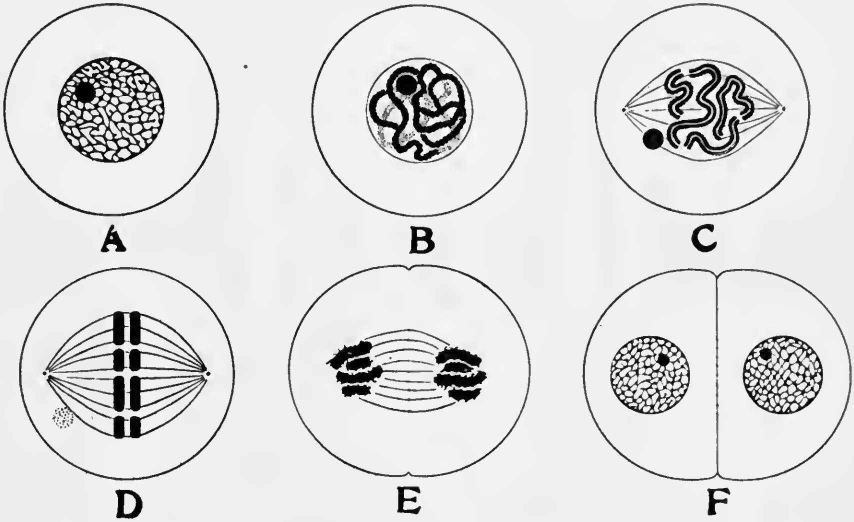


FIG. 28.—Diagram of mitosis in a species having four chromosomes in its cells. *A*, The "resting" cell. *B*, Formation of the spireme-thread. *C*, Longitudinal division of the spireme-thread and transverse segmentation into four chromosomes. *D*, Separation of the daughter chromosomes formed by longitudional splitting of spireme-thread. *E*, Beginnings of nuclear reconstruction and division of the cell body. *F*, Cell division complete and daughter nuclei in the "resting" stage.

tion figure shown at *F*, the significant feature of which is the fact that each of the daughter nuclei resulting from this division receives only two chromosomes instead of the four which the original cell at *A* contained. Since the original cell contained one pair of larger and one pair of smaller chromosomes, the daughter cells which are formed each receive one larger and one smaller chromosome.

Cytological investigation is not yet in agreement as to the interpretation of synapsis especially as to the manner in which the phenomena therein concerned are connected with preceding mitotic divisions. Considering certain cytological investigations and the results of research in heredity together, it appears that the threads which pair in stage *B* represent pairs of chromosomes with homologous chromomeres occupying corresponding positions along their entire length. Likewise the contraction stage at *C* is taken to represent a conjugation of the members of pairs of chromosomes which later again separate. Other cytological evidence indicates that in some forms the conjugation of pairs of homologous chromosomes is brought about in another way. However, the essential fact is the same in either case. In the reduction figure the members of each pair of chromosomes are distributed to the opposite poles of the spindle so that the daughter nuclei received only one member of each pair.

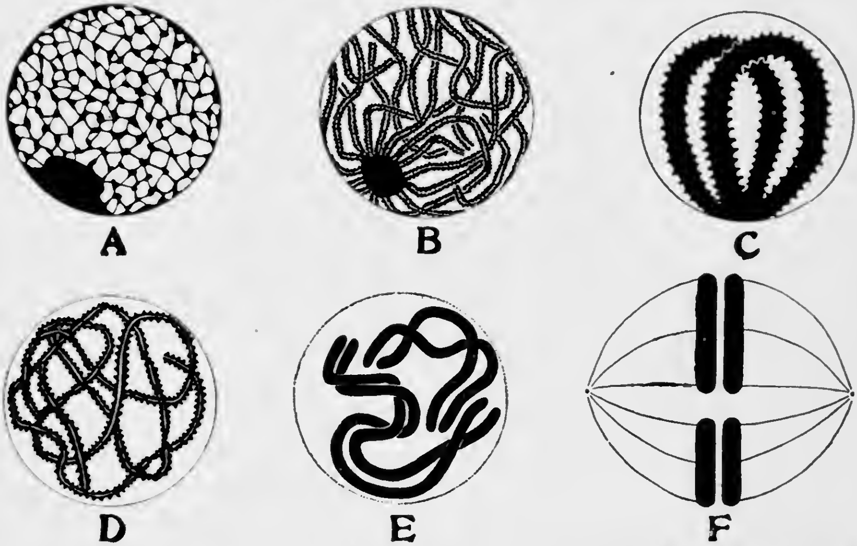


Fig. 29.—The reduction division as represented for a species whose diploid number is four. *A*, "Resting" nucleus of a primary germ cell. *B*, Formaton of paired threads of chromomeres. *C*, Conjugation of homologous chromosomes (synapsis). *D*, Loosening of the synaptic knot. *E*, Condensation of the chromosomes and disappearance of the nuclear membrane. *F*, Homologous chromosomes about to pass to opposite poles, thus giving each secondary germ cell a member of each pair and one-half the somatic number.

The significance of synapsis lies in the conjugation of homologous chromosomes. In the mitoses which have preceded this particular division, the chromosomes were each time conceived to be reformed from the identical group of chromomeres which they contained originally. In synapsis, however, as shown at *B* there is a certain amount of intertwining of the paired threads and in the unraveling of the chromosomes after the contraction stage there is likewise a twisting of the filaments about each other. The indications are, therefore, that in synapsis there is a possibility of interchange of chromatin material between the members of a pair of homologous chromosomes. In all cases, however, in order to uphold our conception of the definite organization of the chromosomes with respect to the chromomeres which they contain, this interchange of material must involve exactly equivalent portions of the two chromosomes. The chromosomes of the reduction division shown at *F* may not, therefore, be identical with the four originally present in *A*, but may represent various combinations of portions of both members of a particular pair of chromosomes. The results of such interchange between members of homologous pairs of chromosomes is shown in Fig. 30. At the left is shown a pair of chromosomes one in outline the other in full black. In the middle the steps in chromatin interchange are diagrammed and finally at the right this interchange results in a pair of chromosomes each of which is made up of parts of both members of the original pair of chromosomes. Various combinations may result depending on the points at which interchange takes place, but in every case the exchange involves corresponding portions of the two chromosomes.

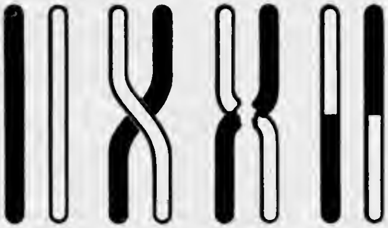


Fig. 30.—Diagram of chromatin interchange between homologous members of a pair of chromosomes. (*After Muller.*)

Independent Distribution of Chromosomes.—In Fig. 31 are illustrated diagrammatically the chromosomes of Drosophila, with particular reference to their size and form relations and to their characteristic pairing in the cell. One member of each of these pairs of chromosomes was contributed by the female parent and one member by the male parent. In the reduction divisions these chromosomes are separated so that each germ cell contains one member of each pair of chromosomes. The simplest condition which could obtain is that of independent distribution in each pair of chromosomes such that the particular member of one pair which went to a given pole of the reduction spindle would have no influence on the distribution of the members of any other pair. Such independent distribution of chromosomes appears to be actually the type followed in reduction. As a consequence the germ cells contain various combinations of chromosomes with respect to their original parental derivation. In Fig. 31 the types of combinations of maternal and paternal chromosomes and their mode of derivation in Drosophila are shown diagrammatically. Two germ cells, one from the female with the chromosomes in outline, and the other from the male with the chromosomes in full black, unite to form the female zygote shown in the middle of the figure. The combinations of maternal and paternal chromosomes which

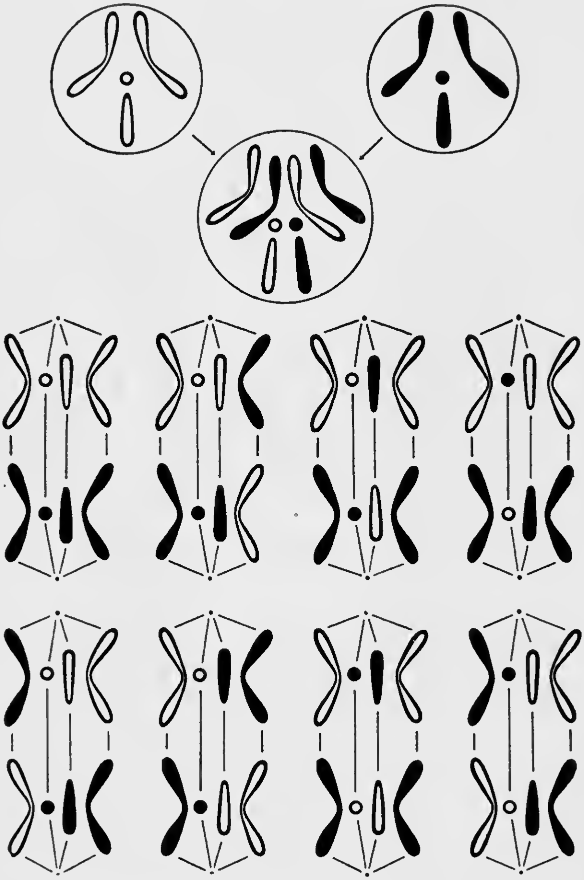


FIG. 31.—Diagram showing consequences of independent segregation of chromosomes in *Drosophila ampelophila.*

result in the production of germ cells in such an individual are shown diagrammatically in the lower portion of the figure. There are eight different ways in which the chromosomes may be grouped in the reduction figures and on the basis of chance any one of these types is as likely to occur as any other. As a result there are sixteen possible combinations of chromosomes in the germ cells with respect to the original derivation of the chromosomes, whether from the female or from the male parent. This of course represents only the total number of possible combinations of entire chromosomes. By exchange of chromatin material between homologous chromosomes resulting in the formation of combination-chromosomes the number of actual combinations is greatly increased.

The number of chromosome combinations resulting from independent distribution is that number possible when each pair of chromosomes is considered separately, and every combination has an equal chance of occurrence. With a form having but two pairs of chromosomes there would be only four possible combinations, three pairs would give eight, four pairs sixteen, and in general the number of possible combinations is given by the expression 2^n in which n is the number of pairs of chromosomes in the individual in question. In tobacco which has 24 pairs of chromosomes the number of possible combinations in the germ cells reaches the enormous total of 16,777,216. This means that in the formation of zygotes in a self-fertilized tobacco plant the actual parental combinations, *i.e.*, combinations identical with those of the germ cells which united to form the individual in question, occur only twice in over sixteen million times, and this proportion is still further lessened when the interchange of chromatin material between homologous chromosomes is taken into account. The condition of independent distribution although simple in itself results in a rapid increase in complexity with the increase in the number of pairs of chromosomes involved.

Chromosomes and Sex in Drosophila.—The relation between inheritance and the chromosome mechanism is perhaps most simply displayed in the inheritance of sex in those animal forms in which the sexes occur in approximately equal proportions. Thus in Drosophila as indicated in Fig. 32 there are three pairs of autosomes which are alike in both the male and the female. The remaining pair of chromosomes, however, differ, for the female possesses two X-chromosomes whereas in the male a single X-chromosome is paired with a Y-chromosome and these differences are characteristic of all normal males and females of this species. The bearing of these differences on the inheritance of sex is shown diagrammatically in Fig. 32. Beginning with the parents, the diploid number is shown in the circles representing the female and the male.

In the female the three pairs of autosomes are outlined and the X-chromosomes only are drawn in black to indicate that they are the ones primarily concerned in the determination of sex. Similarly in the male the three pairs of autosomes which are exactly like those in the female are outlined but the X-chromosome and the Y-chromosome are drawn in black. The reduction division in the female results in a separation of the members of each pair of chromosomes, so that every secondary germ cell (or egg) contains two large curved autosomes, a small autosome, and an X-chromosome. Consequently as far as chromosome content goes the eggs are all exactly alike. In the male, however, the separation of

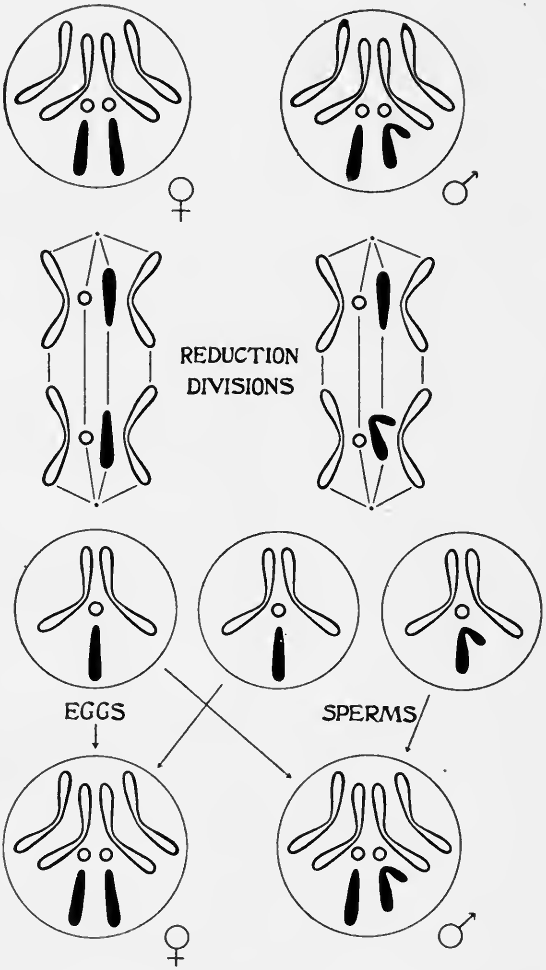


Fig. 32.—Diagram to show chromosome relations in the inheritance of sex in *Drosophila ampelophila*.

the members of the chromosome pairs results in sperms half of which contain an *X*-chromosome and half a *Y*-chromosome in addition to the three autosomes. The reduction division in the male insures an equality in numbers for the two kinds of sperm cells and the chances that either kind of sperm will fertilize an egg-cell are equal. By this arrangement the numerical equality of the sexes is maintained. When, later, the egg cells of the female are fertilized by the sperm cells of the male, as shown in the lower portion of the figure, half of them being fertilized by sperm cells which contain an *X*-chromosome will give females, and half uniting with sperm cells which contain *Y*-chromosomes will produce males. The inheritance of sex in Drosophila provides a beautiful illustration of the parallel behavior of the chromosome mechanism and a somatic difference, in this case sex.

To recapitulate, the essential phenomena of cell behavior which furnish the mechanism for the distribution of hereditary factors are these.

1. Every species is characterized by a definite number of chromosomes, each of which is made up of a definitely organized group of chromomeres. The chromosomes occur in pairs, in each of which one member is derived from each parent. In ordinary somatic mitosis the distribution of chromatin is such that each daughter cell receives a full complement of chromosomes which are equivalent qualitatively to those of the mother cell.

2. In germ cell formation the homologous chromosomes conjugate during synapsis, then separate, and pass into a division figure in which entire homologous chromosomes are opposed to each other. The resulting reduction division gives daughter cells with half the number of chromosomes characteristic of the species, the half number being made up of one member of each pair of chromosomes. During synapsis there is an opportunity for the members of a pair of chromosomes to exchange chromatin material. When such interchange takes place equivalent portions of chromosomes both qualitatively and quantitatively are involved. In the reduction division segregation within one pair of chromosomes is entirely independent of that of any other pair so that the combinations of parental chromosomes in the germ cells represent all those to be expected on the basis of chance distribution.

The student should constantly endeavor to harmonize this conception of the distributing mechanism of the chromatin material with the Mendelian interpretations of hereditary phenomena which will be presented in what follows, to the end that he may obtain a clear and definite idea of the interrelations between the known facts of heredity and cell behavior.

CHAPTER V

INDEPENDENT MENDELIAN INHERITANCE

Essentially Mendelism is an attempt to explain the result of heredity on a rigid, statistical basis. Morgan has stated that the cardinal feature of Mendelism is the fact that when the hybrid forms germ cells the factors segregate from each other without having been contaminated one by the other. The presence or absence of any contamination of factors is still a debatable subject as will be apparent from later discussions, but for all practical purposes the absence of such contamination may be regarded as an established fact. The other implications of this statement that the two germ-cells which unite to produce the individual each contribute an homologous set of hereditary units or factors which determine the characters of the individual and that these units again separate from each other in germ-cell formation are the fundamental conceptions of Mendelism. When the units are considered pair by pair one member of each of which has been derived from each parent, it is clear that the important feature of Mendel's discovery lies in the segregation of the members of each pair in germ-cell formation.

The statistical laws of segregation of characters were first announced by Johann Gregor Mendel, Augustinian monk and later Prälat of the Königskloster at Brünn, Austria. In 1865 after 8 years of thorough and painstaking research which is even today a model of genetic investigation, he read the results of his investigations before a meeting of a local scientific society, the Natural History Society of Brünn, and the following year the paper was published in the transactions of this society. Unfortunately, however, the announcement of the work was made at a time when the scientific world was not in a position to appreciate its full significance and was busy with other things. The results, therefore, were neglected until in 1900, the independent investigations by the three botanists, Correns, von Tschermak, and de Vries, led to similar conclusions and to the rediscovery of Mendel's paper. By that time experimental research had so far advanced that the importance of Mendel's work was immediately recognized and it was not long before a vast series of investigations had been reported in confirmation of it.

The Monohybrid.—The operation of Mendelism is best followed by considering an actual experiment. Mendel crossed tall and dwarf peas and obtained hybrid plants, all of which were tall like the tall parent.

When the progeny of these tall hybrid plants were grown three-fourths of the plants were tall, like the original tall variety, and one-fourth were dwarf, like the original dwarf variety. Although like the tall plant in appearance, therefore, the tall hybrid plants which were produced by crossing a tall and a dwarf plant displayed their hybrid nature in the kind of progeny they produced. To distinguish them from the tall parents which produced only tall plants, they are accordingly called tall hybrids. Continuing this experiment, Mendel found that the dwarf segregants of the second generation bred true, they produced only dwarf plants; but of the tall plants one-third only bred true, and the other two-thirds proved to be tall hybrids, for three-fourths of their progeny were tall plants and one-fourth dwarfs. The progeny of the original tall hybrid plants, therefore, when subjected to this analysis was found to consist of 1 tall : 2 tall hybrid : 1 dwarf. The experimental results of the hybridization of tall and dwarf peas may accordingly be diagrammed as in Fig. 33.

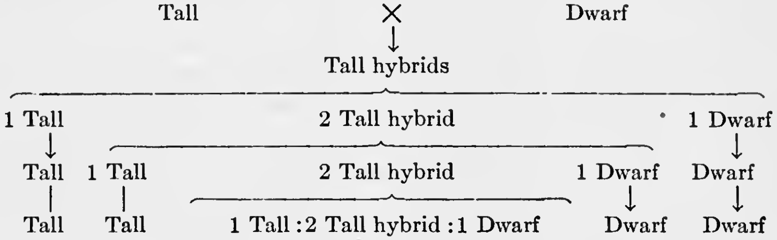


FIG. 33.—Results of hybridization of tall and dwarf peas.

Mendel studied hybrids involving several different pairs of contrasted characters and found that in every case one member of each pair of characters was expressed unchanged in the hybrids, whereas the other member of the pair became latent and its presence could be detected only by growing the progeny of the hybrid. Those characters which were expressed unchanged in the hybrid Mendel termed dominant, the latent characters he called recessive. In the above experiment, for example, tallness was dominant and dwarfness, recessive. Mendel saw that the dominant character, therefore, in these experiments possessed a double significance, that of parental character in which case a uniform progeny of dominants is produced and that of a hybrid character in which case one-fourth of the offspring display the contrasted recessive character. In the above experiment the parental dominants are the tall parents and the hybrid dominants are the tall hybrids. The condition of dominance for a character, therefore, is determined by the fact that in the hybrid that character is expressed to the exclusion of its contrasted character. Dominance is by no means a universal phenomenon, but in Mendel's experiments it so happened that one member of each of the seven pairs of characters displayed complete dominance.

The explanation for the appearance of the recessive character in the second generation and in subsequent generations rests on the fact that the contrasted characters are represented in the germ cells by units or factors. The factor for tallness may be represented by *T* and the factor for the contrasted character dwarfness by *t*. The relations which exist when plants bearing these different factors are crossed are shown in Fig. 34. In the tall race of plants the gametes all bear the factor *T*, so that since any individual of this race arises from the union of two germ cells its genetic constitution with respect to this particular factor is *TT*. Similarly the genetic constitution of any plant of the dwarf race is represented by *tt* and it produces germ cells each of which bears the factor *t*. When tall and dwarf plants are crossed, the hybrid receives a factor *T* from one germ cell and a factor *t* from the other, so that the tall hybrids which are produced are of the genetic constitution *Tt*.

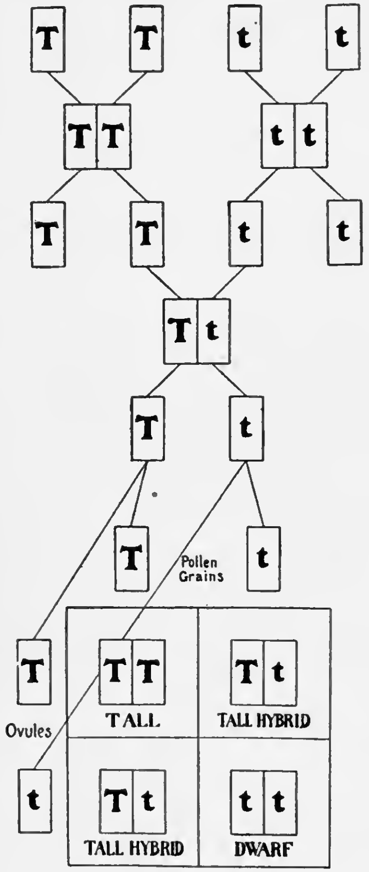


Fig. 34.—Diagram showing factor history in a cross between tall and dwarf peas.

In the production of germ cells and in the union of these germ cells to produce the individuals of the second generation is seen the operation of Mendelian principles. The contrasted units *T* and *t* separate in the germ cells of the offspring so that a particular germ cell receives only one of these factors, either *T* or *t*. Half the germ cells consequently bear the factor *T* and half bear the factor *t*, and this is true of both pollen grains and ovules.

When a tall hybrid plant is self-fertilized, therefore:

a *T* ovule may be fertilized by a *T* pollen grain producing a *TT* plant, tall,
a *T* ovule may be fertilized by a *t* pollen grain producing a *Tt* plant, tall hybrid,
a *t* ovule may be fertilized by a *T* pollen grain producing a *Tt* plant, tall hybrid,
a *t* ovule may be fertilized by a *t* pollen grain producing a *tt* plant, dwarf.

Since there is an equal chance for the occurrence of any one of these types of combinations the progeny of a tall hybrid plant are in the ratio 3 tall : 1 dwarf. One-third of the tall plants are of the genetic constitution *TT* and they consequently will produce only tall plants, whereas the other two-thirds are of the genetic constitution *Tt* and will display segregation in the ratio 3 tall : 1 dwarf. The dwarfs are all of the genetic constitution *tt*, consequently they can produce only dwarf plants. The explanation, therefore, satisfies all the requirements laid down by the experimental results.

Mendelian Terminology.—As a result of the rapid development of Mendelism during the past few years, a special terminology has grown up which is used by practically all investigators in heredity. For those terms which are in most common use, the following brief statements are intended as interpretations of meanings and significance rather than as mere definitions.

The germinal representatives of Mendelian characters are variously termed genes, factors, or determiners, three terms which are used synonymously in Mendelian literature. A Mendelian factor may be defined as an independently inheritable element of the genotype by the presence of which the development of some particular character in the organism is made possible. The word gene was introduced by Johannsen to designate an internal condition or element of the hereditary material upon which some morphological or physiological condition of the organism is dependent. These definitions do not hold rigidly as is always the case with attempts to define something about which very little is known. Of the terms, the term gene as introduced by Johannsen expressly denies any assumptions as to the ultimate nature of the unit in question. The word determiner on the other hand since it implies a rigid relation between an hereditary unit and its end product, the character, is falling into disrepute, for very probably many hereditary units are concerned in the production of all characters. The term factor, as applied to the units of Mendelian heredity is perhaps more frequently used than any other and is just as free from undesirable implications as to the nature of these units on the one hand or their relation to the characters of the individual on the other hand. It will consequently be used more frequently in this book.

Unit characters are those characters of the individual which behave as units in heredity. Thus tallness and dwarfness in peas, since they behave as units in heredity are called unit characters. To behave strictly as units in heredity, character contrasts must depend on single factor contrasts, as for example the character contrast of tall *vs.* dwarf in peas depends upon a contrast of the factors *T* and *t*. The term is a survival of the early days of Mendelism when attention was focussed on the character rather than on the factor as is today the case; and we now have numerous examples of characters which behave as units in certain contrasts, but in others behave as compound characters. It is, therefore, questionable whether in a rigid sense there are any such things as unit characters, but the term has been much used in Mendelian literature, and the conception to which it gives rise, namely that particular individuals or races possess a number of unit characters which may be dissociated from them and recombined in various fashions with the unit characters of related individuals or races, is a useful one and is strictly in accordance with experimental results.

Allelomorphs are contrasted factors or characters. More rigidly as applied to characters, an allelomorph is one of a pair of characters which display alternative inheritance, *i.e.*, inheritance in which one or both of the contrasted characters, although obscured, retain their identity and emerge unchanged from the hybrid. With respect to factors allelomorphism is a relation between two factors such that they are separated into sister gametes in germ-cell formation; they never both enter the same gamete. The allelomorphic characters in our sample are characters tallness and dwarfness, and correspondingly the factors T and t are allelomorphs.

The genotype is the constitution of an organism with respect to the factors of which it is made up. Rigidly the genotype is the sum total of genes or factors of an individual, but it is customary to speak of the sum total of analyzed factors which are under immediate consideration as the genotype. The genotype of the tall race of peas in the above experiment was TT, of the dwarf race tt. The factor arrangement of an individual is also called its genetic constitution when a particular set of factors are concerned and this term is also employed to designate a particular set of factors carried by a gamete. Genotypes of the constitution TT or tt, or in general those which receive the same factors from both gametes are homozygous, whereas those which receive different factors from the two germ cells or gametes are heterozygous, as for example plants of the genetic constitution Tt. Similarly an individual contains a duplex dose of a given factor when it receives that factor from both parents, or a simplex dose if the factor comes in in only one of the germ cells. The substantives corresponding to the adjectives homozygous and heterozygous are homozygote and heterozygote, respectively.

The phenotype is the aggregate of the externally obvious characters of an individual or a group of individuals. Thus in the second generation of the above experiment there were two phenotypes, tall and dwarf, and all the second generation plants belonged to one or the other of these classes. Moreover all members of a phenotype do not necessarily possess the same genetic constitution. In the above example the tall phenotype included tall plants of the genetic constitution TT and tall hybrids of the genetic constitution Tt. The distinction between the genotypes of a given phenotype is only possible by further breeding tests. In general a hybrid is best detected by crossing it to the recessive form in which case it will produce half dominants and half recessives, whereas the pure dominant will produce only dominants. Such a cross is known as a back cross or sesqui-hybrid.

With respect to history an extracted dominant or recessive is one which has been derived from a hybrid form. The historical fact with regard to an extracted form that the parent or other known ancestor did not breed true for the character in question is the only distinguishing feature about it, the factors which it contains are the same as those in the parent races.

The parents of a hybrid are generally called the P_1 generation. The progeny obtained by crossing two distinct races is the first filial generation, conveniently designated the F_1. The progeny of the F_1 are the F_2 generation and so on.

The above terms are constantly employed in even the most simple cases and their application will soon become clear to the student. Other terms are used in connection with more complex cases, but these will be introduced only when their significance may be made clear from the manner in which they are employed.

The Chromosome Interpretation.—The chromosome interpretation of a case of monohybridism is very simple. It depends on the assumption for the case of tall *vs.* dwarf peas that the factor T is a chromomere occupying a definite position in each member of a certain pair of chromosomes of the tall race. The factor t is correspondingly located in exactly the same pair of chromosomes in the dwarf race. Aside from this difference in one pair of chromomeres which occupy identical positions in corresponding pairs of chromosomes the chromosomes of the two races bear exactly the same set of factors. Accordingly, of the seven pairs of chromosomes in the cells of the garden pea, only that pair need be considered which bears the factor T, or in the dwarf races its allelomorph, the factor t. In the hybrid produced by crossing a tall and a dwarf pea one member of the pair of chromosomes bears the factor T, and the other the factor t. In the reduction divisions the members of this pair of chromosomes are separated and distributed to different germ cells, consequently half the number of germ cells will receive that member which bears the factor T, and half that member which bears the factor t. Recombination of these gametes gives the offspring in the ratio 3 tall : 1 dwarf, which has been pointed out previously. If in Fig. 34 the rectangles containing the factors T and t are taken to represent the members of this pair of chromosomes instead of entire gametes, this figure may be used to illustrate the history of this pair of chromosomes in hybridization. Since chromosome relations have been determined more definitely in Drosophila, we shall follow out in detail a selected case in this species. We have pointed out previously that aside from the pair of sex-chromosomes, the pairs of chromosomes in both the male and female of Drosophila are alike and bear the same factors. But in the male the Y-chromosome appears to have no effect upon the development of the body characters so that the male depends upon a single X-chromosome for the development of those characters determined by the factors borne in this chromosome. The Y-chromosome may, therefore, be regarded as a neutral mate for the X-chromosome in the male. Since the distribution of this pair of chromosomes is unique as we have pointed out in the discussion of the inheritance of sex in Drosophila, the history of factors carried by the X-chromosomes furnishes a beautiful illustration of the parallelism existing between chromosome behavior and factor distribution. The inheritance of white-eye color in Drosophila is a case in point. Wild races of Drosophila have red eyes, but Morgan discovered a few white-eyed male mutants in an inbred strain of "wild" flies, *i.e.*, flies which were directly descended from wild flies. From this mutation it was found possible to establish a white-eyed race of flies which breed true to this new eye character. When a white-eyed male is mated to a red-eyed female the offspring all have red eyes, because red eye in Drosophila is dominant to white. In F_2 red- and white-eyed flies are produced in the proportion of 3 red : 1 white. All the females in this generation are red-eyed, but of the males half have red and half white eyes. When the reciprocal cross is made, *i.e.*, when a white-eyed female is mated to a red-eyed male the results are different. In the F_1 of such a mating the female flies have red eyes and the males all have white eyes. When the F_1 flies are bred together an F_2 is obtained half the females of which have red eyes and half white eyes, and likewise among the males half have red eyes and half white eyes.

The explanation of this type of inheritance is shown diagrammatically in Figs. 35 and 36. The factor for white eyes is represented by w and it is borne in the X-chromosome. The factor W for red eyes, allelomorphic to w, is carried by the X-chromosome of the red-eyed race of flies at exactly the same locus as that of w in the white-eyed race. Since these two factors occupy the same locus in the X-chromosome obviously they can never be contained in the same chromosome. In Fig. 35, the two X-chromosomes of the red-eyed female both contain the factor W for red eyes. In a convenient shorthand system the genetic constitution for such a fly may be designated $(WX)(WX)$, the parenthesis indicating that the factor W is carried by the X-chromosome. Each egg from such a female will contain an X-chromosome with a factor for red eyes—in our shorthand notation they will all be (WX). On the other hand, the white-eyed male will produce sperm cells half of which have an X-chromosome and half a Y-chromosome. The X-chromosome of the sperm cells carries a factor w for white eyes, but the Y-chromosome does not bear

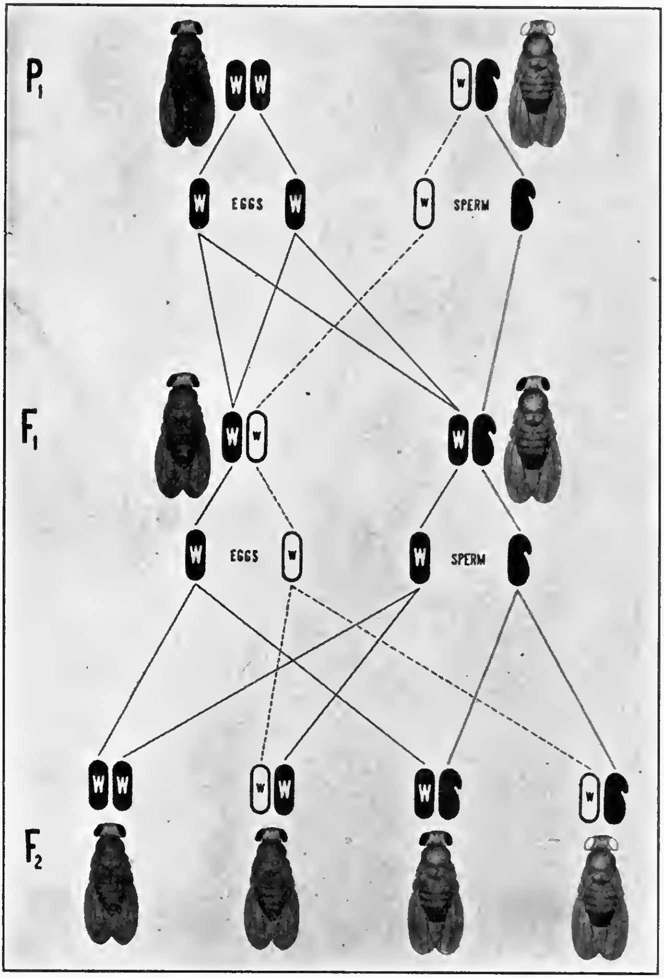


Fig. 35.—Inheritance of white eye color in Drosophila. Red-eyed female mated to white-eyed male. Solid lines indicate history of chromosomes of female; dotted and gray lines, of the male. (*Adapted from Morgan.*)

this factor. In the shorthand notation these two kinds of sperm are represented by (wX) and Y respectively. The Y-chromosome is drawn in black to indicate its unknown constitution with respect to the factors it contains. When an egg-cell (WX) of the red-eyed female is fertilized by a (wX) sperm cell, a female is produced of the genetic constitution

$(WX)(wX)$, and it will be red-eyed because red is dominant over white. When such an egg is fertilized by a Y-bearing sperm a male is produced of the genetic constitution $(WX)Y$ and it is red-eyed because the X-chromosome of the egg-cell carries the factor W. In the F_1 female the reduction divisions separate the X-chromosome bearing the factor for red eyes from the X-chromosome bearing the factor for white eyes. Consequently the F_1 female produces two types of eggs, (WX) and (wX). In the F_1 male the sperm cells similarly produced will be of two kinds (WX) and Y. As shown in the diagram there are four possible combinations of such

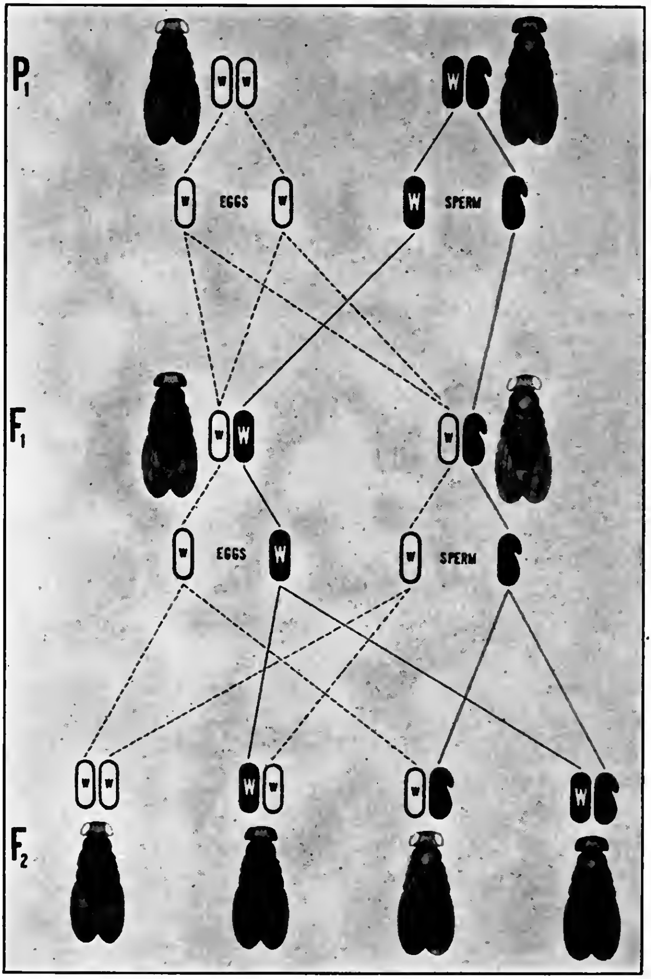


FIG. 36.—Inheritance of white eye color in Drosophila. White-eyed female mated with red-eyed male. Dotted lines indicate history of chromosomes of female; solid and gray lines, of the male. *(Adapted from Morgan.)*

egg and sperm cells in F_2 and these give red-eyed females half of which are homozygous $(WX)(WX)$ and half heterozygous $(WX)(wX)$ and equal numbers of red-eyed and white-eyed males $(WX)Y$ and $(wX)Y$ respectively.

In the reciprocal cross, Fig. 36, the white-eyed female contains two X-chromosomes each bearing a factor for white eyes. Her genetic constitution, therefore, is $(wX)(wX)$. All the eggs from such a female will be of the genetic constitution (wX)—they contain an X-chromosome bearing a white-eye factor. When such eggs are fertilized by an X-bearing sperm cell from the male, the female produced will be of the genetic constitution $(WX)(wX)$. It will be red-eyed because of the red-eyed factor carried by the X-chromosome of the sperm. On the other hand, when such an egg is fertilized by a Y-bearing sperm cell, the male thus produced will be of the genetic constitution $(wX)Y$. It will be white-eyed, because of the white-eye factor in the X-chromosome of the egg-cell. Breeding two such F_1 individuals together will result in the F_2 distribution shown in the diagram. Females will be produced half of which are of the genetic constitution $(WX)(wX)$ and half $(wX)(wX)$, hence red-eyed and white-eyed respectively; and males half of the genetic constitution $(WX)Y$ and half $(wX)Y$, hence red-eyed and white-eyed respectively. The peculiar relations exhibited in the inheritance of white-eye color in Drosophila, therefore, admit of a logical chromosome interpretation, if we assume that the factors involved are borne by the X-chromosomes. The type of inheritance which is apparently dependent on factors borne in the sex-chromosomes is called sex-linked inheritance. It will be treated more fully in Chapter XI.

Mathematical Adequacy of Mendelism.—Mendelian principles do not apply to isolated phenomena of inheritance alone, but they are of general significance. It is consequently of interest to know how well experimental results agree with theoretical expectations when Mendelian analyses are rigidly applied. Particularly is this true of the mathematical relations involved, which have often been used to confute the arguments of Mendelian interpretations. We shall accordingly consider the results of Mendel's original investigation from this standpoint, and a few other cases which have been investigated in particularly large progenies and under circumstances which practically eliminate personal bias.

Mendel's investigations with peas included a consideration of seven pairs of contrasted characters as follows:

1. *The Difference in Form of Ripe Seeds.*—These are either round or roundish, the depressions, if any, occur on the surface, and are at most only shallow as in the indent type; or they are irregularly angular and deeply wrinkled.

2. *The Difference in Color of the Cotyledons.*—The cotyledons of the ripe seeds are either pale yellow, bright yellow, or orange-colored, or they possess a more or less intense green tint.

3. *The Difference in Color of the Seed Coat.*—This is either white, with which character white flowers are constantly correlated; or it is gray, gray-brown, leather brown, with or without violet spotting, in which case the color of the standards is violet, that of the wings purple, and the stem at the base of the leaves is of a reddish tint.

4. *The Difference in 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.

5. *The Difference in Color of the Unripe Pods.*—They are either light to dark green, or vividly yellow, in which coloring the stalks, leaf veins, and calyx participate.

6. *The Difference in Position of the Flowers.*—They are either axillary, 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 cross-section.

7. *The Difference in Length of the Stem.*—The length of the stem is very various in some forms; it is, however, a constant character for each, in so far that healthy plants, grown in the same soil, are only subject to unimportant variations. In the experiments a long axis of 6 to 7 feet was always crossed with a short one of ¾ to 1½ feet.

The results of segregation in F_2 in these seven series of experiments have been summarized from Mendel's paper in Table VII:

TABLE VII.—SUMMARY OF MENDEL'S EXPERIMENTS WITH PEAS

No.	Character contrast	No. in F_2	Dominants	Recessives	Ratio per 4
1	Form of seed..........	7,324	5,474	1,850	2.99 : 1.01
2	Color of cotyledons.....	8,023	6,022	2,001	3.00 : 1.00
3	Color of seed coats.....	929	705	224	3.04 : 0.96
4	Form of pod...........	1,181	882	299	2.99 : 1.01
5	Color of pod...........	580	428	152	2.95 : 1.05
6	Position of flowers......	858	651	207	3.03 : 0.97
7	Length of stem.........	1,064	787	277	2.92 : 1.08
	Totals................	19,959	14,949	5,010	2.996 : 1.004

Mendel observed no transitional forms in these experiments so that the ratios he obtained are based entirely on unprejudiced observations. The ratios in no case differ significantly from the ideal 3:1 ratio. Several investigations have furnished confirmatory evidence as to the correctness of these observations, particularly with respect to that pair of characters concerned with cotyledon color. Johannsen has summarized these results and examined them with reference to their agreement with the conditions imposed by the laws of chance. Table VIII which has been adapted from Johannsen shows that in a sum total of 179,399 counts by seven different investigators the ratio was 3.0035:0.9965. The probable error for this number of observations is ± 0.0028 so that the deviation from the ideal ratio is slightly greater than the probable error, but only so great that such a deviation would be expected approximately twice in five times.

Another case which has been investigated with very large numbers is that of the contrasted characters starchy and sweet endosperm in maize. Those varieties of maize which have starchy endosperms have smooth opaque grains whereas the varieties with sweet endosperms have translucent, wrinkled grains. The difference is due to the fact that in ripening there is a progressive formation of starch in starchy races, but in sweet races the starch grains formed are small and angular and there is an actual breaking down of endosperm materials into various kinds of sugars. Correns has shown that starchiness is completely dominant and segregation is sharp and unquestionable aside from very exceptional cases of intergrading. Fig. 37 illustrates very well how sharply segregation occurs in hybrid ears. The results of East and Hayes' extensive investigations of segregation for this pair of characters are summarized in Table IX. In this table families have been entered separately so that

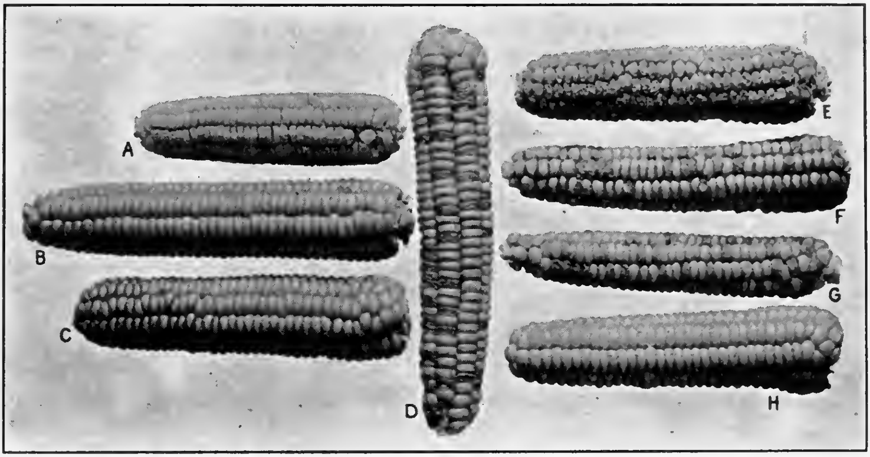


Fig. 37.—Results of crossing starchy and sweet corn: *a*, Sweet parent; *c*, starchy parent; *b*, the F_1 showing complete dominance of starchiness; *d*, the F_2 showing monohybrid segregation; *e*, *f*, *g*, and *h*, F_3 populations, the last three obtained by planting F_2 starchy grains, the sweet ear, *e*, by planting an F_2 sweet grain. (*After East and Hayes.*)

the close correspondence to expectation can be seen all along the line. Moreover, these families represent crosses between many different starchy and sweet races, so that the observations are not based on a single hybrid. The deviation of the total ratio from the 3:1 ratio is very slight and falls far within the probable error set by mathematical conditions.

Table VIII. —Summary of Investigations on Inheritance of Cotyledon Color in Pisum (*After Johannsen*)

Investigator	Yellow	Green	Total	Ratio per 4	Probable errors
Mendel, 1865...	6,022	2,001	8,023	3.0024 : 0.9976	±0.0130
Correns, 1900..	1,394	453	1,847	3.0189 : 0.9811	±0.0272
Tschermak, 1900	3,580	1,190	4,770	3.0021 : 0.9979	±0.0169
Hurst, 1904....	1,310	445	1,755	2.9858 : 1.0142	±0.0279
Bateson, 1905..	11,902	3,903	15,806	3.0123 : 0.9877	±0.0093
Lock, 1905.....	1,438	514	1,952	2.9467 : 1.0533	±0.0264
Darbishire, 1909	109,060	36,186	145,246	3.0035 : 0.9965	±0.0030
Totals.......	134,707	44,692	179,399	3.0035 : 0.9965	±0.0028

Table IX.—Segregation of Starchy vs. Sweet Endosperm in Maize

Family No.	Starchy	Sweet	Total	Ratio
(15 × 54)	1,746	623	2,369	2.948 : 1.052
(15 × 54) – 2	2,293	728	3,021	3.036 : 0.964
(24 × 54)	2,288	801	3,089	2.963 : 1.037
(24 × 54) – 1	771	269	1,040	2.965 : 1.035
(5 × 18)	1,509	492	2,001	3.017 : 0.983
(11 × 18)	873	319	1,192	2.930 : 1.070
(17 × 54) – 1	328	102	430	3.051 : 0.949
(18 × 58) – 1	332	102	434	3.060 : 0.940
(7 × 54)	872	268	1,140	3.060 : 0.940
(8 × 54)	1,505	530	2,035	2.958 : 1.042
(8 × 54) – 1	3,524	1,163	4,687	3.008 : 0.992
(8 × 54) – 5	2,190	725	2,915	3.005 : 0.995
(19 × 7)	783	230	1,013	3.092 : 0.908
(19 × 7) – 5	304	109	413	2.944 : 1.056
(19 × 8)	1,813	602	2,415	3.003 : 0.997
(60 – 5 × 54)	1,150	379	1,529	3.009 : 0.991
(60 – 3 × 54)	799	267	1,066	2.998 : 1.002
(60 – 8 × 54)	451	138	589	3.063 : 0.937
Totals.........	23,531	7,847	31,378	2.9997 : 1.0003
Probable error				±0.0062

These two cases illustrate very well how closely the results of Mendelian investigations fulfill mathematical requirements, and their significance cannot be doubted when it is considered how little difficulty is experienced in classifying this particular kind of material. Nevertheless the mathematical requirements are very often not fulfilled on account of the action of external conditions of various kinds. Here as elsewhere the disturbing influence of biological factors must ever be kept in mind in judging the significance of the application of any strict mathematical tests.

Dihybridism.—When two pairs of factor differences are involved in a hybrid the same laws apply in segregation and recombination as apply in the monohybrid. The two pairs of factors segregate independently of each other and give character combinations in F_2 to be expected on the basis of chance factor distribution. In maize there are varieties which have a deep purple aleurone color which gives the entire grain a black appearance. When such varieties are crossed with certain white varieties which possess no aleurone color the F_1 is purple and in F_2 the grains are in the ratio of 3 purple : 1 white. An ear displaying such F_2 segregation is shown in Fig. 38. The factors involved in this case are W for pigment production in the aleurone layer and w for no pigment production in this tissue. The hybrid Ww since it is a monohybrid will, therefore, give in F_2 genotypes in the ratio 1 WW : 2 Ww : 1 ww, which are distributed in two phenotypes in the ratio 3 purple : 1 white. We have shown similarly how starchy corn when crossed with sweet gives a starchy F_1 and in F_2 3 starchy : 1 sweet. Here the factors involved are S for starchiness and s for sweet. A purple sweet corn, therefore, will have the genetic constitution $WWss$ with respect to the above factors, and a white starchy corn, the genetic constitution $wwSS$.

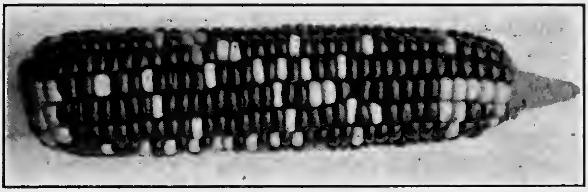


FIG. 38.—Maize ear showing F_2 segregation of grains in the ratio of 3 purple, 1 white.

When a purple sweet corn is crossed with a white starchy corn the F_1 will be purple starchy—it will display the dominant characters of both parents to the exclusion of the recessive characters, white and sweet. From the purple sweet corn the F_1 receives gametes of the genetic constitution Ws and from the white starchy wS. Consequently its genetic constitution is $WwSs$, and it contains two pairs of factor contrasts. Such a hybrid produces gametes representing all possible combinations containing one member of each pair of factors. The gametes, therefore, will be produced in the combinations and proportions

$$1\ WS{:}1\ Ws{:}1\ wS{:}1\ ws.$$

This series of gametes will be represented in both the pollen grains and ovules, so that if each kind of ovule has an equal chance of being fertilized by any one of the four kinds of pollen grains the following combinations will result.

Table X.—Combinations of Factors and Characters Resulting from Self-fertilization of a Purple Starchy Corn of the Composition $WwSs$.

WS ovule and WS pollen grain gives $WWSS$, purple starchy
WS ovule and Ws pollen grain gives $WWSs$, purple starchy
WS ovule and wS pollen grain gives $WwSS$, purple starchy
WS ovule and ws pollen grain gives $WwSs$, purple starchy

Ws ovule and WS pollen grain gives $WWSs$, purple starchy
Ws ovule and Ws pollen grain gives $WWss$, purple sweet
Ws ovule and wS pollen grain gives $WwSs$, purple starchy
Ws ovule and ws pollen grain gives $Wwss$, purple sweet

wS ovule and WS pollen grain gives $WwSS$, purple starchy
wS ovule and Ws pollen grain gives $WwSs$, purple starchy
wS ovule and wS pollen grain gives $wwSS$, white starchy
wS ovule and ws pollen grain gives $wwSs$, white starchy

ws ovule and WS pollen grain gives $WwSs$, purple starchy
ws ovule and Ws pollen grain gives $Wwss$, purple sweet
ws ovule and wS pollen grain gives $wwSs$, white starchy
ws ovule and ws pollen grain gives $wwss$, white sweet

When the F_2 grains are classified according to their phenotype, they are distributed as follows:

9 grains with *purple* aleurone and *starchy* endosperm
3 grains with *purple* aleurone and *sweet* endosperm
3 grains with *white* aleurone and *starchy* endosperm
1 grain with *white* aleurone and *sweet* endosperm

Just as the 3 : 1 ratio is typical for the monohybrid when one of the contrasted characters is dominant, so the 9:3:3:1 ratio is characteristic of dihybrids when one member of each pair of characters is dominant. This ratio is clearly derivable from the simple 3 : 1 ratio, for considering first aleurone color, the segregation is in the ratio 3 purple:1

white. When the endosperm segregation into starchy and sweet is taken into account in the same hybrid the segregation will be in the ratio of 3 starchy:1 sweet in each of these classes, for these characters segregate independently of the aleurone color. This gives, therefore, 3 purple (3 starchy : 1 sweet) : 1 white (3 starchy : 1 sweet) which becomes on expansion 9 purple starchy : 3 purple sweet : 3 white starchy : 1 white sweet.

The correlation of the above facts with chromosome behavior is again very simple. The factors *W* and *w* lie in identical positions in one pair of chromosomes and the factors *S* and *s* lie in identical positions in a different pair of chromosomes. If the difference between the two varieties of maize is only in these factors, then all the other pairs of chromosomes in the varieties bear the same set of factors. Accordingly of the ten pairs of chromosomes of maize only those two need be considered which bear the above factors. The relations then are shown diagrammatically in Fig. 39. The parents in both cases produce gametes which are all alike. The crossing of these parents produces a zygote in which two pairs of the chromosomes differ in their factor content. One member of one pair bears *W* and the other *w* and in the other pair one member bears *S* and the other *s*. Two types of F_1 reduction division are possible and these give four kinds of gametes as shown in the diagram. Since this has occurred in the formation of both ovules and pollen grains, in the self-fertilization of such a plant there are sixteen possible combinations of gametes, which distribute themselves in four phenotypes in the ratio 9 purple starchy:3 purple sweet:3 white starchy:1 white sweet. This feature of the case has already been discussed fully and need not be repeated here.

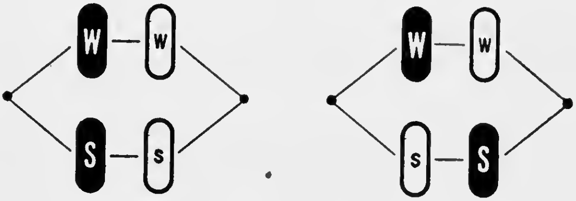


FIG. 39.—Chromosome behavior in reduction in F_1 from a cross between purple sweet and white starchy corn. Factor symbols: *w* = white, *W* = purple, *s* = sweet, *S* = starchy.

The actual agreement of this analysis with experimental results has been shown by several investigators but particularly by East and Hayes. In one case they crossed a white flint corn, Rhode Island White Cap, with a purple sweet corn, Black Mexican. The F_1 grains were purple starchy and in F_2 there was sharp segregation for purple and white aleurone and starchy and sweet endosperm. In some cases splashed

Table XI.—Class Frequencies Among Grains From F_2 and F_3 Ears From the Cross Purple Sweet X White Starchy *(From East and Hayes)*

Generation	Ear No.	Purple starchy	Purple sweet	White starchy	White sweet	Total
F_2	(24 × 54)–1	207 *207*	67 *69*	67 *69*	27 *23*	368
	(24 × 54)–2	170 *164*	54 *55*	49 *55*	19 *18*	292
	(24 × 54)–6	197 *194*	65 *65*	59 *65*	24 *22*	345
	(24 × 54)–8	159 *148*	41 *50*	41 *50*	23 *16*	264
	(24 × 54)–10	166 *152*	40 *51*	46 *51*	19 *17*	271
	(24 × 54)–11	166 *163*	55 *54*	47 *54*	22 *18*	290
	(24 × 54)–13	205 *208*	81 *69*	59 *69*	25 *23*	370
F_3	(24 × 54)–1–2	161 *155*	55 *52*	46 *52*	13 *17*	275
	(24 × 54)–1–6	171 *168*	56 *56*	52 *56*	19 *19*	298
	(24 × 54)–1–8	180 *183*	71 *61*	55 *61*	19 *20*	325
	(24 × 54)–1–9	79 *80*	29 *27*	27 *27*	7 *9*	142
F_2	Totals.......	1,270 *1,237*	403 *413*	368 *413*	159 *137*	2,200
F_3	Totals.......	591 *585*	211 *195*	180 *195*	58 *65*	1,040
Combined Totals ..	....	1,861 *1,822*	614 *608*	548 *608*	217 *202*	3,240

purple grains were obtained, but further breeding tests showed that these were simply heterozygous for purple coloration. A real exception must, however, be made for certain families which showed aleurone color segregation in the ratio 9 purple:7 white. Such results depend on the presence of two color factor differences and they will be explained later. The results in F_2 and F_3 for these plants of the genetic constitution *WwSs* are tabulated in Table XI. The expected results in each case are given in italics.

Throughout the results in this table are substantially in agreement with theoretical requirements. The hypothesis has, however, been subjected to the further test of growing F_3 populations. Table XII shows the kind of F_3 populations which are to be expected when F_2 grains from this cross are planted. All these types of populations were secured. The case, therefore, provides an excellent illustration of the way in which a Mendelian experiment is carried out and of the excellent agreement with theory which is given in such experiments.

TABLE XII.—F_3 RATIOS TO BE EXPECTED FROM THE DIFFERENT GENOTYPES IN THE CROSS *WWss* × *wwSS*

Phenotype	Genotype	Ratio in F_3			
		Purple starchy	Purple sweet	White starchy	White sweet
Purple starchy.....	WWSS	All			
	WWSs	3	1		
	WwSS	3	....	1	
	WwSs	9	3	3	1
Purple sweet......	WWss	....	All		
	Wwss	....	3	....	1
White starchy.....	wwSS	....	....	All	
	wwSs	....	....	3	1
White sweet.......	wwss	....	....	....	All

In the animal kingdom important work has been done in establishing Mendelian principles by the use of small animals, particularly mice, rats, guinea-pigs and rabbits. Such animals are particularly favorable for investigations in heredity because a large number of generations may be reared in a relatively short space of time. Castle has reported an excellent case of dihybridism in the guinea-pig. Rough coat is dominant to smooth and colored coat to the albino condition. When a smooth black is crossed with rough white the hybrids are rough black. In F_2

the segregation is in the ratio 9 rough black : 3 rough white : 3 smooth black : 1 smooth white. These relations are shown diagrammatically in Fig. 40. The factor relations are very simple. The genetic constitution of the smooth black race is *rrCC* and of the rough white race *RRcc*, where *R* is a factor for rough coat and its allelomorph *r* a factor for smooth coat, and *C* and *c* are factors for colored and albino coat respectively. The F_1 *RrCc* is rough black because of the dominance of these two characters over their allelomorphs. When F_1 individuals are bred together the F_2 segregates in accordance with normal dihybrid expectations as shown in the checkerboard in Fig. 41.

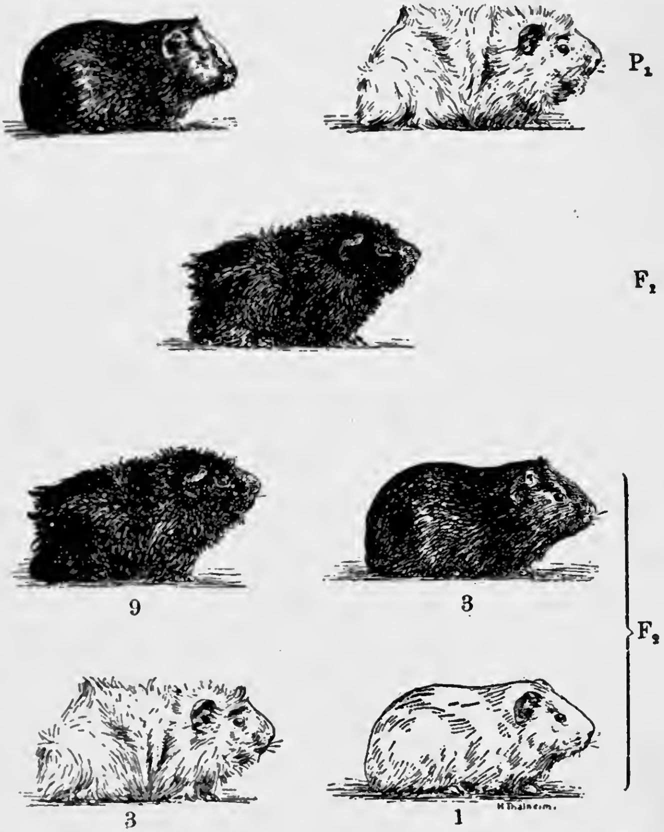


Fig. 40.—Results of crossing smooth black and rough white guinea-pigs. F_1 is rough black. F_2 is in the ratio 9 rough black : 3 rough white : 3 smooth black : 1 smooth white. (*After Baur.*)

This experiment shows how easily new races may be established, for in F_2 two entirely new combinations of characters were obtained, namely, rough black and smooth white. Of the rough black individuals only one in nine were homozygous for both dominant factors as may be determined from the checkerboard analysis. Consequently for this combination of characters it would be necessary to make extensive tests of the individuals in order to determine their genetic constitutions. Mating those which had been determined to be of the genetic constitution *RRCC* together would insure the production of a race of rough black guinea-pigs which would breed true for these characters. On the other hand, all those which are smooth white are of the genetic constitution *rrcc;* they are therefore homozygous and will produce a uniform progeny when bred together.

Dihybridism in Drosophila.—We shall not attempt to follow out the chromosome relations for the guinea-pig hybrid because they are exactly the same as those in maize. In Drosophila, however, the peculiar relations displayed by the sex-chromosomes gives more striking instances of parallelism of chromosome behavior and factor distribution. The inheritance of white-eye color in Drosophila has already been described in detail. Another character, vestigial wings, shows a different type of inheritance. When vestigial-winged flies are crossed with normal long-winged flies the F_1 flies of both sexes are long-winged in the reciprocal crosses, and in F_2 segregation is in the ratio of 3 long : 1 vestigial in both sexes. The factor for vestigial wings, therefore, must be located in one of the pairs of autosomes. We shall call this factor v and its normal allelomorph in the long-winged race V. The formula for a vestigial-winged white-eyed female then becomes $vv\ (wX)(wX)$ and for a long-winged red-eyed male $VV(WX)Y$.

	RC	*Rc*	*rC*	*rc*
RC	*RRCC* rough black	*RRCc* rough black	*RrCC* rough black	*RrCc* rough black
Rc	*RRCc* rough black	*RRcc* rough white	*RrCc* rough black	*Rrcc* rough white
rC	*RrCC* rough black	*RrCc* rough black	*rrCC* smooth black	*rrCc* smooth black
rc	*RrCc* rough black	*Rrcc* rough white	*rrCc* smooth black	*rrcc* smooth white

FIG. 41.—Checkerboard showing F_2 segregation in the cross, smooth black × rough white in guinea-pigs.

The chromosome relations involved in crossing a vestigial white female and a long red male are shown diagrammatically in Fig. 42. Two pairs of chromosomes are involved, the sex-chromosomes and a pair of autosomes. A vestigial white female produces eggs all of which contain an X-chromosome bearing the factor w and an autosome bearing the factor v. Half the sperms, on the other hand, contain an X-chromosome bearing the factor W and an autosome bearing the factor V, and half contain a Y-chromosome and an autosome bearing the factor V. Consequently when the sperm cells which contain X-chromosomes fertilize the eggs, F_1 females of the genetic constitution $Vv(WX)(wX)$ will be produced. Phenotypically they will be long red. When the sperm cells which contain Y-chromosomes fertilize the same kind of eggs the F_1 males which result will be of the genetic constitution $Vv(wX)Y$. Phenotypically they will be long white. The reduction divisions in the F_1 female will result in the production of four kinds of eggs as shown diagrammatically in the figure. They will be of the genetic constitutions:

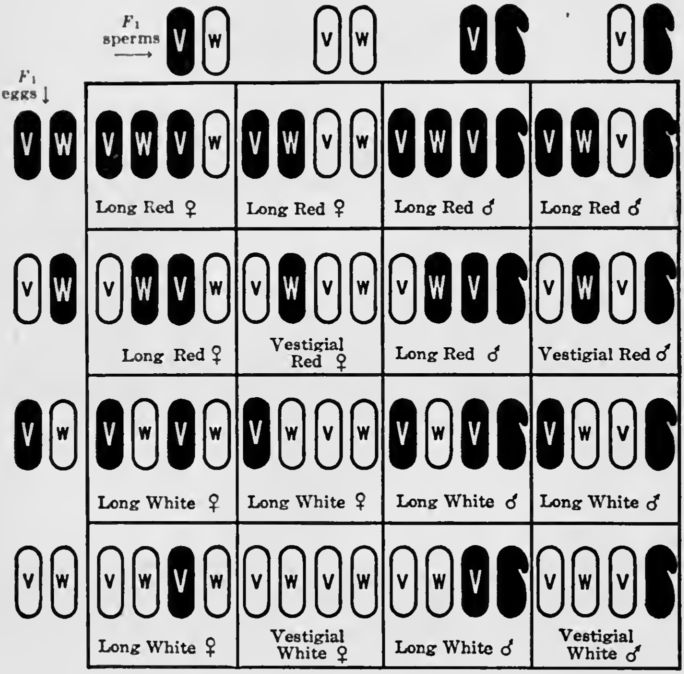


FIG. 42.—F_1 gametes and F_2 zygotes from the cross, vestigial white female × long red male. Factor symbols: v = vestigial, V = long, w = white, W = red.

$$V(WX) \qquad v(WX) \qquad V(wX) \qquad v(wX).$$

Similarly four kinds of sperm cells will be produced by the F_1 male and they will be of the genetic constitutions:

$$V(wX) \qquad v(wX) \qquad VY \qquad vY.$$

The F_2 population produced by mating two F_1 individuals will be made up of F_1 gametes as shown in the checkerboard analysis in Fig. 43. When like phenotypes are collected the ratio in each sex is 3 long red:3 long white:1 vestigial red:1 vestigial white. This is very different from the typical 9:3:3:1 ratio of a dihybrid, but it is strictly in agreement with experimental observations and chromosome behavior.

The reciprocal cross gives different results and for that reason we shall go through it briefly to show that this difference is a necessary consequence of the chromosome behavior. When a long red female, genetic formula $VV(WX)(WX)$, is mated to a vestigial white male, $vv(wX)Y$, the F_1 individuals are long red females, $Vv(WX)(wX)$, and long red males, $Vv(WX)Y$. The F_1 females then give the same four types of eggs as those of the reciprocal cross, viz.,

	$V(wX)$	$v(wX)$	VY	vY
$V(WX)$	$VV(WX)(wX)$ long red ♀	$Vv(WX)(wX)$ long red ♀	$VV(WX)Y$ long red ♂	$Vv(WX)Y$ long red ♂
$V(wX)$	$VV(wX)(wX)$ long white ♀	$Vv(wX)(wX)$ long white ♀	$VV(wX)Y$ long white ♂	$Vv(wX)Y$ long white ♂
$v(WX)$	$Vv(WX)(wX)$ long red ♀	$vv(WX)(wX)$ vestigial red ♀	$Vv(WX)Y$ long red ♂	$vv(WX)Y$ vestigial red ♂
$v(wX)$	$Vv(wX)(wX)$ long white ♀	$vv(wX)(wX)$ vestigial white ♀	$Vv(wX)Y$ long white ♂	$vv(wX)Y$ vestigial white ♂

FIG. 43.—Checkerboard analysis of the F_2 obtained by crossing vestigial white ♀ with long red ♂ in Drosophila.

	$V(WX)$	$v(WX)$	VY	vY
$V(WX)$	$VV(WX)(WX)$ long red ♀	$Vv(WX)(WX)$ long red ♀	$VV(WX)Y$ long red ♂	$Vv(WX)Y$ long red ♂
$V(wX)$	$VV(WX)(wX)$ long red ♀	$Vv(WX)(wX)$ long red ♀	$VV(wX)Y$ long white ♂.	$Vv(wX)Y$ long white ♂
$v(WX)$	$Vv(WX)(WX)$ long red ♀	$vv(WX)(WX)$ vestigial red ♀	$Vv(WX)Y$ long red ♂	$vv(WX)Y$ vestigial red ♂
$v(wX)$	$Vv(WX)(wX)$ long red ♀	$vv(WX)(wX)$ vestigial red ♀	$Vv(wX)Y$ long white ♂	$vv(WX)Y$ vestigial white ♂

FIG. 44.—Checkerboard analysis of the F_2 obtained by crossing long red ♀ with vestigial white ♂. Reciprocal of cross analyzed in Fig. 43.

$$V(WX) \quad V(wX) \quad v(WX) \quad v(wX).$$

The males, however, produce the following series of sperms:

$$V(WX) \quad v(WX) \quad VY \quad vY.$$

Mating F_1 flies of this cross, therefore, results in the F_2 population shown in the checkerboard in Fig. 44. When these are collected into like phenotypes the ratio obtained is 9 long red:3 long white:3 vestigial red: 1 vestigial white, but this agreement with the typical dihybrid ratio is only apparent. When the females alone are considered the ratio is 6 long red: 2 vestigial red, and the males are in the ratio 3 long red:3 long white: 1 vestigial red:1 vestigial white. The disturbance in the ratio is occasioned by the unique behavior of the white-eye character which behaves exactly as it did in the simple case which was analyzed previously. The reciprocal ratio, therefore, is additional evidence as to the adequacy of the chromosome theory.

The Trihybrid.—The same line of reasoning of course applies to cases in which three pairs of factors are involved. Such for example is a case which Baur has described in the common garden snapdragon, *Antirrhinum majus.* In this particular case the factors involved have the following relations.

Z—a factor which conditions the development of the zygomorphic type of blossom which is characteristic of the species. The factor *z*, its allelomorph, conditions the production of peloric blossoms, *i.e.*, blossoms which display radial symmetry. The normal form is nearly completely dominant.

R—a factor for red color of the blossoms. The allelomorph *r* gives flowers which are flesh colored.

I—a factor for ivory coloration of the blossoms. The allelomorph *i* in this case conditions the production of yellow flowers. *R* with *I* gives flowers red on an ivory background, a magenta type of coloration, whereas *R* with *i* gives flowers which are red on a yellowish background. It is possible to distinguish these two classes in a mixed population.

Table XIII.—Distribution of Classes Among the Progeny of an F_1 Hybrid Snapdragon of the Composition *ZzRrIi*

Ratio	Phenotypes	Observed	Expected
27	Zygomorphic, red on ivory	64	52
9	Zygomorphic, red on yellow	14	17
9	Zygomorphic, flesh-colored, on ivory	10	17
3	Zygomorphic, flesh-colored, on yellow	23	17
9	Peloric, red, on ivory	6	6
3	Peloric, red, on yellow	1	6
3	Peloric, flesh-colored, on ivory	4	6
1	Peloric, flesh-colored, on yellow	2	2

The F_1 hydrid *ZzRrIi* was the normal flower form and produced blossoms of a magenta coloration, *i.e.*, red on ivory. From self-fertilized seed of such plants there were produced 124 plants distributed with respect to their phenotypes as shown in Table XIII. For so small a population, in number of individuals only about twice that necessary to obtain a triple recessive, the agreement is good.

To account for these hybrid results on a chromosome basis it is necessary to assume merely that the three pairs of allelomorphs are borne in different pairs of chromosomes. When germ cells are formed in the F_1 hybrids the members of the three pairs of chromosomes separate independently so that eight different kinds of gametes are formed. In Fig. 45 are shown diagrammatically the reduction divisions in an F_1 snapdragon of the genetic constitution *ZzRrIi*. Since any one of these types of reduction has a good as chance of occurrence as any other one, the eight kinds of gametes are produced in substantially equal numbers. When such a plant is self-fertilized there are 64 possible combinations as shown in the checkerboard in Fig. 46. In the description of phenotypes in this checkerboard certain differences between homozygous and heterozygous forms have been disregarded. This is true particularly for the *Rr* individuals as contrasted with the homozygous *RR* individuals. The

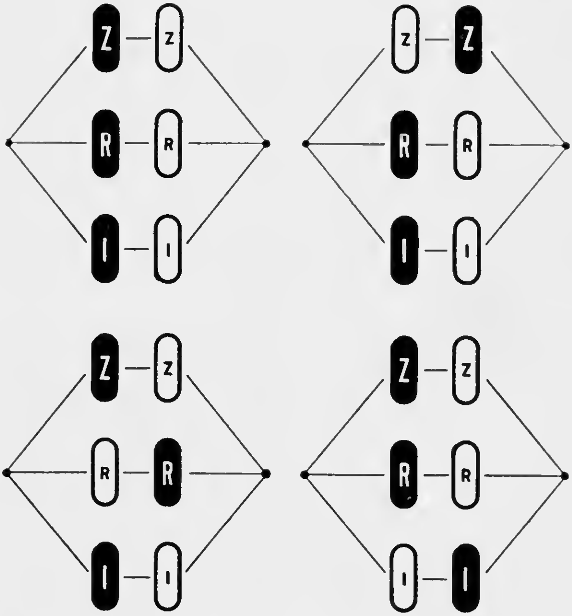


FIG. 45.—Diagrammatic representation of reduction divisions in an F_1 snapdragon of the genetic constitution *ZzRrIi*.

	ZRI	*ZRi*	*ZrI*	*Zri*	*zRI*	*zRi*	*zrI*	*zri*
ZRI	*ZRI* *ZRI* zygomorphic red ivory	*ZRi* *ZRI* zygomorphic red ivory	*ZrI* *ZRI* zygomorphic red ivory	*Zri* *ZRI* zygomorphic red ivory	*zRI* *ZRI* zygomorphic red ivory	*zRi* *ZRI* zygomorphic red ivory	*zrI* *ZRI* zygomorphic red ivory	*zri* *ZRI* zygomorphic red ivory
ZRi	*ZRI* *ZRi* zygomorphic red ivory	*ZRi* *ZRi* zygomorphic red yellow	*ZrI* *ZRi* zygomorphic red ivory	*Zri* *ZRi* zygomorphic red yellow	*zRI* *ZRi* zygomorphic red ivory	*zRi* *ZRi* zygomorphic red yellow	*zrI* *ZRi* zygomorphic red ivory	*zri* *ZRi* zygomorphic red yellow
ZrI	*ZRI* *ZrI* zygomorphic red ivory	*ZRi* *ZrI* zygomorphic red ivory	*ZrI* *ZrI* zygomorphic flesh-colored ivory	*Zri* *ZrI* zygomorphic flesh-colored ivory	*zRI* *ZrI* zygomorphic red ivory	*zRi* *ZrI* zygomorphic red ivory	*zrI* *ZrI* zygomorphic flesh-colored ivory	*zri* *ZrI* zygomorphic flesh-colored ivory
Zri	*ZRI* *Zri* zygomorphic red ivory	*ZRi* *Zri* zygomorphic red yellow	*ZrI* *Zri* zygomorphic flesh-colored ivory	*Zri* *Zri* zygomorphic flesh-colored yellow	*zRI* *Zri* zygomorphic red ivory	*zRi* *Zri* zygomorphic red yellow	*zrI* *Zri* zygomorphic flesh-colored ivory	*zri* *Zri* zygomorphic flesh-colored yellow
zRI	*ZRI* *zRI* zygomorphic red ivory	*ZRi* *zRI* zygomorphic red ivory	*ZrI* *zRI* zygomorphic red ivory	*Zri* *zRI* zygomorphic red ivory	*zRI* *zRI* peloric red ivory	*zRi* *zRI* peloric red ivory	*zrI* *zRI* peloric red ivory	*zri* *zRI* peloric red ivory
zRi	*ZRI* *zRi* zygomorphic red ivory	*ZRi* *zRi* zygomorphic red yellow	*ZrI* *zRi* zygomorphic red ivory	*Zri* *zRi* zygomorphic red yellow	*zRI* *zRi* peloric red ivory	*zRi* *zRi* peloric red yellow	*zrI* *zRi* peloric red ivory	*zri* *zRi* peloric red yellow
zrI	*ZRI* *zrI* zygomorphic red ivory	*ZRi* *zrI* zygomorphic red ivory	*ZrI* *zrI* zygomorphic flesh-colored ivory	*Zri* *zrI* zygomorphic flesh-colored ivory	*zRI* *zrI* peloric red ivory	*zRi* *zrI* peloric red ivory	*zrI* *zrI* peloric flesh-colored ivory	*zri* *zrI* peloric flesh-colored ivory
zri	*ZRI* *zri* zygomorphic red ivory	*ZRi* *zri* zygomorphic red yellow	*ZrI* *zri* zygomorphic flesh-colored ivory	*Zri* *zri* zygomorphic flesh-colored yellow	*zRI* *zri* peloric red ivory	*zRi* *zri* peloric red yellow	*zrI* *zri* peloric flesh-colored ivory	*zri* *zri* peloric flesh-colored yellow

Fig. 46.—Checkerboard Analysis of the F_2 Obtained from a Cross Involving the Three Pairs of Factors, *Z–z, R–r, I–i*

former are intermediate in coloration between the full-colored *RR* individuals and the flesh-colored *rr* individuals, and form a distinct class in themselves. But disregarding these differences the phenotypes in F_2 are in the following ratio:

27 Plants with zygomorphic, red on ivory flowers.
9 Plants with zygomorphic, red on yellow flowers.
9 Plants with zygomorphic, flesh-colored on ivory flowers.
9 Plants with peloric, red on ivory flowers.
3 Plants with zygomorphic, flesh-colored on yellow flowers.
3 Plants with peloric, red on yellow flowers.
3 Plants with peloric, flesh-colored on ivory flowers.
1 Plant with peloric, flesh-colored on yellow flowers.

This 27:9:9:9:3:3:3:1 ratio is typical for trihybrids, if dominance occurs in the three pairs of factors involved. Like the dihybrid ratio it is derivable from the monohybrid 3:1 ratio by subdividing the members of each term in the 3:1 ratio and then by again subdividing each term of the dihybrid ratio thus obtained in the ratio 3 : 1. To illustrate with our example, if the contrasted characters zygomorphic and peloric are considered segregation is in the ratio 3 zygomorphic: 1 peloric. When the contrasted characters red against flesh-colored, which also segregate in the simple ratio, are introduced into the analysis the ratio becomes 3 zygomorphic (3 red : 1 flesh-colored) : 1 peloric (3 red : 1 flesh-colored) = 9 zygomorphic red : 3 zygomorphic flesh-colored : 3 peloric red : 1 peloric flesh-colored. When finally the contrasted characters ivory against yellow are introduced this becomes 9 zygomorphic red (3 ivory : 1 yellow) : 3 zygomorphic flesh-colored (3 ivory : 1 yellow): 3 peloric red (3 ivory : 1 yellow) : 1 peloric flesh-colored (3 ivory : 1 yellow). This gives the final distribution tabulated above.

It is important to note that in this phenotypic ratio one member only of each phenotype is homozygous for all its factors and will breed true thereafter. From a Mendelian standpoint an individual is either homozygous or heterozygous for a given factor, if it is homozygous it is pure bred with respect to that factor and will breed true thereafter, irrespective of its derivation. It is therefore possible in F_2 to obtain a pure race with respect to any combination of parental factors provided only that a large enough F_2 generation is grown and tested. The increasing difficulty of fulfilling these conditions as the number of factors involved increases is obvious, so that from the standpoint of practicability it is usually necessary to work with crosses involving a relatively small number of factor differences.

Another fact which is apparent from this trihybrid case is the greater ease with which homozygous individuals may be obtained from the classes which are represented in the smallest numbers. In the above example peloric snapdragons with flowers flesh-colored on yellow are least frequent, but they all breed true on self-fertilization. In the case of the most frequent class, however, the zygomorphic red on ivory only one plant in 27 is homozygous for the three factors involved and consequently would breed true. These are features of Mendelism which have a direct practical application.

Multi-factor Hybrids.—Very few cases have been worked out which demonstrate conclusively, that more than three pairs of independently Mendelizing characters were involved. Not only are the experimental difficulties in such cases too great, but the scientific interest attached to them is not considerable. From a scientific standpoint accuracy of analysis is of chief importance, and accuracy is best attained by working with small numbers of factors at a time.

Little and Phillips, however, have conducted an experiment involving four pairs of independently Mendelizing factors in mice. The factors and the character expressions which they produce are listed below:

A—factor for agouti coloration. In this type of coloration the pigment is disposed in bands in the hairs giving the peculiar gray or agouti coloration of the wild mouse. The allelomorph *a* conditions a uniform distribution of pigment in the hairs.

B—a factor for black coat color. In this experiment the allelomorph *b* conditions the production of brown coat color.

D—a factor for intensity of coat coloration. Animals with the factor *D* were full colored, whereas those with *d* were "dilute" colored.

P—a factor for eye coloration. *P* conditions a dark eye coloration; the allelomorph *p* pink-eye color.

TABLE XIV.—FOUR-FOLD FACTOR SEGREGATION OF MICE (*From Little and Phillips*)

Phenotype	Formula	Observed	Expected	Observed ratio	Theoretical ratio
Black agouti	*ABDP*	436	373	94.5	81
Black	*aBDP*	127	124	27.5	27
Brown agouti	*AbDP*	103	124	22.3	27
Dilute black agouti	*ABdP*	130	124	28.2	27
Pink-eyed black agouti	*ABDp*	103	124	22.3	27
Brown	*abDP*	40	41	8.7	9
Dilute brown agouti	*AbdP*	31	41	6.7	9
Dilute black	*aBdP*	37	41	8.0	9
Pink-eyed black	*aBDp*	35	41	7.6	9
Pink-eyed brown agouti	*AbDp*	38	41	8.2	9
Pink-eyed dilute black agouti	*ABdp*	38	41	8.2	9
Dilute brown	*abdP*	11	14	2.4	3
Pink-eyed brown	*abDP*	12	14	2.6	3
Pink-eyed dilute brown agouti	*Abdp*	15	14	3.3	3
Pink-eyed dilute black	*aBdp*	17	14	3.7	3
Pink-eyed dilute brown	*abdp*	7	5	1.5	1

For the experiment a wild male of the genetic formula *AABBDDPP* was mated to a pink-eyed dilute brown female of the genetic constitution *aabbddpp*. The F_1s, *AaBbDdPp*, displayed all four dominant characters and were like the wild males. The F_2 segregation is shown in Table XIV. For 1180 individuals only about four times the number of genetic combinations for a four-factor hybrid, the agreement is satisfactory.

As for the chromosome interpretation, it may be made in the same way as in other cases by assuming that four different pairs of chromosomes bear the factors. Sixteen different kinds of gametes would be formed by such a hybrid, and these together would give the 256 gametic combinations of the F_2 generation.

For higher numbers of pairs of factors the same manner of independent distribution may hold as for those cases which have been outlined in detail. For independent distribution, the chromosome condition is simply that the different pairs of factors be borne in different pairs of chromosomes. Since, however, the total number of factors in any species must greatly exceed the number of pairs of chromosomes, it cannot be expected that every multi-factor hybrid will display independent segregation for all its factors. The number of pairs of chromosomes in Drosophila is four, consequently no crosses in this species involving more than four pairs of factors can possibly display independent segregation, if the chromosome theory be valid. Moreover, on the basis of the laws of probability, the chances that any particular case of even fourfold factor hybridization in this species would display independent segregation are extremely slight. Abundant evidence in this species has established the validity of these theoretical deductions. The same principles may logically be extended to other species so that for even as small a number of pairs of factors as five in wheat, which has eight pairs of chromosomes, in peas which have seven, and in corn which has ten, independent segregation would be an exception rather than the rule. Cases where independent segregation does not occur are treated in the next chapter, which deals with linkage.

Methods of Dealing with Genetic Data.—Many different methods have been devised for representing the results of Mendelian studies, and as yet the work of any large group of investigators is marked by a considerable lack of uniformity in this respect. Often the same investigator employs at one time one method of representation, and at another time, another. This is as it should be, for it can hardly be expected in a field of investigations marked by as rapid strides as had been characteristic of genetics in recent years that the ideal method of presentation should have been discovered while only a comparatively small portion of the evidence is at hand. Moreover, the method of presentation is merely a shorthand account of the operation of certain principles; it should not, therefore, greatly matter what methods are adopted so long as they represent clearly and adequately the operation of these principles. It is necessary for the student to familiarize himself with at least some of the more widely employed methods, remembering that with the basic principles clearly in mind, it should be possible to interpret very easily the methods employed in the presentation of any body of Mendelian data.

For ordinary work it is well to have a definite system of interpreting problems. In the following treatment only cases involving the category of independently segregating pairs of factors are considered, but it should be possible to extend the system without great difficulty to other categories as will be pointed out in those sections dealing with such categories.

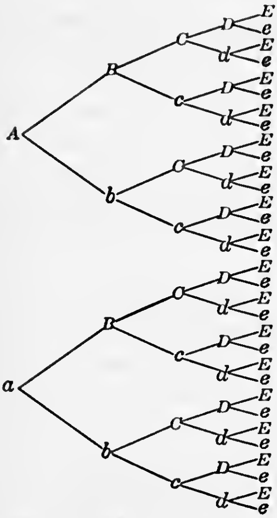


Fig. 47.—Method of writing all possible combinations of any number of pairs of factors.

When an individual is heterozygous for one pair of factors two types of gametes are possible. If the factors involved are represented by *A* and *a*, the genotypic constitution of such an individual is *Aa*, and the two types of gametes are *A* and *a*. If an individual is heterozygous for two pairs of factors, its genotypic formula will be *AaBb*, and there are then possible four different kinds of gametes, namely *AB*, *Ab*, *aB* and *ab*. As the number of heterozygous factors increases, therefore, the number of possible combinations of factors increases geometrically so that it is necessary to adopt a method of writing down these possible combinations. The method of dichotomy may be used in such cases, and the diagram, Fig. 47, explains its operation without further comment.

With as few as five pairs of factors, therefore, there are possible no less than thirty-two different kinds of gametes as follows:

ABCDE
ABCDe
ABCdE
ABCde
ABcDE
ABcDe
ABcdE
ABcde

AbCDE
AbCDe
AbCdE
AbCde
AbcDE
AbcDe
AbcdE
Abcde

aBCDE
aBCDe
aBCdE
aBCde
aBcDE
aBcDe
aBcdE
aBcde

abCDE
abCDe
abCdE
abCde
abcDE
abcDe
abcdE
abcde

By following this method consistently it is possible to write out readily the possible combinations of any series of factors. Fortunately or unfortunately the limits of experimental facilities usually preclude the possibility of working with large numbers of factors in any single experiment, so that it rarely becomes necessary to handle any large number of combinations.

Since F_2 results are commonly obtained by selfing the F_1 individuals in the case of plants, or interbreeding them in the case of animals, the F_2 ratios ordinarily represent the product of two like gametic series each consisting of all possible combinations of the different factors involved. There are several methods of obtaining these ratios, each of which has its special advantages. The simplest of these is the algebraic method which merely depends upon the multiplication of the two series together as illustrated in the following general example for two factor differences.

$$\begin{array}{ll} \text{Female gametes} & AB + Ab + aB + ab \\ \text{Male gametes} & AB + Ab + aB + ab \end{array}$$

F_2 zygotes:

$$\begin{array}{l} AABB + AABb + AaBB + AaBb \\ \qquad AABb \qquad\qquad + AaBb + AAbb + Aabb \\ \qquad\qquad AaBB + AaBb \qquad\qquad\qquad + aaBB + aaBb \\ \qquad\qquad\qquad AaBb \qquad\quad + Aabb \qquad\quad + aaBb \quad + aabb \\ \hline \end{array}$$

F_2 genotypes:

$$AABB + 2AABb + 2AaBB + 4AaBb + AAbb + 2Aabb + aaBB + 2aaBb + aabb$$

Collecting these F_2 genotypes into their respective phenotypes we get the following results:

$9AB$	$3Ab$	$3aB$	$1ab$
$1AABB$	$1AAbb$	$1aaBB$	$1aabb$
$2AABb$	$2Aabb$	$2aaBb$	
$2AaBB$			
$4AaBb$			

This tabulation of the genotypes since it shows that the genotypes within a phenotype are in definite ratios to each other immediately suggests the method of progression of writing down the F_2 phenotypic and genotypic distributions on the basis of the symmetrical relations displayed by them. The ratio of phenotypes in F_2 in a cross involving n pairs of factors is conveniently obtained in cases of complete dominance by the expansion of the expression $(3 + 1)^n$ or by continuously dividing the terms of a simpler ratio in the ratio 3:1 until the number of pairs of factor differences involved is satisfied. In the following table the phenotypic ratios obtained by the expansion of $(3 + 1)^n$ for values of n up to five have been given in condensed form.

TABLE XV.—PHENOTYPIC RATIOS OBTAINED BY EXPANSION OF THE BINOMIAL $(3 + 1)^n$.

Pairs of factors	$(3 + 1)^n$	Phenotypic ratio	Number of combinations
1	$(3 + 1)^1$	$3 + 1$	4
2	$(3 + 1)^2$	$3^2 + 2.3 + 1$	16
3	$(3 + 1)^3$	$3^3 + 3.3^2 + 3.3 + 1$	64
4	$(3 + 1)^4$	$3^4 + 4.3^3 + 6.3^2 + 4.3 + 1$	256
5	$(3 + 1)^5$	$3^5 + 5.3^4 + 10.3^3 + 10.3^2 + 5.3 + 1$	1,024
n	$(3 + 1)^n$	$3^n + n.3^{n-1} + \frac{n(n-1)}{\underline{\lvert 2}} 3^{n-2} + \frac{n(n-1)\,(n-2}{\underline{\lvert 3}} 3^{n-3} + .\ . + 1$	4^n

For three pairs of factors, therefore, we interpret this table to mean that the distribution with respect to phenotypes is as follows:

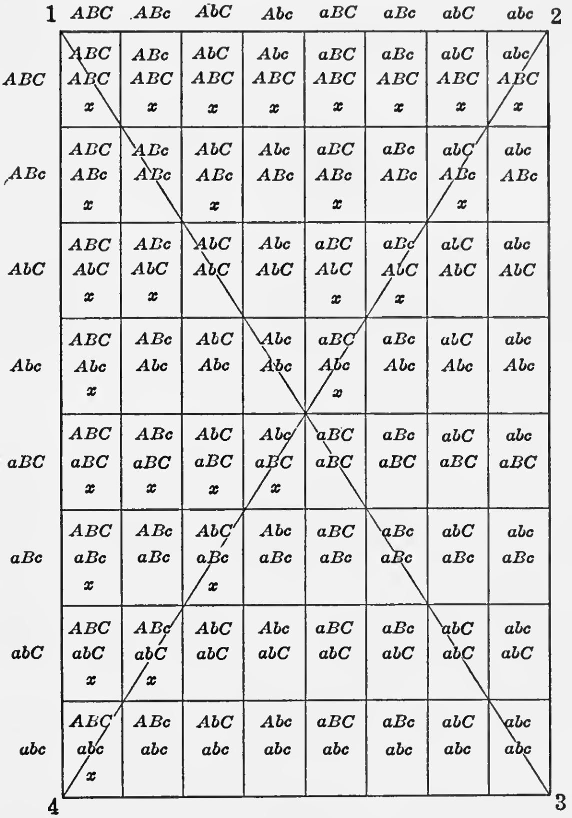
$$27ABC : 9ABc : 9AbC : 9aBC : 3Abc : 3aBc : 3abC : 1abc$$

If it is desired now to write down the numbers of each particular genotype in a given phenotype, the procedure according to the method of progression is very simple. Let us select the class $27ABC$ the genotypes of which are as follows:

$1AABBCC$
$2AABBCc$
$2AABbCC$
$2AaBBCC$
$4AABbCc$
$4AaBBCc$
$4AaBbCC$
$8AaBbCc$

It may be noted that there is one phenotype in each class homozygous for all its factors. In this class starting with this phenotype, we double the number of individuals each time an additional pair of factors becomes heterozygous. Thus there are three genotypes possible with only one heterozygous factor, and there will be two individuals of each of these, there will be three different genotypes having two heterozygous factors, and each of these will be represented by four individuals, and finally there is only one genotype with three heterozygous factors and it is represented by eight individuals. The method of progression is based upon the symmetrical relations which exist in the phenotypic ratios and in the ratios of genotypes within a phenotype and is a very convenient method for general use.

For illustrative purposes when it is desired to bring out relations graphically the checkerboard method of Punnett is much used. This method has already been employed in this book and needs no extended discussion here. The accompanying general checkerboard for three pairs of factors will illustrate the relations obtaining when this method is employed consistently. As shown in Fig. 48 the gametic series is written down at one side and at the top of the checkerboard and any square is filled out by writing down the genetic formula of the gamete at the top of its column and the one at the end of its row. If the series are written in the order shown the diagonal 1–3 will pass through all homozygous combinations. The number of these is evidently equal to the number of possible combinations in the gametic series. The diagonal 2–4 passes through all those combinations in which all three pairs of factors



	ABC	ABc	AbC	Abc	aBC	aBc	abC	abc
ABC	ABC ABC x	ABc ABC x	AbC ABC x	Abc ABC x	aBC ABC x	aBc ABC x	abC ABC x	abc ABC x
ABc	ABC ABc x	ABc ABc	AbC ABc x	Abc ABc	aBC ABc x	aBc ABc	abC ABc x	abc ABc
AbC	ABC AbC x	ABc AbC x	AbC AbC	Abc AbC	aBC AbC x	aBc AbC x	abC AbC	abc AbC
Abc	ABC Abc x	ABc Abc	AbC Abc	Abc Abc	aBC Abc x	aBc Abc	abC Abc	abc Abc
aBC	ABC aBC x	ABc aBC x	AbC aBC x	Abc aBC x	aBC aBC	aBc aBC	abC aBC	abc aBC
aBc	ABC aBc x	ABc aBc	AbC aBc x	Abc aBc	aBC aBc	aBc aBc	abC aBc	abc aBc
abC	ABC abC x	ABc abC x	AbC abC	Abc abC	aBC abC	aBc abC	abC abC	abc abC
abc	ABC abc x	ABc abc	AbC abc	Abc abc	aBC abc	aBc abc	abC abc	abc abc

Fig. 48.—Checkerboard method of analyzing expected results in F_2 from a cross involving three pairs of allelomorphs. The "x" zygotes belong to phenotype ABC. *Cf.* p. 98.

are heterozygous, and the number of these is also equal to the number of kinds of gametes. The bottom row gives the ratio which would be obtained by crossing the F_1 back to the triple recessive form. The student will be able to determine other relations existing in checkerboards of this type.

From a mathematical standpoint, students of genetics are interested in two things, the number and proportion of various types of individuals, and in methods of testing the mathematical validity of segregation ratios. Table XVI gives the mathematical relations which obtain in the production of gametes in F_1 individuals and in their union to form the F_2 zygotes. It is assumed throughout that one factor of each pair of allelomorphs is dominant.

TABLE XVI.—PROPORTIONS EXISTING IN MENDELIAN EXPERIMENTS INVOLVING VARIOUS NUMBERS OF FACTOR DIFFERENCES

Number of pairs of factors	1	2	3	4	5	6	n
Number of different kinds of gametes....	2	4	8	16	32	64	2^n
Number of combinations of gametes......	4	16	64	256	1,024	4,096	4^n
Number of homozygotes in F_2...........	2	4	8	16	32	64	2^n
Number of heterozygotes in F_2..........	2	12	56	240	992	4,032	$4^n - 2^n$
Number of kinds of genotypes in F_2......	3	9	27	81	243	729	3^n
Number of kinds of homozygous genotypes	2	4	8	16	32	64	2^n
Number of kinds of heterozygous genotypes..............................	1	5	19	65	211	665	$3^n - 2^n$

From this table it is clearly apparent how rapidly Mendelian problems increase in complexity with increases in the number of factor differences. With only five pairs of factors the number of individuals necessary to represent the F_2 population is 1024 and in order to be sure to have all classes represented it would be necessary to grow four or five times as many individuals as this. In such an experiment there would be 243 different genotypes distributed among thirty-two phenotypes. Naturally the chances of selecting a homozygous individual would vary according to the phenotype within which such selection was made, but the average chance of selecting a homozygote would be one in thirty-two, and the chance of selecting such an individual in the class displaying all five dominant characters would be only one in 243. The practical difficulties of dealing with large numbers of factor differences are therefore of considerable importance in planning and carrying out Mendelian experiments.

Methods of testing the "goodness of fit" of Mendelian ratios depend upon the application of the mathematical theory of probabilities. It is beyond the province of this book to enter into any exhaustive treatment of this subject, the present discussion is intended merely to point out the mathematical requirements which must be fulfilled, if no factors are present which tend to disturb the ratio constantly in a given direction. For most problems of this kind it is sufficiently accurate to consider the standard deviation of a Mendelian ratio = $\pm\sqrt{N(K-N}$ where N represents a particular term of a Mendelian ratio and K represents the sum of all the terms of such a ratio. This gives for the probable error E_n of a given term N of a Mendelian ratio the value

$$E_n = \pm\ 0.6745 \sqrt{\frac{N(K - N)}{n}}.$$

In this formula n = the total number of individuals classified.

The actual application of this formula may be illustrated by the use of data from East and Hayes given in Table XI. The totals in this table give observed frequencies as shown in Table XVII.

Table XVII.—Goodness of Fit in a Mendelian Experiment

Phenotypes	Observed	Observed ratio	Theoretical ratio	E	Probability
Purple starchy....	1,861	9.190	9	±0.094	1:4.64
Purple sweet......	614	3.032	3	±0.074	1:1
White starchy.....	548	2.706	3	±0.074	1:142.26
White sweet.......	217	1.072	1	±0.046	1:2.57
Totals..........	3,240	16.000	16		

The results are expected to be in agreement with a 9:3:3:1 ratio; therefore these observed results are first reduced to the form of a ratio per 16 by dividing each term by $\frac{1}{16}$ of the total number of individuals, or by $\frac{3240}{16} = 202.5$. By this method the observed ratio in Table XVII was calculated.

To obtain the probable error for the purple starchy class values are substituted in the above formula as follows:

$$E_9 = \pm\ 0.6745 \sqrt{\frac{9(16 - 9)}{3240}} = \pm\ 0.094$$

The observed deviation 0.19 is approximately twice the value of the probable error. For practical purposes a deviation less than three or four times the probable error is not considered significant. A deviation of the above magnitude in comparison to the probable error occurs about once in four times. In Table XVII the values of the probable error have been calculated for all four of the terms of this ratio. One term lies considerably within the probable error and its probability has been put down as 1:1. This is not strictly correct but serves the purposes of these calculations. It will be noted that there is one serious deviation, that of the white starchy class which could occur only once in 142 times. This deviation is not serious enough, however, to lead us to reject the hypothesis of two factor differences for this case, but it may indicate that other disturbing forces are in operation in this experiment.

A better method of testing goodness of fit has been suggested by Harris. The formula employed is

$$X^2 = \Sigma \frac{(o - c)^2}{c}.$$

In this formula o = the observed frequency of any class; c, the calculated frequency of that class; and Σ indicates that all values of the type $\frac{(o - c)^2}{c}$ are added together. When this formula is applied to the case treated above the values obtained are as given in Table XVIII. The value of X^2 is 8.14. The number of phenotypic classes is four. To determine the significance of this value it is necessary to refer to Elderton's tables for calculating goodness of fit. The value for P, the probability, for this case derived from such a table is 0.0437. The chances that the deviations shown in this ratio are merely due to random sampling are about one in twenty-three, again confirming our previous statement that some unknown slightly disturbing forces may be operating in this case. The deviation, however, is not enough to establish this certainly, for such a deviation might be expected to occur in about 4 per cent. of cases.

TABLE XVIII.—GOODNESS OF FIT IN A MENDELIAN EXPERIMENT

Phenotypes	Observed	Calculated	$\frac{(o - c)^2}{c}$
	o	c	
Purple starchy	1,861	1,822.5	0.81
Purple sweet	614	607.5	0.07
White starchy	548	607.5	5.83
White sweet	217	202.5	1.43
	3,240	3,240.0	8.14 = X^2

Mathematically the method suggested by Harris is preferable. It has also the advantage that it gives a measure of the goodness of fit of the ratio as a whole; which particular terms are most seriously at variance may be determined by simple inspection of the values of $\frac{(o - c)^2}{c}$. For determining the significance of X^2, it is necessary to have available Elderton's table for test of goodness of fit. These are given in Pearson's tables for statisticians and biometricians. It must ever be held in mind that forces which tend to disturb Mendelian ratios may not necessarily be of significance as bearing upon the essential feature of the analysis, namely, that a given number of independent factors are concerned in a certain experiment. There is always a chance that biological conditions of necessity may disturb a ratio, for after all a ratio is only the end point of a series of phenomena which we pretend to describe step by step. Unless constantly guarded against, such biological conditions as differences in viability, variations in phenotypic expression, etc., may result in selective elimination of a certain number of zygotes at some time previous to classification, or in error in the classification of some individuals.

CHAPTER VI

LINKAGE RELATIONS IN MENDELISM

Thus far Mendelian experiments have been considered in which the different pairs of factors segregate independently, and it has been shown that such cases may be explained very simply on the assumption that different pairs of chromosomes carry independent factors. However, there are several different species of plants and animals in which the number of known factor differences exceeds the number of pairs of chromosomes. Since it is reasonable to believe that only a small proportion of the possible number of factorial differences in any species has been analyzed, the conclusion appears justifiable that the number of factors in any species of plant or animal greatly exceeds the number of pairs of chromosomes; in fact our present evidence leads us to believe that the number of hereditary units in any organism must reach into the thousands. If the chromosome view of heredity is valid, therefore, each chromosome must carry a very great number of factors. In the present chapter it is proposed to discuss that class of Mendelian phenomena which depend upon factors which tend to remain together during segregation rather than to undergo independent assortment. Assuming that such factors are borne by the same chromosome, it will be shown how the chromosome mechanism provides an adequate physical basis for all the relations exhibited by such factors. Linkage and factor coupling are terms applied to that type of inheritance in which the factors tend to remain together in segregation. Linkage of factors is definitely an exception to one of the principles which Mendel laid down, namely, that of independent character segregation. Nevertheless by common consent the term Mendelism has been extended to include all phenomena of inheritance based on the unit factor hypothesis. For a long time only a few cases of linkage were known, and these were regarded in effect as anomalies. But the advocates of the chromosome theory of heredity have zealously prosecuted the study of linkage because of the many ways in which linkage relations parallel chromosome behavior. Moreover as the number of definitely recognizable factors within a species increases it becomes more and more important to determine the relations which the factors display among themselves. Linkage relations among factors, therefore, are of primary importance, and have been the direct means of giving us a clear and illuminating picture of the constitution of the hereditary material and of the operation of the chromosome mechanism in the distribution of the hereditary units.

Purple Aleurone and Waxy Endosperm in Maize.—A typical example of the relations which obtain for linked factors is given in the experiments which involve purple aleurone color and waxy endosperm in maize. We have shown in Chapter V that aleurone color in maize in certain cases depends on a single factor difference, so that in F_2 segregation is in the ratio 3 purple : 1 white. For waxy endosperm, when contrasted with starchy endosperm, Collins has shown that starchiness is dominant and that in F_2 segregation is in accordance with the normal monohybrid ratio, 3 starchy : 1 waxy. The factors involved in these two cases are C for aleurone coloration and its recessive allelomorph c for colorless aleurone, and W for starchy endosperm and its recessive allelomorph w for waxy endosperm. Collins found that when purple starchy corn, $CCWW$, is crossed with white waxy, $ccww$, F_1 is purple starchy, $CcWw$; but F_2 does not segregate in the expected dihybrid ratio 9 purple starchy : 3 purple waxy : 3 white starchy : 1 white waxy. The data which he actually obtained from six ears are given in Table XIX. The calculated ratio based on independent segregation evidently falls far short of agreement with the observed results, even though, when each pair of characters is considered separately, the agreement with the monohybrid ratio is very satisfactory. Thus for purple and white the observed totals are 2037:699 giving a ratio of 2.98 : 1.02, and for starchy and waxy the observed totals are 2053:683 giving a ratio of 3.00 : 1.00. The latter ratio is so close that it would be perfect if only one kernel were shifted from the starchy to the waxy class. Taking each pair separately, there-

Table XIX.—F_2 Segregation of Cross Purple Starchy × White Waxy
(*After Collins*)

Ear number	Number of grains	Purple starchy	Purple waxy	White starchy	White waxy
152	183	112	20	22	29
301	579	372	62	63	82
302	536	343	52	53	88
303	627	409	57	62	99
325	650	434	55	61	100
380	161	104	17	18	22
Observed totals.	2,736	1,774	263	279	420
Calculated.......9 : 3 : 3 : 1		1,539	513	513	171
Calculated 22.6 crossing-over...		1,775	276	276	409

fore, the factors evidently segregate in the normal Mendelian fashion, but the excess of purple starchy and white waxy kernels indicates that the factors C and W which came from one parent and c and w which came from the other have been distributed to the same gametes more often than would occur on the basis of independent segregation.

The ordinary gametic ratio for independent segregation in a hybrid of the genetic constitution $CcWw$ is

$$1CW:1\,Cw:1cW:1cw.$$

In this particular case, however, the gametes were produced in about the ratio

$$3.4CW:1Cw:1cW:3.4cw.$$

The factors, therefore, display partial linkage, *i.e.*, the parental combinations of factors tend to remain together more frequently than they tend to form new combinations. The factor W breaks away from C to form a new combination with c only once in about 4.4 times, instead of once in two times as is the case for independent segregation. Necessarily whenever W breaks away from C to form a new combination with c, w forms a new combination with C. This accounts for the symmetrical relations displayed in the gametic ratio. In order to show that the two factors are linked, in this case we represent the genetic constitutions of the parents as $(CW)(CW)$, purple starchy, and $(cw)(cw)$, white waxy; not $CCWW$ and $ccww$ respectively, which is the form used to indicate independent relations between the factors. Correspondingly the F_1 is $(CW)(cw)$, not $CcWw$, and the series of gametes which it forms is written

$$3.4(CW):1(Cw):1(cW):3.4(cw).$$

The method of deriving an F_2 ratio from such a gametic series is shown in the checkerboard in Fig. 49. Here it is necessary to take into account not only the genetic constitutions of the gametes, but also the coefficients which represent their relative frequency.

Summing up the totals for like phenotypes from this checkerboard, we find the F_2 grains are distributed in the following ratio:

50.28 with purple aleurone and starchy endosperm
7.8 with purple aleurone and waxy endosperm
7.8 with white aleurone and starchy endosperm
11.56 with white aleurone and waxy endosperm.

The calculated results based on this ratio are given in Table XIX. They show very close agreement with numbers actually observed, but in judging the significance of this agreement it must be borne in mind that a gametic ratio was arbitrarily selected which would give the closest possible agreement with the observed results.

When the factors enter the hybrid in different relations, the segregation ratio is different. Thus when purple waxy, (*Cw*)(*Cw*), is crossed with white starchy, (*cW*)(*cW*), the F_1 is purple starchy as in the previous case. The resemblance, however, is not complete except as to phenotypic expression, for its genetic constitution is (*Cw*)(*cW*), instead of (*CW*)(*cw*) as in the first cross. It produces a series of gametes in the ratio

	3.4 (*CW*)	1 (*Cw*)	1 (*cW*)	3.4 (*cw*)
3.4 (*CW*)	11.56 (*CW*)(*CW*) purple starchy	3.4 (*CW*)(*Cw*) purple starchy	3.4 (*CW*)(*cW*) purple starchy	11.56 (*CW*)(*cw*) purple starchy
1 (*Cw*)	3.4 (*Cw*)(*CW*) purple starchy	1 (*Cw*)(*Cw*) purple waxy	1 (*Cw*)(*cW*) purple starchy	3.4 (*Cw*)(*cw*) purple waxy
1 (*cW*)	3.4 (*cW*)(*CW*) purple starchy	1 (*cW*)(*Cw*) purple starchy	1 (*cW*)(*cW*) white starchy	3.4 (*cW*)(*cw*) white starchy
3.4 (*cw*)	11.56 (*cw*)(*CW*) purple starchy	3.4 (*cw*)(*Cw*) purple waxy	3.4 (*cw*)(*cW*) white starchy	11.56 (*cw*)(*cw*) white waxy

Fig. 49.—F_2 checkerboard of cross between purple starchy and white waxy maize.

	1 (*CW*)	3.4 (*Cw*)	3.4 (*cW*)	1 (*cw*)
1 (*CW*)	1 (*CW*)(*CW*) purple starchy	3.4 (*CW*)(*Cw*) purple starchy	3.4 (*CW*)(*cW*) purple starchy	1 (*CW*)(*cw*) purple starchy
3.4 (*Cw*)	3.4 (*Cw*)(*CW*) purple starchy	11.56 (*Cw*)(*Cw*) purple waxy	11.56 (*Cw*)(*cW*) purple starchy	3.4 (*Cw*)(*cw*) purple waxy
3.4 (*cW*)	3.4 (*cW*)(*CW*) purple starchy	11.56 (*cW*)(*Cw*) purple starchy	11.56 (*cW*)(*cW*) white starchy	3.4 (*cW*)(*cw*) white starchy
1 (*cw*)	1 (*cw*)(*CW*) purple starchy	3.4 (*cw*)(*Cw*) purple waxy	3.4 (*cw*)(*cW*) white starchy	1 (*cw*)(*cw*) white waxy

Fig. 50.—F_2 checkerboard of cross between purple waxy and white starchy maize.

1(*CW*) : 3.4(*Cw*) : 3.4(*cW*) : 1(*cw*).

In this ratio the numerical proportions of the gametes are reversed. This is due to the fact that here the original factor combinations, *C* and *w*, and *c* and *W*, although the reverse of those in the former case, tend to remain together in the same ratio.

When F_1 plants of the genetic constitution, (*Cw*)(*cW*), are selfed segregation occurs in F_2 as shown in the checkerboard in Fig. 50. When like phenotypes are collected into classes, the following distribution is obtained:

39.72 with purple aleurone and starchy endosperm
18.36 with purple aleurone and waxy endosperm
18.36 with white aleurone and starchy endosperm
1.00 with white aleurone and waxy endosperm.

This ratio is strikingly different from that obtained for the former cross, although exactly the same characters are involved. Unfortunately data supporting this part of the analysis have not yet been presented in a satisfactory manner, but the results so far as reported do show a positive linkage between the factors. Moreover other cases which we shall discuss in this chapter demonstrate beyond doubt that the relations described above hold rigidly for cases of factor linkage. The different results obtained when factors enter a cross in different combinations are, therefore, simply due to the fact that the original combinations tend to be preserved in segregation in a definite fixed proportion of gametes.

To give a chromosome interpretation of linkage we assume that the factors linked are borne in the same chromosome. Thus the factor for purple aleurone color is one of the chromomeres occupying a definite locus in a particular pair of chromosomes in a purple starchy race of corn and the factor *W* for starchy endosperm occupies a different locus in these same chromosomes. In Fig. 51 the chromosome behavior in linkage is shown graphically. In the hybrid one member of a pair of chromosomes bears the factors *C* and *W*, the other member *c* and *w*. During synapsis these chromosomes conjugate, and when the threads representing the two chromosomes separate after conjugation they may in consequence of their twisted condition break at certain points and, reuniting, the free ends of different threads may join together. In a certain percentage of cases this breaking of the filaments may occur between *C* and *W*, so that the chromosomes afterward reconstituted will contain the factors *C* and *w*, and *c* and *W* rather than the original combinations. More frequently the chromosomes will untwist without exchanging chromatin material or after having exchanged it in such a way as not to disturb the original factor combinations. Exchange of chromatin material between homologous chromosomes is called crossing-over. This term is also applied to the formation of new combinations of linked factors, and these new combinations are called cross-overs. In this particular case the end result is that for the factors *C* and *W* and their allelomorphs crossing-over occurs in 22.6 per cent. of cases. Accordingly the gametes are formed in the ratio:

$$\underbrace{38.7\text{ per cent. }(CW) : 38.7\text{ per cent. }(cw)}_{77.4\text{ per cent. non-cross-overs}} : \underbrace{11.3\text{ per cent. }(Cw) : 11.3\text{ per cent. }(cW)}_{22.6\text{ per cent. cross-overs.}}$$

It follows, therefore, that linkage may be interpreted as due to association of factors within the same chromosomes and that crossing-over or breaking apart of linked factors may be regarded as a consequence of chromatin exchange between homologous chromosomes during synapsis. The factors may be thought of as the purely passive objects with which the chromosome mechanism deals, they are linked together because they are borne in the same chromosome, they show breaks in linkage in a certain percentage of cases because in synapsis breaks occur between the loci which they occupy in the chromosome such that new combinations of the factors are formed. The chromosome relations are the same even when chromatin interchange results in no new combinations of factors,

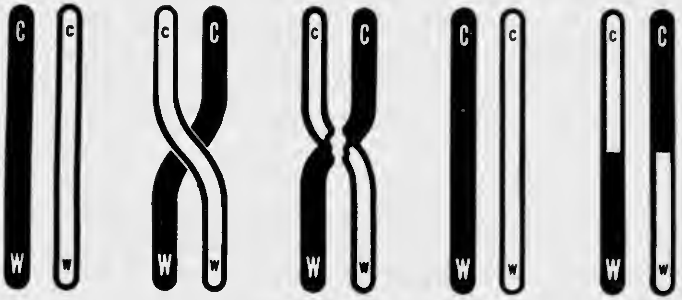


FIG. 51.—Diagrammatic representation of crossing-over and results. At the left, the two original chromosomes. In the middle, the twisted condition of the chromosomes in synapsis and their subsequent separation. At the right, the four types of chromosomes which result and their proportions.

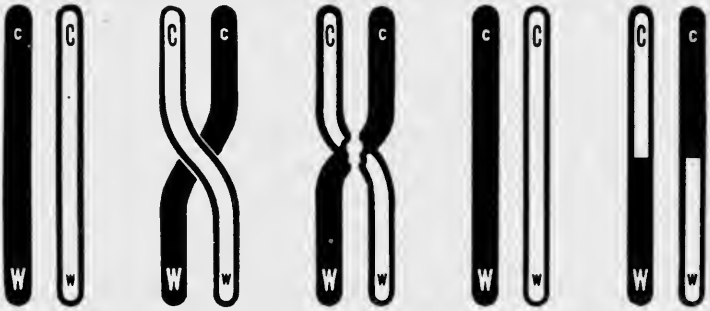


FIG. 52.—Diagrammatic representation of crossing-over and its results when the factors enter in the opposite combination from that shown in Fig. 51.

it is only when there are factor differences between the homologous chromosomes that the operation of the mechanism can be detected and some conception gained of its mode of operation.

Linkage in Drosophila.—To Morgan and his associates through their investigations with mutations of *Drosophila ampeloplila* we owe directly practically our entire conception of the linkage relations displayed by factors. No other single species has provided such a wealth of data or proved so favorable for genetic investigations. This body of data is still growing very rapidly and is adding new conceptions all the time, but even at this time it is no exaggeration to say that the Zoölogical Laboratories of Columbia University, like the old garden of the Königskloster at Brünn, have yielded results which will be accounted among the epochal advances in genetics. Mendel's work showed that the characters of the organism were dissociable elements of its makeup which could be recombined and shuffled about in genetic experiments. From this starting point the factor conception of heredity, which assumes that characters of the individual may be referred to the action of definite factors in the hereditary material, was developed by a host of investigators. Morgan's work has also furnished an overwhelming body of evidence supporting the factor conception of heredity, but its most important contribution to genetics has been in the establishment of the relations existing between the factors of heredity and the chromosome mechanism of the cell.

The Four Groups of Factors in Drosophila.—According to the chromosome theory of heredity a factor is located at a particular locus in the chromosome mechanism. Consequently since linkage depends upon factor relations within the same chromosome it follows that the factors should display linkage relations such that they would be thrown into groups corresponding to the number of pairs of chromosomes. In Drosophila the linkage relations existing among over a hundred factor mutations have been studied. The factors fall into four groups corresponding to the four pairs of chromosomes in Drosophila, and furthermore the relative sizes of these groups corresponds roughly to the relative sizes of the different pairs of chromosomes. There is a large group of sex-linked factors all of which display the same type of inheritance as white-eye color, which has already been described. This group corresponds to the *X*-chromosomes. There are two large groups of factors which correspond to the two large pairs of autosomes, and finally there is a small group, consisting as yet of only two factors, which corresponds to the small pair of autosomes. The following list of the groups of factors in Drosophila, although incomplete, gives some idea of the number and kinds of factors which have been studied in this species (Table XX).

The type of behavior shown in linkage in Drospohila may be illus-

TABLE XX.—PARTIAL LIST OF THE FOUR GROUPS OF FACTORS IN *Drosophila ampelophila* SHOWING THE PRINCIPAL CHARACTER AFFECTED BY EACH FACTOR.

Group I		Group II		Group III		Group IV	
Name of factor	Character affected	Name of factor	Character affected	Name of factor	Character affected	Name of factor	Character affected
Abnormal	Abdomen	Antlered	Wings	Band	Thorax	Bent	Wings
Bar	Eye-shape	Apterous	Wings	Beaded	Wings	Eyeless	Eyes
Bifid	Wings	Arc	Wings	Cream III	Eye-color		
Bow	Wings	Balloon	Wings	Deformed	Eyes		
Cherry	Eye-color	Black	Body-color	Dichaete	Bristles and wings		
Chrome	Body-color	Blistered	Wings	Dwarf	Body-size		
Club	Wings	Comma	Thorax	Ebony	Body-color		
Depressed	Wings	Confluent	Wing-venation	Giant	Body-size		
Dot	Thorax	Cream II	Eye-color	Kidney	Eye-shape		
Eosin	Eye-color	Curved	Wings	Low-crossover	Crossing-over		
Facet	Eyes	Dachs	Legs	Maroon	Eye-color		
Forked	Bristles	Extra veins	Wing-venation	Peach	Eye-color		
Furrowed	Eyes	Fringed	Wings	Pink	Eye-color		
Fused	Wing-venation	Jaunty	Wings	Rough	Eyes		
Garnet	Eye-color	Limited	Abdominal bands	Safranin	Eye-color		
Green	Body-color	Little crossover	Crossing-over	Sepia	Eye-color		
Jaunty I	Wings	Morula	Eyes	Sooty	Body-color		
Lemon	Body-color	Olive	Body-color	Spineless	Spines		
Lethals, 15	Life	Plexus	Wing-venation	Spread	Wings		
Miniature	Wings	Purple	Eye-color	Trident	Thorax		
Notch	Wings	Speck	Wings	Truncate intensifier	Wings		
Reduplicated	Legs	Strap	Wings	White head	Thorax		
Ruby	Eyes	Streak	Thorax	White occlli	Simple eyes		
Rudimentary	Wings	Trefoil	Thorax				
Sable	Body-color	Truncate	Wings				
Shifted	Wing-venation	Vestigial	Wings				
Short	Wings						
Spoon	Wings						
Spot	Body-color						
Tan	Body-color						
Truncate intensifier	Wings						
Vermilion	Eye-color						
White	Eye-color						
Yellow	Body-color						

trated by the cross yellow white female by gray red male. The genetic formula of a yellow white female is $(ywX)(ywX)$, and of a gray red male $(YWX)Y$. In these formulæ y stands for the factor for yellow body-color and w for white eye-color, and the capital letters for the corresponding dominant allelomorphs present in the wild type. When two such flies are bred together the F_1 consists of females of the genetic constitution $(YWX)(ywX)$ and males of the genetic constitution $(ywX)Y$. The F_1 females, therefore, have gray bodies and red eyes and the males have yellow bodies and white eyes. Gray red females of the genetic constitution $(YWX)(ywX)$ produce four kinds of eggs in the following proportions:

$$\underbrace{(YWX)\ 49.45 \text{ per cent.}\quad (ywX)\ 49.45 \text{ per cent.}}_{98.9 \text{ per cent. non-cross-over gametes.}}\qquad \underbrace{(YwX)\ 0.55 \text{ per cent.}\quad (yWX)\ 0.55 \text{ per cent.}}_{1.1 \text{ per cent. cross-over gametes.}}$$

When such a female is bred to a yellow white male, genetic constitution $(ywX)Y$, which produces only two kinds of sperms, (ywX) and Y, the progeny in both sexes obviously will be in the ratio

49.45 gray red:49.45 yellow white:0.55 gray white:0.55 yellow red.

Table XXI shows the results which have been secured, mostly from matings of this type.

The relations shown when the factors enter in the reverse combinations may be determined by mating a gray white female, genetic constitution $(YwX)(YwX)$ to a yellow red male, genetic constitution $(yWX)Y$. This gives F_1 gray red females of the constitution $(YwX)(yWX)$, and gray white males of the genetic constitution $(YwX)Y$. In this case the F_1 females produce four kinds of eggs in the following proportions:

$$\underbrace{(YwX)\ 49.45 \text{ per cent.} : (yWX)\ 49.45 \text{ per cent.}}_{98.9 \text{ per cent. non-cross-ever gametes.}}\ :\ \underbrace{(YWX)\ 0.55 \text{ per cent.} : (ywX)\ 0.55 \text{ per cent.}}_{1.1 \text{ per cent. cross-over gametes.}}$$

TABLE XXI.—FACTOR LINKAGE IN GRAY RED FEMALE DROSOPHILAS OF THE TYPE $(YWX)(ywX)$

Reported by	Number of flies classified	Non-cross-overs		Cross-overs		Percentage of crossing-over
		Gray red	Yellow white	Gray white	Yellow red	
Dexter	14,939	8,093	6,672	93	81	1.16
Morgan and Cattell	1,818	1,075	729	14	0	0.77
Morgan and Cattell	854	513	334	2	5	0.82
Morgan and Bridges	3,424	1,807	1,600	7	10	0.50
Totals	21,035	11,488	9,335	116	96	1.01

When, therefore, the F_1 females are mated to yellow white males of the genetic constitution $(ywX)Y$ the progeny will give directly in its phenotypic ratio the proportions in which the gametes are produced as follows:

49.45 gray white:49.45 yellow red:0.55 gray red:0.55 yellow white. The actual experimental results from this type of mating are summarized in Table XXII. The actual linkage value obtained is 1.13 which is substantially the same as that shown in the previous table. On the basis of summarized data of counts of 81,299 flies, Morgan and Bridges fix the value for crossing-over between these two loci at 1.1 per cent. This is the value we have used in deriving the above gametic ratios. Other factors have been studied in the same way and give different percentages of crossing-over. Thus Morgan and Bridges report the value for crossing-over between white and miniature based on counts of 110,701 flies at 33.2 per cent., between white and vermilion from 27,962 flies at 30.5, between vermilion and bar from 23,522 flies at 23.9, and so on for the whole series of factors in the first group.

TABLE XXII.—FACTOR LINKAGE IN GRAY-RED FEMALE DROSOPHILAS OF THE TYPE $(YwX)(yWX)$

Reported by	Number of flies classified	Non-cross-overs		Cross-overs		Percentage of crossing-over
		Gray white	Yellow red	Gray red	Yellow white	
Dexter	1,348	440	889	16	3	1.41
Morgan and Cattell	3,258	1,841	1,412	4	1	0.15
Morgan and Cattell	9,027	4,292	4,605	86	44	1.44
Totals	13,633	6,573	6,906	106	48	1.13

Factors in the second and third groups display the same type of linkage relations as those in the first group. As an example we may take the recessive factors black and curved which lie in the second group. A black curved female of the genetic constitution $(bc_v)(bc_v)$ crossed with a gray normal male $(BC_v)(BC_v)$ gives in F_1 gray long females and males of the genetic constitution $(BC_v)(bc_v)$. When such F_1 females are crossed back to black curved males the results as reported by Sturtevant and Bridges are given in Table XXIII. The observed percentage of crossing-over between the loci B and C_v in the second chromosome in this experiment amounts to 24.04 per cent.

When gray curved females $(Bc_v)(Bc_v)$ are mated to black normal males $(bC_v)(bC_v)$ the F_1 flies are gray normal as in the previous case, but genetically they are of the constitution $(Bc_v)(bC_v)$. Such females mated to black curved males, according to the same investigators, gave the results tabulated in the last two columns in Table XXIII. Here the percentage of crossing-over amounted to 22.74 per cent., a value substantially in agreement with the results of the reverse factor tests.

TABLE XXIII.—CROSSING-OVER BETWEEN B AND C_v IN DROSOPHILA

Phenotype	Black curved ♂ $(bc_v)(bc_v)$ mated to			
	Gray normal ♀ $(BC_v)(bc_v)$		Gray normal ♀ $(Bc_v)(bC_v)$	
	Non-cross-overs	Cross-overs	Non-cross-overs	Cross-overs
Gray normal	610	...	.....	644
Gray curved	...	184	2,292	
Black normal	...	226	2,148	
Black curved	652	...	.....	663
Totals	1,262	410	4,440	1,307
Percentage of crossing-over	24.04		22.74	

No Crossing-over in the Male.—The above results show clearly that crossing-over in the female between the loci B and C_v of the second chromosome results in the production of approximately 23 per cent. of cross-over gametes irrespective of the particular combination of the factors concerned. Sturtevant and Bridges, however, have shown that there is no crossing-over in the male so that males of the genetic constitution $(BC_v)(bc_v)$ produce only two types of sperm in the ratio $1(BC_v):1(bc_v)$ and males of the genetic constitution $(Bc_v)(bC_v)$ produce sperms in the ratio, $1(Bc_v):1(bC_v)$.

It is not known just what the absence of crossing-over in the male depends upon. In the case of factors in the X-chromosome or first group, crossing-over would involve exchange of chromatin material between the X- and Y-chromosomes. Since these differ strikingly it is not surprising that interchange of chromatin does not take place between these chromosomes for it is difficult to see how the difference could be preserved if crossing-over should occur. But the other chromosomes are alike in both sexes, nevertheless no matter how high the percentage of crossing-over in the female, none whatever has been observed in the male. This has been found true for factors lying in the third group as well as for those lying in the second group, and it is without doubt a general phenomenon.

The knowledge that no crossing-over occurs in the male has often been turned to advantage in experimental work. When gray curved flies, $(Bc_v)(Bc_v)$ are mated to black normal, $(bC_v)(bC_v)$, the F_1 flies are gray normal and of the genetic constitution $(Bc_v)(bC_v)$. When these are interbred to obtain the F_2 generation the results are shown in the checkerboard in Fig. 53. According to this checkerboard, the F_2 will consist of flies in the ratio

2 gray normal : 1 gray curved : 1 black normal.

No black curved flies are obtained in this cross in F_2, and it is of interest to note that no matter what the amount of crossing-over in the female the flies in F_2 will always be in the ratio 2 : 1 : 1. In F_3 black curved flies may be obtained from a certain percentage of matings of black normal or of gray curved flies.

The failure of the double recessive class to appear in F_2 has been much used by Morgan in determining the factor group to which new mutations belong. For this purpose black-pink flies are crossed with the new mutant type. Since black lies in the second group and pink in the third, if the new factor belongs to either of these groups it will fail to show the corresponding double recessive form in F_2. Whether it belongs to the sex-linked group is of course readily determined from the sex relations obtained in such an experiment, and if the test shows that the factor in question belongs to none of these three groups, by exclusion it must belong to the fourth.

	(Bc_v)	(bC_v)
11.5 (BC_v)	11.5 $(BC_v)(Bc_v)$ gray normal	11.5 $(BC_v)(bC_v)$ gray normal
38.5 (Bc_v)	38.5 $(Bc_v)(Bc_v)$ gray curved	38.5 $(Bc_v)(bC_v)$ gray normal
38.5 (bC_v)	38.5 $(bC_v)(Bc_v)$ gray normal	38.5 $(bC_v)(bC_v)$ black normal
11.5 (bc_v)	11.5 $(bc_v)(Bc_v)$ gray curved	11.5 $(bc_v)(bC_v)$ black normal

FIG. 53.—F_2 obtained by crossing gray curved and black normal flies.

Linear Arrangement of Factors.—It was an old idea of Roux brought forward to explain the division of the chromatin while in the form of a long thin thread that the individual elements of the chromatin are arranged in a linear series in the chromosomes. Later Janssens developed the idea that in synapsis homologous chromosomes twist about each other and in separating tend to break apart at places, and in reuniting exchange chromatin material. Morgan has taken these two ideas and applied them to the results of the Drosophila investigations. The twisting of the chromosomes in synapsis is held to be the physical evidence of the known interchange of factors between chromosomes which takes place in crossing-over. Moreover, if the factors are the individual elements of the chro-

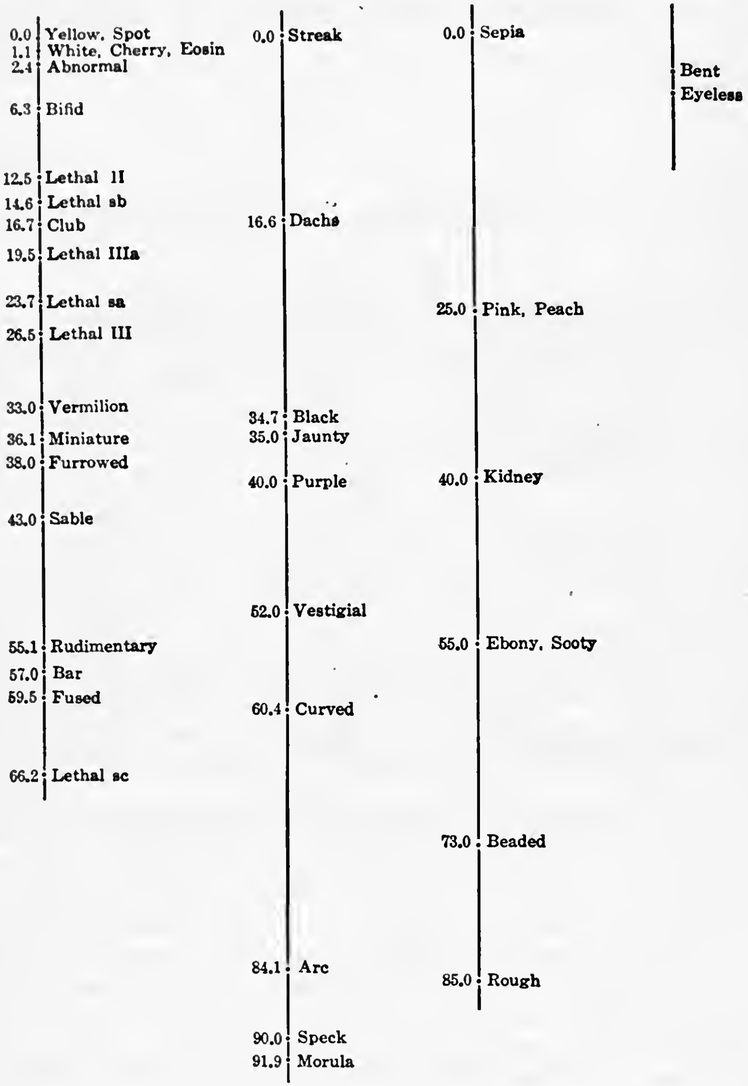


FIG. 54.—Plotted relations of factors in *Drosophila ampelophila.*

matin threads which twist about each other and these elements are held to occupy invariable loci in the chromatin thread, then the percentage of crossing-over between any two loci may be taken as an indication of the distance between the factors. For obviously if the chromatin thread is as likely to break between any two chromomeres as between any other two, then the farther apart two factors lie in the chromatin threads representing homologous chromosomes, the greater is the chance that crossing-over will occur between them.

The results of the application of this idea to the linkage relations existing in Drosophila are shown in Fig. 54. In this chromosome map of Drosophila the factors have been plotted in a linear series according to their relative position in the chromosomes as determined by linkage relations. The evidence as yet is not sufficient to give an accurate picture of the arrangement of all the factors, but the number of factors plotted and the relations which they display provide further evidence of the correspondence between the chromosomes and the factor groups. Morgan has taken 1 per cent. of crossing-over as the unit for expressing linkage relations. Expressed in such units the first chromosome, which contains all the sex-linked factors, has a length of 66.2. The second and third groups, as far as determined, have lengths of 91.9 and 85.0, respectively. These lengths in general correspond fairly well to the known relative sizes of the two large pairs of autosomes when compared with each other and with the *X*-chromosomes. In the fourth group but two factors are known and their loci are so close together that thus far no crossing-over has been observed between them. Accordingly no definite value can be fixed for their linkage relations. From a knowledge of the small relative size of the third autosome Muller, at the time he announced the discovery of the first factor in the fourth group, predicted that factors in this group would show very close linkage values. This prediction has been upheld satisfactorily and it is further evidence that the chromosome theory of heredity works.

The demonstration that factors lie in a linear series in each group provides a unique method of predicting the results of factor behavior. Obviously if a factor is known to belong to a particular group, it is possible to predict confidently that it will display independent segregation with factors belonging to other groups. But further than this when the loci of a number of factors in a given group have been plotted accurately, with a new factor it is only necessary to determine the linkage relations with two of the plotted loci in order to determine its locus. When its locus has been determined, its linkage values with any other members in the group may be predicted from its distance in units from those factors. To illustrate, in Group I, if the position of miniature were unknown, it might be tested with vermilion and sable. It would give about 3 per cent. of crossing-over with vermilion and about 7 per cent. with sable. Knowing the position of the vermilion locus at 33.0 and the sable locus at 43.0, we would be able from these data to fix the locus position of miniature at about 36.0. With this value determined we could confidently predict for example that miniature and white would show somewhat less than 35 per cent. of crossing-over or miniature and bar about 21 per cent. The ability to make such predictions is a unique product of recent investigations in heredity.

How experimental results support the hypothesis of linear arrangement of factors may be illustrated by what Morgan calls a three-point experiment, *i.e.*, an experiment involving three different factors in the same chromosome. We may take three factors which are in widely separated loci in the chromosome, white at locus about 1.0, miniature at about 36.0, and bar at about 57.0. The summaries which Morgan and Bridges have given of the data involving these three loci are included in Table XXIV. White and miniature give directly 33.2 per cent. of crossing-over, and miniature and bar 20.5 per cent. Since the distance between white and miniature plus that between miniature and bar is equal to 53.7, this latter value should represent the distance between white and bar. But direct experimental determinations of the percentage of crossing-over between white and bar give a value of 43.6 per cent., which is 10.1 per cent. short of the calculated value.

TABLE XXIV.—CROSSING-OVER FOR THE LOCI *W*, *M*, and *B′* IN DROSOPHILA. DATA OBTAINED BY MATING FEMALES OF THE CONSTITUTION (*wmB′X*)(*WMb′X*) WITH TRIPLE RECESSIVE MALES (*wmb′X*)*Y*.

Character combinations	Number of flies classified	Number of cross-overs	Per cent. of crossing-over
White miniature....	110,701	31,071	33.2
Miniature bar......	3,112	636	20.5
White bar.........	5,955	2,601	43.6

The reason for this should be plain from a consideration of Fig. 55 which shows diagrammatically how the chromosomes behave in a three-point experiment. On the left in the two upper groups are represented the two chromosomes with the factors in the original positions in which they were derived from the parents. On the right the homologus chromosomes are shown twisted about each other, and at *A*, *B*, *C*, and *D* the types of chromosomes which are obtained after chromatin interchange in synapsis. The numbers below refer to the relative frequency of production of the four types of chromosome pairs in this three-point experiment based on the data of Table XXIV. In *A* (Fig. 55) no exchanges of chromatin have occurred which affect the relations of the factors to each other, so that this type of separation after synapsis gives the non-cross-over gametes (*wmB′X*) and (*WMb′X*). Types *B* and *C* involve single breaks in the chromosomes followed by chromatin interchange in reunion. They are the single cross-overs and give the cross-over gametes (*wMb′X*) and (*WmB′X*) and (*wmb′X*) and (*WMB′X*) respectively. Finally in type *D* the chromosomes have broken and exchanged material at two points. This type is called double crossing-over and results in the production of gametes of the genetic constitutions (*wMB′X*) and (*Wmb′X*). In this last case, although chromatin interchange has occurred between the two chromosomes, the relations between the loci *W* and *B′* remain unchanged.

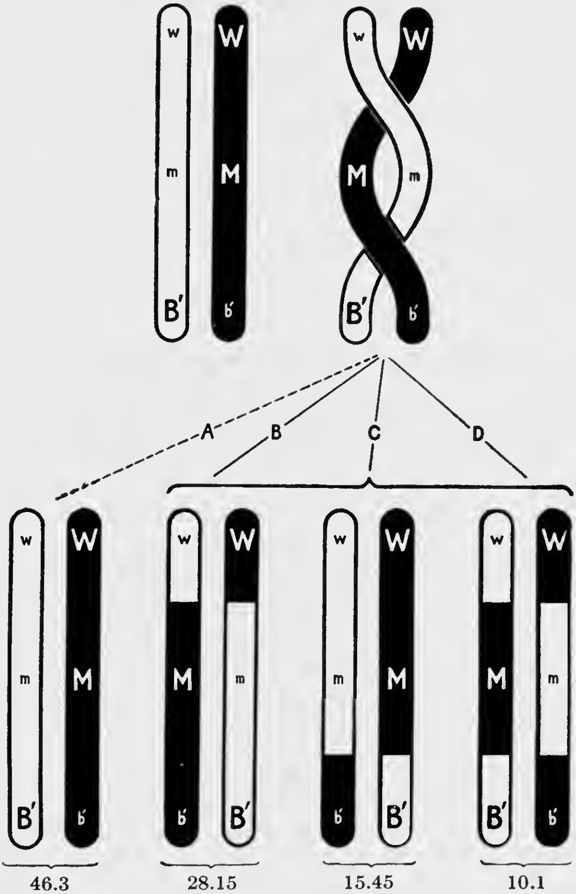


Fig. 55.—Diagram to show crossing-over in a three-factor experiment.

The occurrence of double crossing-over accounts for the low percentage of crossing-over between white and bar as compared with the sum of the values given by white and miniature and miniature and bar.

The value for crossing-over between W and M is given by

$$B + \frac{D}{2} = 28.15 + 5.05 = 33.2 \text{ per cent.}$$

and similarly between M and B'

$$C + \frac{D}{2} = 15.45 + 5.05 = 20.5 \text{ per cent.}$$

consequently the distance between W and B' as measured by adding together the values for W and M and M and B' gives the equation

$$B + C + D = 53.7.$$

Since double crossing-over of the type D does not involve a rearrangement of the loci, W and B', however, the actual crossing-over obtained experimentally must fall short of the computed distance by a value equal to D as given by the equation

$$B + C = 43.6 \text{ per cent.}$$

The lowering of the percentage of crossing-over when extreme distances are involved is, therefore, a logical consequence of the relations existing between linked factors. Obviously double crossing-over occurs much less frequently in short distances than in long ones. Consequently since a factor map is designed to give the total values for crossing-over between the different loci, such a map is prepared so far as possible from experiments involving short factor distances. If such data are not at hand simple methods of interpolation are used to locate the loci.

It should be noted in passing that variations in linkage values sometimes occur among members of a given set of factors. Bridges has pointed out that in some cases at least the percentage of crossing-over depends somewhat on the age of the female, and Plough has detected definite effects of extremely high or low temperatures on the percentage of crossing-over between factors of the second chromosome in Drosophila, although crossing-over in the first and third chromosomes was not influenced by the changes in temperature. Besides such variations, however, definite factors have been discovered (Sturtevant) which lower the percentage of crossing-over. Muller has shown that such a factor exerts a particularly disturbing action in the third chromosome in which it is located. But even in cases of variation in linkage values the order of the factors in the chromosome is not disturbed. The relations shown, therefore, in cases involving variations in linkage are in harmony with the conception of linear arrangement of factors in the chromosomes.

The most striking confirmation of the hypothesis of linear arrangement is found in the case of "deficiency" in the X-chromosome, which was investigated by Bridges (see p. 155) and in which the location of forked spines within the deficient region "was detected and proved as a result of deliberate search among those genes which had *previously been mapped closest to bar!*"

The Mode of Interchange in Crossing-over.—Factor interchange conceivably might take place by interchange of isolated factors here and there along adjacent threads or it might follow as a consequence of interchange of relatively large sections of chromatin between chromosomes. The sectional mode of chromatin interchange appears to have more cytological evidence in its support and Plough's recent studies on the effect of temperature on crossing-over corroborate Muller and Bridges' inference that crossing-over takes place in the fine thread stage of synapsis, which would be the most favorable stage for sectional interchange. But breeding investigations of themselves clearly establish this hypothesis. Thus Muller made up females which contained twelve sex-linked mutant factors. These females received from one parent the factors for yellow body color, white eye color, abnormal abdomen, bifid wings, vermilion eye color, miniature wings, sable body color, rudimentary wings, forked spines, and from the other parent the mutant factors cherry eye color, club wings and bar eyes. Using the system of writing the genetic formulæ which has been followed in this text, these females were of the genetic constitution.

$$(ywA'b_i\ C_lvmsrfb'X)(Yw^ca'B_ic_lVMSRFB'X).$$

Muller found in tests of 712 individuals arising from gametes from such females, that the proportions of crossing-over between factor loci in the formation of gametes occurred according to the figures given in Table XXV. The results show that in this experiment there was no crossing-over in 54.4 per cent. of cases; single crossing-over in 41.7 per cent., and double crossing-over in 4.2 per cent. No example of triple crossing-over was found among these flies, but a few such cases have been observed. The values agree satisfactorily with those calculated from the three-point experiments involving the loci W, M, and B' in this same chromosome.

If we consider the double cross-overs which were obtained in this experiment we find abundant evidence in support of the sectional mode of chromatin interchange. It is difficult to visualize the relations from the numerical data, consequently Fig. 56 has been prepared to illustrate diagrammatically the types of double crossing-over obtained in these experiments. In all but one case the points of crossing-over are far removed from each other, and even in the exceptional case the distance between the points of crossing-over may have been as great as nineteen units distance.

TABLE XXV.—CLASSIFICATION OF FACTOR COMBINATIONS TRANSMITTED BY FEMALES OF DROSOPHILA HAVING THE GENETIC CONSTITUTION $(ywA'b_iC_lvmsrfb'X)(Yw^ea'B_jc_lVMSRFB'X)$

No crossing-over	186	200	386
Crossing-over between the loci	Number of yellow flies	Number of gray flies	Totals
Yellow and white	2	5	7
White and abnormal	3	5	8
Abnormal and bifid	4	11	15
Bifid and club	17	27	44
Club and vermilion	46	51	97
Vermilion and miniature	7	9	16
Miniature and sable	18	19	37
Sable and rudimentary	28	38	66
Rudimentary and forked	..	5	5
Forked and bar	..	1	1
Total single cross-overs			296

Double crossing-over			Totals
Y and W : C_l and V	1	..	1
Y and W : M and S	..	1	1
Y and W : S and R	1	1	2
Y and W : R and F	1	..	1
W and A' : C_l and V	1	..	1
W and A' : R and F	1	..	1
A' and B_i : C_l and V	..	1	1
A' and B_i : S and R	1	..	1
B_i and C_l : M and S	1	1	2
B_i and C_l : S and R	4	3	7
C_l and V : V and M	..	1	1
C_l and V : S and R	7	1	8
C_l and V : R and F	2	..	2
C_l and V : F and B'	1	..	1
Total double cross-overs			30

Interference.—Interference is merely a consequence of the sectional mode of chromatin interchange between homologous chromosomes. The term is used to designate the observed fact that when crossing-over takes place at a particular point in the chromosome the regions for some distance on both sides are protected from coincident crossing-over. The operation of interference is well illustrated in Muller's data, although the numbers are not sufficient to warrant a quantitative determination of its effect. With long distances interference decreases, which is in accordance with expectation. Even for relatively long distances, however, as for the loci W, M and B' which we have already considered in detail there is still some evidence of interference. Based purely on the laws of chance, if crossing-over occurs between *W* and *M* in 33.1 per cent. of cases and between *M* and *B'* in 20.5 per cent., then the chance of coincident crossing-over is equal to the product of the independent chances of crossing-over. This gives a value of 6.8 per cent. which is slightly greater than the value 5.05 per cent. calculated from the experimental data.

A three-point experiment involving shorter distances, however, gives a clearer idea as to the extent of interference. Morgan and Bridges have reported such an experiment involving the loci for vermilion, sable, and bar with the results given in Table XXVI. From this table the total percentage of crossing-over between vermilion and sable is 9.8 per cent. and between sable and bar 13.8 per cent. The expected percentage of double crossing-over for these values obtained by taking 9.8 per cent. of 13.8 per cent. would be 1.35 per cent. The observed amount of double crossing-over, 0.25 per cent., is only about one-fifth of this value.

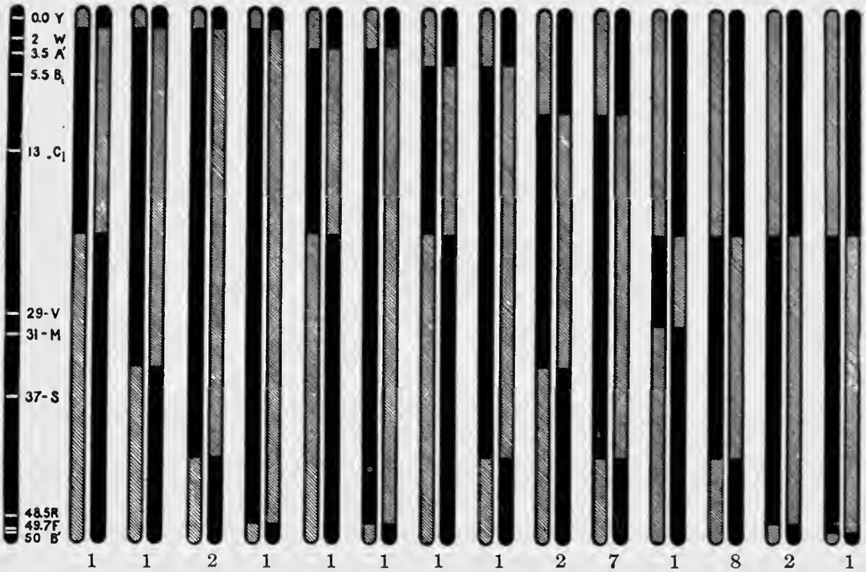


Fig. 56.—Diagram showing types of double crossing-over in females of Drosophila heterozygous for twelve sex-linked factors. The figures below indicate the number of times the type occurred in 712 cases. (The loci indicated in the "map" at the left are only approximately correct according to recent data of Morgan and Bridges, but they are sufficiently accurate for the purpose of this diagram.)

That interference is normally to be expected from the method of chromatin interchange in synapsis may be seen clearly by a consideration of Fig. 57. Thus if the chromosomes have a modal length in loop twisting about each other in synapsis, then a crossing-over at point *B*

TABLE XXVI.—LINKAGE OF VERMILION, SABLE, AND BAR IN DROSOPHILA

Characters	Non-cross-overs	Single cross-overs between		Double cross-overs
		Vermilion and sable	Sable and bar	
Gray red normal	755	110	140	4
Gray vermilion normal	734	92	151	1
Sable red normal	724	97	131	4
Gray red bar	845	87	126	4
Gray vermilion sable	608	80	123	3
Gray vermilion bar	800	95	129	1
Sable red bar	665	81	107	1
Vermilion sable bar	641	74	108	3
Totals	5,772	716	1,015	21
Percentages	76.7	9.53	13.49	0.28

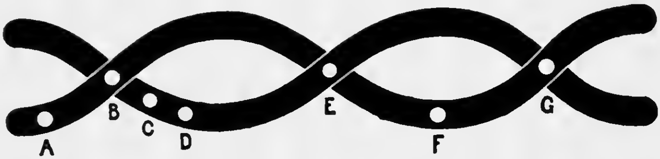


FIG. 57.—Diagram to illustrate interference in crossing-over.

would protect the loci *A*, *C*, and *D* on either side of it from crossing-over because there would be no close twisting of the chromosomes at these points. As we move on toward *E*, however, the frequency of double crossing-over would become greater and greater until at *E* where the modal length of loop was attained double crossing-over values approaching those expected on the basis of pure chance would be obtained. Muller has actually shown that such conditions are fulfilled in his twelve-point experiments and he has been able to plot a curve showing that the observed frequency of double crossing-over gradually increases until when the modal length is reached the curve coincides with that based on pure chance. Thus we see again how another point of attack has lent support to the conception that the factors are arranged in a linear series and that the linkage relations of factors are referable to the mechanical consequences of relative positions in the linear series.

Bridges points out that interference stands in about the same relation to linkage as linkage does to free Mendelian assortment. Also that the development of the idea of interference is an illustration of the advantage of the chromosome hypothesis. The existence of this phenomenon was originally deducted by Muller and Sturtevant from a consideration of linkage as a chromosome hypothesis.

Linkage Phenomena in Other Plants and Animals.—Our extended discussion of linkage relations has been based practically entirely on *Drosophila ampelophila* because the factor analysis in this species provides us with a body of data incomparably superior to that provided by any other species. Nevertheless there are other scattered cases of linkage in many species of plants and animals.

In plants Bateson first described the phenomenon of linkage in sweet peas for the characters round pollen and red flower color. Later the factor for hooded standard was found to be linked to the factors for these two characters. Later Punnett discovered linkage in a second group of factors consisting of those for green axils, cretin flower shape, and sterile anthers. Gregory has described a group of five factors in the Chinese primrose, those for red stigma, red flower color, long style, dark stems, and light corolla tube. In garden peas, Vilmorin and Bateson have both reported linkage between the factors for round as opposed to wrinkled seed and tendrilled as opposed to non-tendrilled or "acacia" leaves, and Hoshino has suggested coupling between red flower color and a factor for late flowering. Very recently O. E. White has investigated or compiled the data on thirty-five factor differences in Pisum and has presented data for four linked groups of characters. In the garden snapdragon, Baur found linkage between the factors for red flower color and for the "picturatum" type of color pattern in the flower and also clear cut evidence of linkage between some other factors. Surface has shown that in oats the factors for pubescence on the back of the lower grain, pubescence on the back of the upper grain, and black grain color are closely linked. Enough cases have also been reported for other plants to demonstrate that linkage relations are of general occurrence in plants.

In animals, Castle and Wright have suggested that linkage occurs in rats between the factors for red eye-color and pink eye-color. A clear case also has been established by Tanaka in the silkworm moth in which a series of factors for larva pattern are linked to factors for yellow and white cocoon color. Besides these cases there are a large number of cases of sex-linked inheritance in many animal forms. These will be discussed in Chapter XI.

It is clear from what we have stated above that aside from our knowledge of linkage in Drosophila, we have not progressed far in the investigation of linkage relations. Several factors have contributed to this condition. Most of the forms which have been used in genetic investigations have a larger number of chromosomes than Drosophila, a fact which considerably complicates such investigations. Most genetic data have been obtained from experiments which involve but few factors. If the chromosome number is large, the chances of such experiments showing factor linkage are slight. Finally there are experimental difficulties in the way of securing an adequate body of data for most animals and for practically all plants. It is necessary to conduct most technical investigations in heredity with relatively meager financial support, consequently the expenditures necessary to obtain sufficient data of this kind would be prohibitive for most of the larger animals and plants. Moreover, on account of the time required to raise a sufficient number of generations and to classify the individuals a considerable time must elapse before a body of data can be gathered in any species sufficient to submit it to the critical tests necessary to establish the chromosome theory. Drosophila with its prolific breeding tendencies, short life cycle, and ease of handling provides a form far superior to any other thus far investigated for the elucidation of factor relations in general. It is safe to say that our ideas of linkage for some time to come will be largely determined by the results of the Drosophila investigations. Particularly is this true because thus far none of the linkage phenomena exhibited by other animals and by plants have yielded evidence contradictory to the chromosome theory. The number of factors which have been investigated in several species exceeds the number of pairs of chromosomes, nevertheless in no single case has there been a clear demonstration that the number of independently Mendelizing factors exceeds the number of pairs of chromosomes. Moreover, those cases of linkage which have been discovered are largely of factors for wholly unrelated characters, just as in Drosophila. Added to this the ratios are of the same diverse orders of magnitude and the linkage relations in general show no essential difference from those which are displayed by Drosophila. It would be nothing short of inconceivable, in fact, that the conclusions reached from the Drosophila investigations are not applicable in all their essential features to plant and animal forms in general.

On the basis of the sweet pea and Primula investigations, the English school of geneticists, represented particularly by Punnett and Trow, has developed a theory of linkage very different from that outlined in this chapter, which is called reduplication. According to this hypothesis segregation occurs in a series of cell divisions preceding the reduction divisions, and for linked factors gives gametic series mostly of the form

$$\text{For coupling } (n-1):1:1:(n-1)$$
$$\text{For repulsion } 1:(n-1):(n-1):1.$$

In these ratios n is some power of two. Interaction of two such series may give secondary reduplications which give different values for the terms of the ratio. This theory of linkage cannot, however, lay claim to the experimental support which the chromosome theory has obtained, nor is it based on any known cytological phenomena. The series of ratios which lent original support to the theory appear to be no more frequent than should be the case on the basis of chance, and many which are supposed to fall into the series have been placed there on evidence which is entirely inadequate. The large series of linkage values which have been obtained in Drosophila demonstrate clearly that all intermediate ratios can be obtained, and since all other conditions are satisfied by the chromosome theory it seems unreasonable to give it up for an hypothesis which has no cytological support and an uncertain amount of experimental support. Moreover, it may be safely stated that all cases of linkage thus far reported may be explained according to the chromosome theory of linkage.

The mathematical relations existing in linkage phenomena are of interest because they provide a method of determining the genetic relationships involved in certain cases of somatic correlations. If two factors are linked in inheritance it follows that a larger proportion of the population will display the corresponding two characters than would be the case, if the factors were inherited independently. Consequently character correlations of this type are an index to factor linkage.

In Tables XXVII and XXVIII the results of various strengths of factor linkage and the consequences with respect to the gametic and phenotypic ratios are given. These tables show clearly that the only satisfactory method of determining the presence of linkage and its value is to cross back the heterozygous individual to individuals recessive for both factors. In such crosses the phenotypic ratio corresponds exactly to the gametic ratio, and it is, therefore, possible to determine the percentage of crossing-over by this method with a much greater degree of precision than from ordinary F_2 populations. When the two dominant factors enter the cross from opposite sides it is practically impossible to determine the linkage values by simply mating F_1 individuals together, for comparatively large differences in linkage value may affect the phenotypic ratio so slightly that the deviations, in small populations at least, might be ascribed merely to the operation of the laws of chance. The significant feature of such ratios is the small proportion of double recessives which appear. Thus with crossing-over values exceeding 20 per cent., this class practically disappears in experiments involving the usual number of individuals in a population. Moreover, matings in species which display crossing-over only in the sex-homozygotes as shown in Table XXVIII give the ratio 2:1:1 for all percentages of crossing-over when one dominant factor enters the cross from one parent and the other dominant factor from the other parent. A careful consideration of these two tables will show clearly how difficult it is to determine linkage values precisely except by properly planned experiments, and in this difficulty lies the reason for many errors of interpretation.

TABLE XXVII.—LINKAGE RELATIONS—CROSSING-OVER IN BOTH SEXES

P_1	Percentage of crossing-over	Gametic ratio	Phenotypic ratio per thousand			
		AB:*Ab*:*aB*:*ab*	*AB*	*Ab*	*aB*	*ab*
Ab × *aB*	1	1:99.0:99.0:1	500.025	249.975	249.975	0.025
	2	1:49.0:49.0:1	500.100	249.900	249.900	0.100
	3	1:32.3:32.3:1	500.225	249.775	249.775	0.225
	4	1:24.0:24.0:1	500.400	249.600	249.600	0.400
	5	1:19.0:19.0:1	500.625	249.375	249.375	0.625
	6	1:15.7:15.7:1	500.900	249.100	249.100	0.900
	7	1:13.3:13.3:1	501.225	248.775	248.775	1.225
	8	1:11.5:11.5:1	501.600	248.400	248.400	1.600
	9	1:10.1:10.1:1	502.025	247.975	247.975	2.025
	10	1: 9.0: 9.0:1	502.500	247.500	247 500	2.500
	20	1: 4.0: 4.0:1	510.000	240.000	240.000	10.000
	30	1: 2.3: 2.3:1	522.500	227.500	227.500	22.750
	40	1: 1.5: 1.5:1	540.000	210.000	210.000	40.000
	50	1: 1 : 1 :1	562.500	187.500	187.500	62.500
AB × *ab*	40	1.5:1:1: 1.5	590.000	160.000	160.000	90.000
	30	2.3:1:1: 2.3	622.500	127.500	127.500	122.500
	20	4.0:1:1: 4.0	660.000	90.000	90.000	160.000
	10	9.0:1:1: 9.0	702.500	47.500	47.500	202.500
	9	10.1:1:1:10.1	707.025	42.975	42.975	207.025
	8	11.5:1:1:11.5	711.600	38.400	38.400	211.600
	7	13.3:1:1:13.3	716.225	33.775	33.775	216.225
	6	15.7:1:1:15.7	720.900	29.100	29.100	220.900
	5	19.0:1:1:19.0	725.625	24.375	24.375	225.625
	4	24.0:1:1:24.0	730.400	19.600	19.600	230.400
	3	32.3:1:1:32.3	735.225	14.775	14.775	235.225
	2	49.0:1:1:49.0	740.100	9.900	9.900	240.100
	1	99.0:1:1:99.0	745.025	4.075	4.075	245.025

TABLE XXVIII.—LINKAGE RELATIONS—CROSSING-OVER ONLY IN THE SEX HOMOZYGOTE, NON-SEX-LINKED FACTORS

P_1	Percentage of crossing-over	Gametic ratio	Phenotypic ratio per thousand			
		AB:*Ab*:*aB*:*ab*	*AB*	*Ab*	*aB*	*ab*
Ab × *aB*	*n*	$\frac{100-n}{n}:1:1:\frac{100-n}{n}$	500	250	250	0
AB × *ab* or *ab* × *AB*	1	99.0:1:1:99.0	747.5	2.5	2.5	247.5
	2	49.0:1:1:49.0	745.0	5.0	5.0	245.0
	3	32.3:1:1:32.3	742.5	7.5	7.5	242.5
	4	24.0:1:1:24.0	740.0	10.0	10.0	240.0
	5	19.0:1:1:19.0	737.5	12.5	12.5	237.5
	6	15.7:1:1:15.7	735.0	15.0	15.0	235.0
	7	13.3:1:1:13.3	732.5	17.5	17.5	232.5
	8	11.5:1:1:11.5	730.0	20.0	20.0	230.0
	9	10.1:1:1:10.1	727.5	22.5	22.5	227.5
	10	9.0:1:1: 9.0	725.0	25.0	25.0	225.0
	20	4.0:1:1: 4.0	700.0	50.0	50.0	200.0
	30	2.3:1:1: 2.3	675.0	75.0	75.0	175.0
	40	1.5:1:1: 1.5	650.0	100.0	100.0	150.0
	50	1 :1:1: 1	625.0	125.0	125.0	125.0

CHAPTER VII

THE NATURE AND EXPRESSION OF MENDELIAN FACTORS

In previous chapters the formal relations which exist in the transmission of factors from parent to offspring have been discussed. It has been shown that these relations may be ascribed to the locus positions which factors occupy in the chromosomes. This single assumption taken together with the known behavior of the chromosome mechanism in its cycles explains very simply the two great categories of inheritance with respect to distribution of factors, namely independent segregation and linkage. Obviously, however, these are merely formal considerations, it is of considerable importance to know something about the factors themselves and the physiological interactions which they display with one another in the development of characters in the individual. It is to this problem that this and following chapters are addressed.

It is true that as yet we know next to nothing about the factors themselves with respect to their physical and chemical constitution, we know them merely by their actions. We regard them as the loci arranged in a linear series in the chromosome, we know they have certain characteristic effects in development and by these effects we recognize them. It is important to note that our knowledge of their behavior even is based on factor differences, not on a study of the factors themselves. Thus we know that a certain locus in the germinal substance in Drosophila is concerned with the production of red eye color because when it is changed in a particular fashion, the eye color developed is no longer red, but white. We have no means of knowing how profound the relation of this factor to the other factors in the system is, nor can we judge as to the nature of the change in the locus by which the course of development was shifted from red to white in the production of eye color in Drosophila. Nevertheless a few things at least are known concerning the effects of factors in development and even in this vague field more and more facts are being discovered all the time.

Factors are the genetic representatives of certain characters. Thus if a fly has a genetic constitution containing, among other factors for eye color, the factor *w*, then it will develop white eyes. In this particular case the eye color is practically the only character affected. Similarly in corn, if a mutation occurs in one of the basic aleurone color factors, for example, a change in the chromogen factor *C* to *c* then that corn thus developing is white as respects aleurone color. Here apparently only aleurone color is concerned. Similarly in other cases much more insignificant changes may be connected with definite factor differences. Thus a forked condition of the spines in Drosophila is dependent upon a definite factor difference, a recessive factor in this case. One could go on and recount indefinitely factors which cause only very slight character changes. Any character change, therefore, however slight, may be based on genetic factor differences. The only valid genetic test is the pedigree breeding method, at the same time giving due consideration to environmental influences which may obscure or temporarily cover entirely the underlying genetic differences.

Very great somatic differences may also be dependent upon differences in single factors in individuals. Perhaps the most striking of these are large size differences such as are found in beans, peas, and even in animals at times. Thus in beans the main difference between pole and bush beans is dependent upon a single factor difference. The difference between tall and dwarf varieties of peas is of a similar nature and has been fully discussed above. Certain types of dwarfing in man appear to depend upon single factor differences and in Drosophila there are factors which determine the production of giant races and others of dwarf races. Moreover, factor differences show striking relations to one another. Thus in Drosophila there are factors for eye color which change the shade of red in the eye, some resulting in a darker and many in lighter shades, but there is also a single factor difference which results in white eyes or in other words in the entire loss of color in the eyes, and even further there is a factor for an eyeless condition, which when a part of the genetic constitution of a fly results in the production of mere rudiments of eyes or even none at all.

Very frequently single factors may cause such profound changes as to alter the entire appearance of the individual and interfere more or less with all its functions. Such, for example, is the case with fasciated forms in plants, some of which at least are dependent upon simple factor differences. A striking case of this type has been reported by O. E. White in tobacco. In this fasciated variety the number of leaves is greatly increased, from 24 to as high as 80, the stem is flattened and exhibits a characteristic fasciated condition, and the flowers are very abnormal. The abnormality of the flowers extends to every part, the numbers of sepals, petals, stamens, and ovary locules are increased, and striking deformities of these parts give evidence of the disturbing effect of the factor. The abnormal effects of the factor are not confined to external characters, but cytological studies show that the division figures, particularly in reduction, show marked irregularities which may be expressed in an increase in the number of chromosomes, or in a breaking down of cells during division, or in various other peculiar phenomena. The abnormal variety also displays a certain degree of sterility, probably associated with abnormal cell division. In spite of all the differences both external and internal which this mutation displays when compared with the normal variety from which it arose, its behavior in inheritance shows clearly that only a single factor difference is involved. When crossed with the normal type, the F_1 is intermediate, and in F_2 segregation is in approximately the ratio 1 abnormal:2 intermediate:1 normal. The F_2 homozygous segregants are exact duplications of the original pure forms, the normal segregants are in every respect as normal as the normal parent and the abnormal segregants are no less abnormal than those of pure abnormal races. The heterozygous forms are throughout clearly distinguishable from abnormal homozygotes on the one hand and normal homozygotes on the other. Taken as a whole it would be difficult to find a better example of the profound effects which may result from a single factor difference.

Lethal factors also exist which affect vital organs and result in the death of individuals homozygous for them. Excellent examples of such disturbing factors are those which affect the production of chlorophyll in plants. A number of species of plants at times produce races in which under experimental conditions approximately one-fourth of the seedlings are yellow or white instead of green and hence die soon after germination. Such strains are particularly common in cereals, and in maize in almost any variety when a large number of self-fertilized ears are tested, a number of strains may be found which produce seedlings about one-fourth of which die as soon as the food supply of the endosperm is exhausted on account of deficiency in chlorophyll production.

Since the homozygous recessive forms of albino strains die soon after germination, it follows that such strains must be propagated by means of the heterozygous individuals. The operation of such a scheme is illustrated in the following case. The original self-fertilized ear gave on germination 3 fully green seedlings to one which was pure white and which died shortly after germination. If we call the albino factor g in this case and its normal allelomorph present in the green plants G, we may assume that this ear was produced by a heterozygous green plant of the constitution Gg. Half the pollen grains of such a plant carry the factor G and half the factor g; and likewise in the ovules half bear the factor G, and half g. By self-pollination of such a plant, random fertilization of the ovules by the pollen grains results in grains in the ratio $1GG{:}2Gg{:}1gg$. Although grains of these different genotypes are indistinguishable in appearance, those of the genetic constitution GG and Gg produce fully green plants, while those which are gg produce albino seedlings which are incapable of independent existence on account of their lack of chlorophyll. Those green plants of the genetic constitution *Gg* when self-fertilized produce grains one-fourth of which again give albino seedlings as in the previous generation. The green plants of the genetic constitution *GG*, however, since they are homozygous for the factor *G* produce nothing but green plants in succeeding generations.

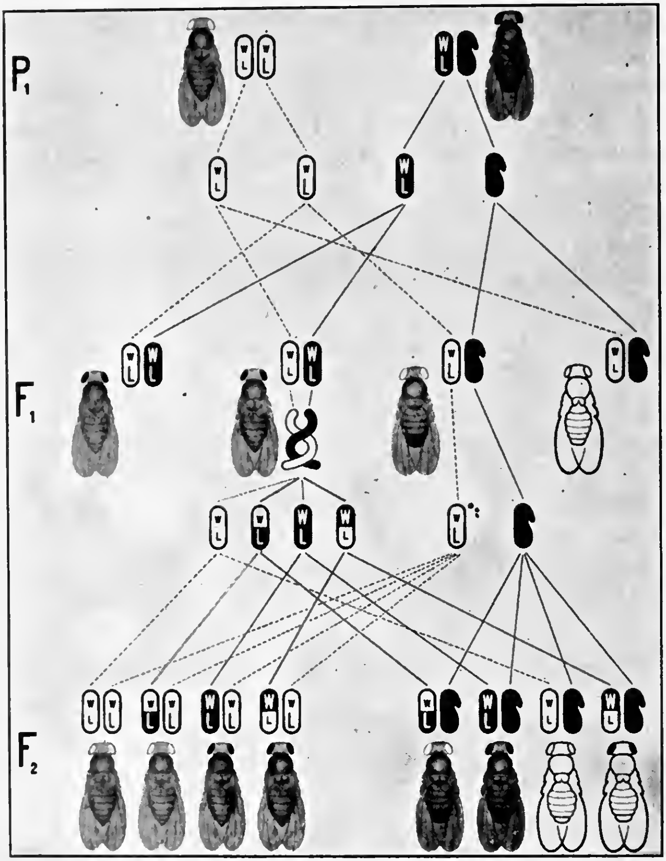


Fig. 58.—Disturbance of phenotypic ratio by a recessive sex-linked lethal factor. Compare with Fig. 36.

Morgan has demonstrated the existence of a number of lethal factors in Drosophila. These factors result in the death of the individuals at some time before they reach the adult stage. They are particularly found among sex-linked factors, because sex-linked recessive factors have no normal allelomorphs in the male. The results of the presence of sex-linked lethal factors is shown diagrammatically in Fig. 58. As in corn, the strains are propagated by means of heterozygous individuals. Since such individuals can only be females in the case of sex-linked factors in Drosophila, it follows that the strains must be propagated by means of females heterozygous for the factors. The diagram shows how such lines are maintained. A heterozygous female produces eggs half of which bear the normal factor L, and half bear the lethal factor l. When mated to a normal male the X-chromosome of which bears the normal factor L, half the daughters are normal homozygotes and half are heterozygous for l. Half the males receive an X-chromosome bearing the factor L, and consequently are normal and half receive an X-chromosome bearing the factor l. These latter die before reaching the adult stage, consequently a heterozygous female produces flies two-thirds of which are females and one-third males The unusual sex-ratio provides a convenient test for heterozygous females and by this means the strain may be continued.

Some of the consequences of the presence of lethal factors when linked with other factors are of importance because of the disturbances to which they give rise in Mendelian experiments. An illustration of such effects may be taken from Lethal III in Drosophila which is located at about the locus 26.5 in the X-chromosome. It is about 25 units distance from the locus for white eyes. If now a white-eyed female heterozygous for Lethal III be crossed with a red-eyed male, as shown diagrammatically in Fig. 58 all the females will be red-eyed but only half will be homozygous for the normal factor L_3. These females, homozygous for L_3, produce flies in the ratio of 1 red ♀ :1 red ♂ :1 white ♀ :1 white ♂ when mated to their brothers. The other half of the F_1 females, on the other hand, will be heterozygous for L_3 and consequently, since crossing-over takes place in 25 per cent. of cases, they produce gametes in the ratio $3(wl_3X):3(WL_3X):1(Wl_3X):1(wL_3X)$. When such a female is mated to an F_1 male fly the ratio is distinctly different from that obtained with the other females, in this case 4 Red ♀ :3 Red ♂ :4 White ♀ :1 White ♂. The ratio of sexes in this latter case is 2 female: 1 male and the same is true in F_1. The sex ratio gives an immediate clue to the disturbing factor and leads to a true explanation of the cause of the disturbance.

Manifold Effects of Factors.—In a preceding section of this chapter it has been shown how far reaching may be the effects of single Mendelian factors, and in the present account it is intended to deal specifically with what Morgan has termed the manifold effects of single factors. Careful study has revealed the fact that although factors are restricted in their conspicuous results to certain characters, nevertheless they may have other less noticeable results which are none the less definite and constant. Baur has observed for example in Antirrhinum that the factor which produces pure white blossoms also yields plants which are distinctly weaker in growth and are smaller than those which possess the normal allelomorph for this factor. Plants possessing the recessive factor may be recognized in the seedling stages by a peculiar coloration of the edges of the leaves and even better by the characteristic epidermis of the leaf blades.

Manifold effects of factors are probably very common but very little definite work has been reported along this line. Morgan, however, has called attention to some cases in Drosophila. Thus there is a factor for club wings, and in strains of this type flies appear the wing pads of which fail to unfold after emergence. But this character is not constant, in fact about 80 per cent. of the flies in a pure strain have normal wings. Subsequent study, however, has shown that in such stocks the absence of spines on the side of the thorax is a constant differential test. These differences are shown in the accompanying figure (59). By employing the absence of spines as the differential test it is possible to classify mixed populations of "normal" and "club" flies accurately without paying any attention to wing characters.

The Variability of Factor Expressions.—Factors also vary in the effects which they produce. We have pointed out that in pure strains of club-winged Drosophila (Fig. 59) only about 20 per cent. of the flies exhibit the unfolded wing pad characteristic of the club mutation. On the other hand, the absence of spines on the side of the thorax determined by the same factor appears to be an invariable characteristic of the club-winged flies.

Sometimes this variability in factor expression may be traced to a definite environmental condition. This is certainly true of the red Primula which produces red flowers under ordinary temperature conditions, but which when placed under abnormally high temperatures produces white flowers. The production of chlorophyll in some strains of corn, likewise, depends on generally favorable environmental conditions. This has been demonstrated by Miles for the yellow-green type of chlorophyll reduction. Plants heterozygous for this factor produce grains three-fourths of which produce fully green plants on germination, but the other one-fourth produce pale yellowish seedlings with a tinge of green. The yellowish seedlings die under ordinary conditions, but in particularly favorable surroundings they continue to live and soon develop the normal chlorophyll coloration. If self-fertilized, they produce only yellowish plants which must again be given very favorable conditions for the production of the normal green leaf color.

In Drosophila a number of environmental relations have been described. Thus Morgan has studied in considerable detail the influence of environment on the development of abnormal abdomen. Flies with the dominant factor for abnormal abdomen should all exhibit the characteristic type of deformed abdomen shown in Fig. 60; but this is not the case, for pure mutant stocks constantly show a high percentage of flies with normal abdomens. This variability in abdomen characters has been found to depend upon the condition of the food. When the food is moist a high percentage of flies have abnormal abdomens, but when the larvæ are raised on dry food nearly all of them have normal abdomens.

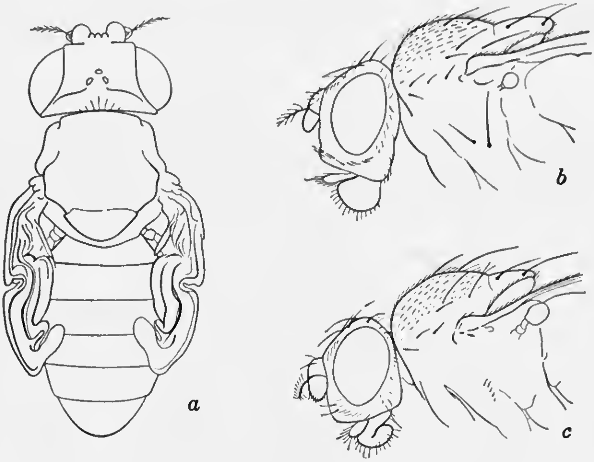


Fig. 59.—Club-winged Drosophila. At *a* characteristic unfolded wing pads. At *c* the absence of spines on the side of the thorax is shown in comparison with the normal conditions, *b*. (*From Morgan.*)

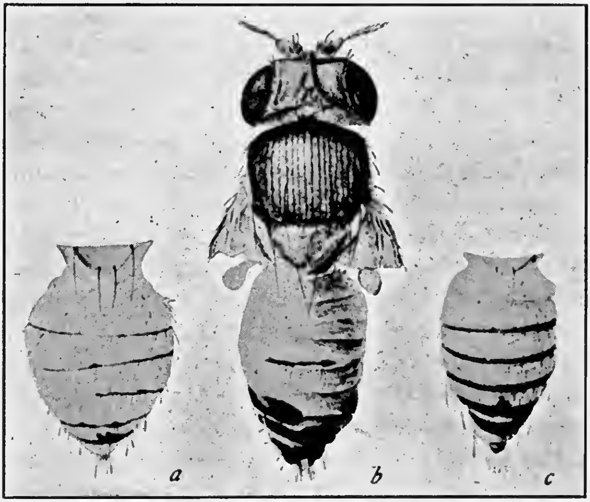


Fig. 60. Mutant type of *Drosophila ampelophila* called abnormal abdomen (the wings have been cut off); *a*, female; *b*, male; *c*, female that approaches the normal type. Development of this character is dependent upon moisture. (*From Morgan.*)

On account of these relations the expected Mendelian behavior of this factor in crosses with normal flies is obscured in cultures grown on dry food, but with moist food Mendelian expectations are completely fulfilled.

Moreover, the variability in the expression of the abnormal condition of the abdomen is not connected with any variability in the factor itself but is merely an expression of a variable reaction of the factor to the environment. Normal flies possessing the factor for abnormal abdomen when given moist food produce offspring just as abnormal as those from abnormal flies. The factor itself is invariable just as in a chemical system the elements which are in the system are invariable but may produce different results according to the dilution, temperature, and other conditions under which the reaction is going on.

The reduplicated stock in Drosophila shows similar relations to environmental conditions. The characteristic feature of this mutation is the production of extra legs or parts of legs. At normal temperatures very few flies show this condition, but when strains are grown at 10°C. a high percentage of them show supernumerary legs. As with abnormal abdomen and moist food, so Miss Hoge has shown that with temperatures below 10° these flies satisfy Mendelian expectations when crossed with normal strains, but at ordinary temperatures of cultivation the phenomena are entirely obscured.

Duplicate Factors.—A number of cases are known where similar or identical effects are produced by factors located in different loci in the germinal substance. A case in point which has been subjected to excellent analysis is that for capsule form in the common shepherd's purse (Bursa). When the form having flattened triangular capsules is crossed with that having top-shaped seed pods, the F_1 plants produce triangular capsules. When the F_2 is grown approximately 15 produce triangular capsules to one which produces top-shaped capsules.

Such a result may be explained by assuming that two recessive factors, *c* and *d*, combine to produce the top-shaped capsule. The top-shaped race then is of the genetic constitution *ccdd*, and the contrasted triangular-shaped race is *CCDD*. The factors *C* and *D* are fully dominant and produce identical results, namely plants bearing the typical triangular-shaped seed pods. Consequently selfing F_1 plants of the genetic constitution *CcDd* gives F_2, 15 plants with triangular pods to 1 with top-shaped pods. The checkerboard for this case is shown in Fig. 61.

If this analysis is valid for the inheritance of capsule form the F_3 and subsequent generations should display a characteristic type of behavior as shown in the checkerboard. In each square is given the ratio in which the particular genotype should segregate in F_3. Thus it will be seen that

7 families should breed true for triangular capsules.
4 families should give 15 triangular:1 top-shaped.
4 families should give 3 triangular:1 top-shaped.
1 family should breed true for top-shaped capsules.

Shull applied this test to his cultures and obtained substantial agreement with theory throughout. Fig. 62 gives a graphic summary of his experimental results.

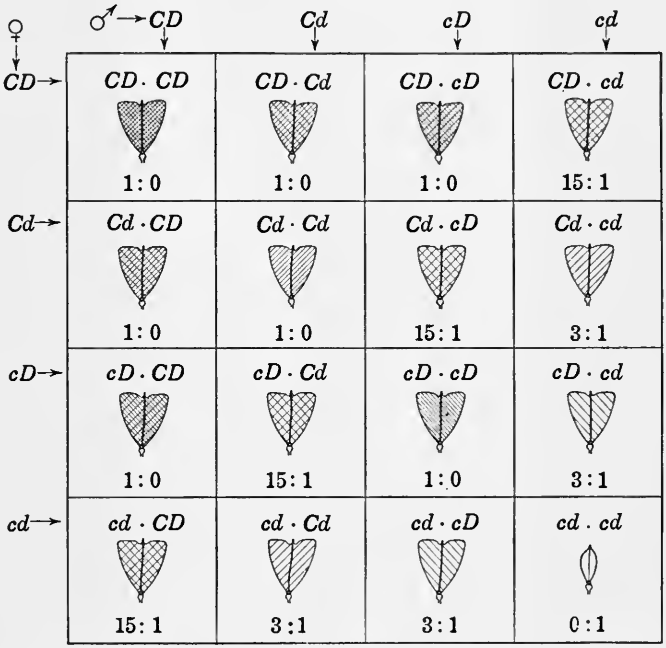


FIG. 61.—Checkerboard diagram to visualize the genetic relations in a dihybrid F_2 family of *Bursa bursa-pastoris* × *Heegeri*, in respect to the capsule-characters. The capsules figured in each square indicate by their outline their phenotype, and by their oblique ruling their genotype, the gene C being represented by lines from upper right to lower left, and D from upper left to lower right. Homozygotes are densely lined, heterozygotes more sparsely. The ratios indicate the expectation in F_3 when a plant having the genotypic constitution indicated in the same square, is self-fertilized. (*After Shull.*)

When three duplicate factors are concerned in a hybrid the ratio in F_2 is 63:1, with four factors, 255:1, and so on. The first case of duplicate factors was that described by Nilsson-Ehle in wheat. Here the red color of certain races of wheat depends on the presence of three dominant Mendelian factors so that such races are to be represented by the genetic formula *RRSSTT* and the contrasted white race by *rrsstt*. The F_1 of a cross between two such races is of a pale red color intermediate between the parental red and white, and in F_2 all shades of red are found from very pale to about the same depth of color as the parent race. In the actual experiment among seven families comprising a total of 440 plants only one produced white grains, but the F_3 generation demonstrated the adequacy of the three-factor analysis. The intermediate shade of red produced in F_1 and the varying shades produced in segregation depend on the cumulative effect of the color factors. In-

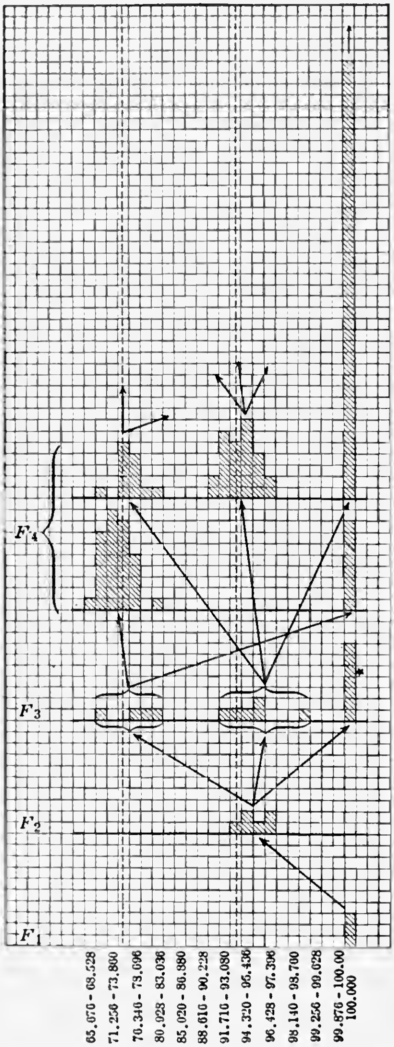


FIG. 62.—Resumé of ratios found in 142 families in the first five generations following the cross between *Bursa bursa-pastoris* and *B. Heegeri*. Each square represents a possible family, the position of a family being determined by the percentage of plants with triangular capsules as indicated at the base of the figure. (*After Shull.*)

stead of displaying complete dominance for any one member of the factor system as Shull found for the triangular capsule factors in Bursa, the factors here have a certain effect in color production which is additive,

			RrSsTt			
			RrSsTt			
			RrSsTt			
			RrSsTt			
			RrSsTt			
		rrSsTt	*RrSsTt*	*RrSSTt*		
		rrSsTt	*RrSsTt*	*RrSSTt*		
		rrSsTt	*RrSsTt*	*RrSSTt*		
		rrSsTt	*rrSsTT*	*RrSSTt*		
		RrssTt	*rrSsTT*	*RrSsTT*		
		RrssTt	*rrSSTt*	*RrSsTT*		
		RrssTt	*rrSSTt*	*RrSsTT*		
		RrssTt	*RRssTt*	*RrSsTT*		
		RrSstt	*RRssTt*	*RRSsTt*		
	rrssTt	*RrSstt*	*RrSStt*	*RRSsTt*	*RrSSTT*	
	rrssTt	*RrSstt*	*RrSStt*	*RRSsTt*	*RrSSTT*	
	rrSstt	*RrSstt*	*RrssTT*	*RRSsTt*	*RRSsTT*	
	rrSstt	*rrssTT*	*RrssTT*	*rrSSTT*	*RRSsTT*	
	Rrsstt	*rrSStt*	*RRSstt*	*RRssTT*	*RRSSTt*	
rrsstt	*Rrsstt*	*RRsstt*	*RRSstt*	*RRSStt*	*RRSSTt*	*RRSSTT*
0	1	2	3	4	5	6

FIG. 63.—F_2 squares of the checkerboard of a cross of red (*RRSSTT*) × white (*rrsstt*) wheat arranged in classes according to the depth of color displayed by the phenotypes.

i.e., two factors produce twice the depth of red coloration in the grain that one produces and all six are necessary for the production of the full color of the parent red wheat. Consequently there are six shades of red in an F_2 population possessing various frequencies with respect to the proportionate number of individuals which display a particular shade of color as shown in the foregoing diagram (Fig. 63). Factors which display summation effects have been conveniently called cumulative factors.

Besides dominant factors which produce similar or identical somatic effects a large number of recessive factors are known which display the same phenomena. The first example of this type which was worked out was that in sweet peas described by Bateson. In sweet peas there are a number of different whites which phenotypically cannot be distinguished from one another. The fact that they are genetically different is shown when they are crossed together, for then instead of producing white sweet peas the F_1 plants bear colored flowers, the particular color depending upon the genetic constitutions of the whites which were crossed. Since the simultaneous action of two dominant factors, neither one of which by itself can produce any color, is necessary for color production, Bateson has proposed to call such factors complementary factors.

The same relations have been found to exist in the production of aleurone color in grains of corn. Certain white varieties of corn are known which when crossed together give red or purple corn according to the genetic constitutions of the races which were crossed. As with dominant duplicate factors this sort of phenomenon gives peculiar Mendelian ratios in F_2 because of the fact that many of the genotypes are indistinguishable phenotypically. Thus for example we may represent a purple corn by the formula *CCPP*, these factors being particularly concerned in the production of aleurone color. A mutation in the locus *C* would give a white corn of the genetic constitution *ccPP*, and likewise a mutation in the locus *P* would give a white corn of the genetic constitution *CCpp*. Phenotypically these two varieties of white corn are indistinguishable, but from a genotypic standpoint the factors for white are located in different chromosomes in the two varieties. Accordingly when two such white varieties are crossed, the F_1 is of the genetic constitution *CcPp*. Since *C* and *P* are both completely dominant over their allelomorphs *c* and *p* such a corn will be purple because the complete set of factors necessary for the production of purple aleurone color has been brought together by crossing these two genetically different whites.

The checkerboard for the F_2 of such a cross is shown in Fig. 64. It will be observed that the phenotypic ratio in F_2 is 9 purple:7 white. This is merely a modification of the typical 9:3:3:1 F_2 ratio, for in this cross the last three classes are phenotypically alike, although genotypically different. Of the nine purples, only one breeds true in F_3, and of the remaining eight purples, four give families which segregate in the ratio of 3 purple : 1 white, and four give families showing segregation in the ratio of 9 purple:7 white. All the whites, although of different genotypes, produce entirely white families. All these relationships are shown clearly in the checkerboard.

In Drosophila a large number of similar cases of like somatic effect have been found to be dependent upon different factors. Here the linkage values of the different factors with other factors have been determined very precisely, and moreover the mutants have for the most part arisen directly from the cultures, so that the relationships have been established much better than in any other form.

	CP	*Cp*	*cP*	*cp*
CP	*CCPP* Purple 1:0	*CCPp* Purple 3:1	*CcPP* Purple 3:1	*CcPp* Purple 9:7
Cp	*CCPp* Purple 3:1	*CCpp* White 0:1	*CcPp* Purple 9:7	*Ccpp* White 0:1
cP	*CcPP* Purple 3:1	*CcPp* Purple 9:7	*ccPP* White 0:1	*ccPp* White 0:1
cp	*CcPp* Purple 9:7	*Ccpp* White 0:1	*ccPp* White 0:1	*ccpp* White 0:1

Fig. 64.—Checkerboard of F_2 of cross white (*ccPP*) × white (*CCpp*) maize, showing phenotypes and F_3 segregation as well as genotypes.

For body color at least three similar mutant factors result in almost identical darker forms. The first of these to be discovered was the black factor which is located in the second group of factors. The factor for ebony body color is in the third group, and sable is a sex-linked factor. Although so nearly alike that a mixed population could not be certainly classified these particular races do show slight differences in coloration. Similarly nearly identical results are obtained from three different jaunty factors which cause the wings to turn up at the ends. Morgan has also pointed out other such similarities in effect of different factors which affect eye and wing characters, color, etc.

Sometimes a dominant and a recessive factor give identical phenotypic results. For an illustration of this we may again turn to aleurone color in corn. Taking into account the white dominant factor for aleurone coloration, the following genotypes may be obtained:

WWccPP = white
wwCCPP = purple
wwccPP = white
wwCCpp = white
wwccpp = white

	WCP	*WCp*	*WcP*	*Wcp*	*wCP*	*wCp*	*wcP*	*wcp*
WCP	*WWCCPP* White 0:1	*WWCCPp* White 0:1	*WWCcPP* White 0:1	*WWCcPp* White 0:1	*WwCCPP* White 1:3	*WwCCPp* White 3:13	*WwCcPP* White 3:13	*WwCcPp* White 9:55
WCp	*WWCCPp* White 0:1	*WWCCpp* White 0:1	*WWCcPp* White 0:1	*WWCcpp* White 0:1	*WwCCPp* White 3:13	*WwCCpp* White 0:1	*WwCcPp* White 9:55	*WwCcpp* White 0:1
WcP	*WWCcPP* White 0:1	*WWCcPp* White 0:1	*WWccPP* White 0:1	*WWccPp* White 0:1	*WwCcPP* White 3:13	*WwCcPp* White 9:55	*WwccPP* White 0:1	*WwccPp* White 0:1
Wcp	*WWCcPp* White 0:1	*WWCcpp* White 0:1	*WWccPp* White 0:1	*WWccpp* White 0:1	*WwCcPp* White 9:55	*WwCcpp* White 0:1	*WwccPp* White 0:1	*Wwccpp* White 0:1
wCP	*WwCCPP* White 1:3	*WwCCPp* White 3:13	*WwCcPP* White 3:13	*WwCcPp* White 9:55	*wwCCPP* Purple 1:0	*wwCCPp* Purple 3:1	*wwCcPP* Purple 3:1	*wwCcPp* Purple 9:7
wCp	*WwCCPp* White 3:13	*WwCCpp* White 0:1	*WwCcPp* White 9:55	*WwCcpp* White 0:1	*wwCCPp* Purple 3:1	*wwCCpp* White 0:1	*wwCcPp* Purple 9:7	*wwCcpp* White 0:1
wcP	*WwCcPP* White 3:13	*WwCcPp* White 9:55	*WwccPP* White 0:1	*WwccPp* White 0:1	*wwCcPP* Purple 3:1	*wwCcPp* Purple 9:7	*wwccPP* White 0:1	*wwccPp* White 0:1
wcP	*WwCcPp* White 9:55	*WwCcpp* White 0:1	*WwccPp* White 0:1	*Wwccpp* White 0:1	*wwCcPp* Purple 9:7	*wwCcpp* White 0:1	*wwccPp* White 0:1	*wwccpp* White 0:1

FIG. 65.—F_2 checkerboard for cross of white (*WWCCPP*) × white (*wwccpp*) corn. In the F_3 segregation ratio the purple is given first as in Fig. 64.

The student will be able to figure out many different relations which exist when such races are crossed. In this section only one will be considered as an illustration of the working of such a system. If a white corn, *WWCCPP*, is crossed with a white corn, *wwccpp*, the F_1 is of the genetic constitution, *WwCcPp*, and is white on account of the action of *W*. The F_2, however, shows some purple grains as will become apparent from a study of the accompanying checkerboard, Fig. 65. In F_2 such a hybrid segregates in the ratio 55 white : 9 purple, and in F_3 the families show the segregation ratios indicated in the proper squares of the checkerboard. As in the previous instance these ratios are merely modifications of the typical Mendelian dihybrid and trihybrid ratios due to the fact that many of the classes are white and hence are merged into one.

It should be apparent from the discussion in this chapter that many complex relations exist as respects the nature and expression of factors. Only some of the best established and most conspicuous cases have been discussed and some of these in rather incomplete fashion, but the material presented is sufficient to establish several facts concerning factors, namely that some factors have very minute, others very far reaching effects, that factors may affect many characters in the individual, that factors may vary in their expression in individuals, that sometimes this variability in factor expression is dependent upon definite environmental conditions and sometimes on obscure or unknown causes, and that at times different factors may have similar somatic expressions. It is difficult to treat such various matters in any systematic fashion, consequently this chapter must be regarded merely as an introduction to the general topic of factor interactions.

CHAPTER VIII

ALLELOMORPHIC RELATIONSHIPS IN MENDELISM

The present chapter is designed to deal with those relationships in which a single locus in the hereditary system is involved.

Mendel worked with seven pairs of contrasted characters and he observed that in all of these one member of the pair controlled the expression of the character when the individual was heterozygous. When tall peas are crossed with dwarf the hybrid is tall, in fact slightly taller even than the tall parent. Similarly yellow cotyledons are dominant over green, and smooth over wrinkled seed. The same is true for the other four pairs of characters. So important did this fact of dominance appear to investigators that for some time after the rediscovery of Mendelism reference was very generally made to the law of dominance, and great significance was attached to any failure to observe dominance in genetic investigations. But subsequent investigations have shown that dominance, far from being a general rule, is merely a special condition met with in certain cases of inheritance. That it is by no means universal must be conceded. How far it obtains and what other conditions are met with in its absence, we shall endeavor to show in what follows.

Dominance is a relation existing between a factor and its allelomorph such that in plants heterozygous for the factor in question the character expression is the same or approximately the same as that when the factor is homozygous. Dominance, therefore, applies only to relations existing between a pair of factors. That two contrasted characters show an intermediate condition is no evidence in itself that dominance is lacking. It must further be demonstrated that this condition is due to the fact that the character expression of a genotype *Aa* lies between that of *AA* and *aa*. Otherwise the intermediate expression of the hybrid character may be the expression merely of the action of several pairs of factors each displaying dominance for one member of each pair, but together giving an intermediate expression.

The Extent of Dominance.—Off hand it would appear that complete dominance is a very common phenomenon in genetic investigations. The seven pairs of contrasted characters in peas could hardly have displayed it in all the pairs unless it were a condition of wide occurrence and considerable significance. Otherwise we should have to consider this a remarkable case of coincidence. Likewise the oft-cited investi-

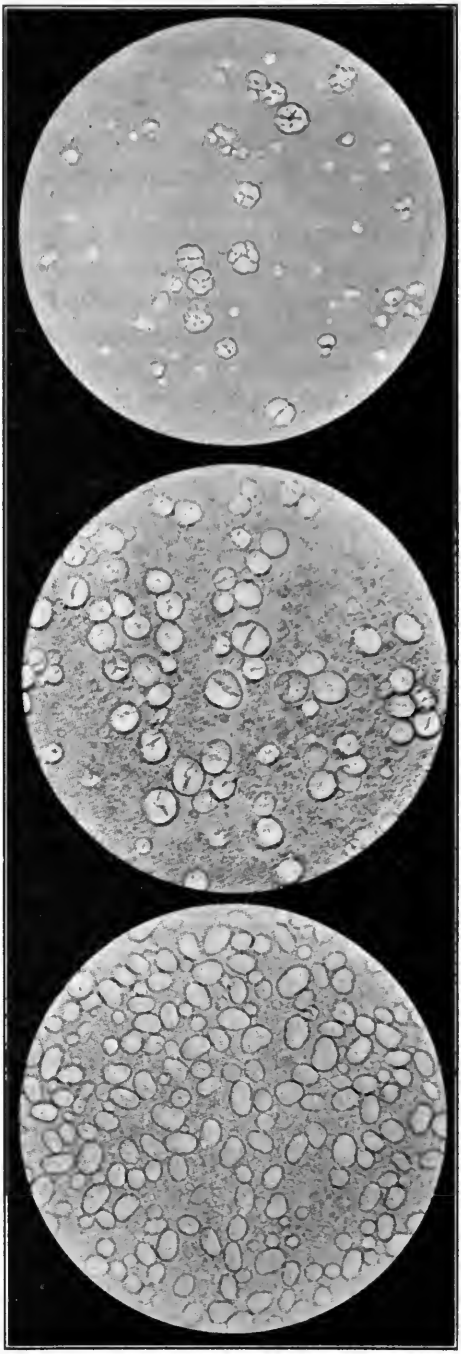


Fig. 66.—At the left, starch grains of round pea; at the right, of the wrinkled pea; and in the middle, of a hybrid between round and wrinkled peas. Magnified about 300 times. (*After Darbishire.*)

gations with Drosophila indicate that usually a normal allelomorph is dominant to a mutant factor, and in fact often to the eye completely dominant. More precise investigations indicate, however, that although for all practical purposes dominance often is so complete as to closely approximate the expression of the homozygous character due to the duplex condition of the dominant factor, still the completeness of dominance is often more apparent than real.

Darbishire has attacked this problem in the case of the cross smooth as contrasted with wrinkled peas. Mendel's experiments showed that smooth or round shape is dominant over the wrinkled shape in peas and as in other cases the dominance appears to the eye complete. Darbishire investigated the cause of the difference between round and wrinkled peas and found it associated with a difference in starch content. Thus during the development of the seed in those races possessing round seeds the sugar is almost wholly converted into starch so that when the seed is ripe and drying it retains water rather firmly and shrinks uniformly to form a round seed. Like the seeds of round races those of wrinkled peas are also round at the height of development, but in peas of such varieties the sugar is very incompletely transformed into starch. Consequently in ripening and drying they give up more water proportionally than round races and do not shrink uniformly. As a result they become very much wrinkled at maturity. This difference in the starch grains of the wrinkled pea is not only a matter of less complete transformation of sugar into starch, but is also associated with less perfect production of starch grains as shown in Fig. 66. Thus in the round races the starch grains are numerous and are large and entire. They show practically no subdivision of the grains. But in the wrinkled peas the grains are not only less numerous, but they show fissures which give them an appearance like that of the compound starch grains of some species of plants. This appearance is probably due to the fact that actual breaking down of starch grains occurs in wrinkled peas during ripening so that the grains remaining are in a partial stage of disintegration. In the hybrid between a round and a wrinkled pea, however, the condition of the starch grains is intermediate between that of the two parents. The grains are intermediate not only in number and shape but also in the degree of disintegration they display. In the contrasted pair of characters, round *vs.* wrinkled seed in peas, the dominance of round is, therefore, merely a superficial character expression. Actually the basic phenomena involved, *i.e.*, the transformation of sugar into starch, show an intermediate condition in the hybrid. The superficial character expression of this intermediate condition happens to be the same as that of the strict parental round condition, so that dominance here is merely dependent on superficial resemblance. We may well hesitate, therefore, in our judgment as to the completeness of dominance in any case until it has been examined with considerable care.

Sometimes the application of more precise character measurements will suffice to detect a difference between the homozygous and heterozygous character expression. This is shown for the case of miniature *vs.* long wings in Drosophila. In miniature-winged flies the wings reach about to the tip of the abdomen, whereas in the long-winged flies they extend considerably beyond the abdomen. The long-winged condition is dominant, to the eye completely, and there is absolutely no difficulty in segregating the long-winged flies of an F_2 population from those which have miniature wings. Nevertheless Lutz has shown that when biometrical methods are employed the length of wings of heterozygous flies compared with the length of legs is shorter than that for flies homozygous for the long-winged factor. The difference in character expression in this case is slight but it can be demonstrated by the employment of precise methods of measurement.

Intermediate Expression in the Hybrid.—From those cases in which dominance is nearly or quite complete we may next pass to those in which the character expression of *Aa* is intermediate to that of *AA* and *aa*. There are numberless instances of this kind, and they are of interest because the heterozygous class may be distinguished in F_2, so that the typical ratio obtained is $1A:2Aa:1a$, instead of $3A:1a$ as in cases where dominance occurs.

For a concrete example we may turn to Baur's case in the snapdragon. Baur and Miss Wheldale have independently conducted very extensive investigations of Mendelian inheritance in Antirrhinum. For most cases one member of a pair of contrasted characters is dominant, but when ivory is crossed with red the F_1 is intermediate in color, it is pale red or pink. When F_2 is grown it is found to consist of 1 red: 2 pink: 1 ivory. In one case among 97 plants, Baur obtained 22 red, 52 pink, and 23 ivory, a satisfactory agreement with Mendelian expectations. The actual proof for this case comes out in growing F_3. When this is done it is found that the red plants and the ivory plants give progeny which are entirely red and ivory, respectively. The pink plants on the other hand are all heterozygous and they give in F_3 and in all succeeding generations plants in the proportion of 1 red:2 pink:1 ivory. The case is very evidently one in which a single factor difference is concerned. If the factor responsible for the production of red in Antirrhinum be designated by *R*, then we may designate its allelomorph present in the ivory race by *r*. The case then works out according to the diagram in Fig. 67.

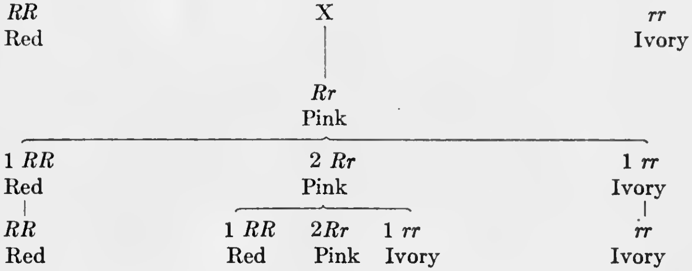


FIG. 67.—Results of crossing snapdragons with red and ivory colored flowers.

In the Four o'clock, *Mirabilis jalapa*, it appears to be the rule that heterozygous plants present visible differences from plants homozygous for color factors. For this reason in breeding experiments this plant gives a rather remarkable diversity of colors with relatively few factors involved. Thus we may start with the primary assumption that in one series of colors we have involved two pairs of factors as follows:

Y = factor for yellow colored sap.
R = factor which turns yellow sap red.

The various homozygous combinations of these two factors give four primary races which breed true as follows:

YYRR = crimson.
YYrr = yellow.
yyRR = white.
yyrr = white.

By hybridizing these races four heterozygous forms may be produced which are of the colors given below:

YYRR (crimson) × *YYrr* (yellow) gives *YYRr* = orange red.
YYRR (crimson) × *yyRR* (white) gives *YyRR* = magenta.
YYRR (crimson) × *yyrr* (white) gives *YyRr* = magenta-rose.
YYrr (yellow) × *yyrr* (white) gives *Yyrr* = pale yellow.

♂	*YR*	*Yr*	*yR*	*yr*
♀ *YR*	*YYRR* Crimson	*YYRr* Orange red	*YyRR* Magenta	*YyRr* Magenta rose
Yr	*YYRr* Orange red	*YYrr* Yellow	*YyRr* Magenta rose	*Yyrr* Pale yellow
yR	*YyRR* Magenta	*YyRr* Magenta rose	*yyRR* White	*yyRr* White
yr	*YyRr* Magenta rose	*Yyrr* Pale yellow	*yyRr* White	*yyrr* White

Fig. 68.—Checkerboard analysis of the progeny of a magenta-rose Mirabilis of the genetic constitution *YyRr*.

We thus have seven distinct color classes as a result of various combinations of two pairs of color factors.

Moreover, this species gives a very good example of the diversity which may be obtained in an F_2 population. Thus Miss Marryat has shown that when magenta-rose, *YyRr*, is selfed, the progeny fulfil the conditions indicated by the accompanying checkerboard analysis in Fig. 68.

Table XXIX.—F_2 Phenotypes and F_3 Phenotypic Ratios Derived from the Original Cross, Crimson, *YYRR* × White, *yyrr*

Color of parent	Number of plants selfed	Number of offspring	Color of offspring
Yellow	2	26	All yellow.
Crimson	2	23	All crimson.
Orange red	3	61	17 crimson : 31 orange red : 15 white.
Magenta	4	64	18 crimson : 32 magenta : 14 white.
Pale yellow	3	46	9 yellow : 25 pale yellow : 12 white.
Magenta-rose	5	70	5 crimson : 9 magenta : 6 orange red : 19 magenta-rose : 3 yellow : 7 pale yellow : 21 white.

When the F_3 was grown from such an F_2 population Miss Marryat obtained excellent agreement with this analysis as is shown by the data in Table XXIX.

Variable Character Expression in the Hybrid.—Sometimes the character expression in F_1 while intermediate displays a range of variation extending almost from one parent to the other. This is shown rather strikingly in the case of bar eyes in Drosophila (Fig. 69). The bar eye factor is a sex-linked mutant factor which is responsible for the production of flies with long narrow eyes instead of the round eyes normal for the species. When a female with bar eyes is crossed to a normal male the F_1 all have bar eyes. In the males especially the eyes are just as narrow as in homozygous races, but among the females some may be found which have eyes nearly as narrow as those characteristic of homozygous bar eye flies and others which have eyes nearly as round as those characteristic of the normal fly. Most of them, however, have eyes which display an intermediate effect of the factor.

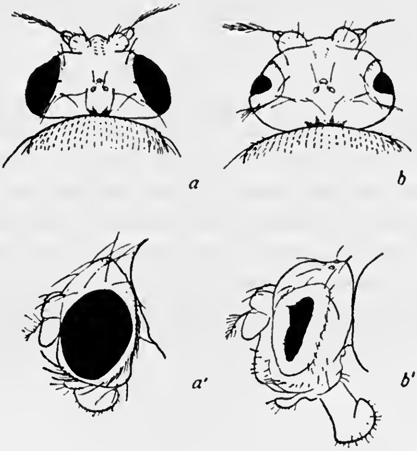


FIG. 69.—Normal (a, a') and bar eye (b, b') of Drosophila; shown in side view and as seen from above. (*After Morgan.*)

This case readily admits of explanation, if the genetic phenomena involved are considered. Since the factor for bar eyes is sex-linked we may represent the bar-eyed female as $(B'X)(B'X)$, following Morgan in employing the primed symbol to indicate a dominant mutant factor. The male with normal eyes is then $(b'X)Y$. When a bar-eyed female is mated to a normal male, bar-eyed females and males are obtained in F_1 as shown in the diagram in Fig. 70.

The F_1 bar-eyed male obtains his only X-chromosome from the female and this chromosome contains the factor for bar eyes. He has exactly the same genetic constitution, therefore, as a male of a pure bar-eyed race, and it is to be expected that he will display the character to the same extent as a male from a pure race. On the other hand the female has one X-chromosome which bears the normal recessive allelomorph of the bar-eye factor. This factor may be considered as exerting a competitive influence against the bar-eye factor of the other X-chromosome, so that the character expression in a sense depends upon a variable equilibrium reached between the two factors. Since they appear to be nearly equal in potency it is possible apparently for this equilibrium to be thrown so much to one side or the other that at times the character expression approaches that of the typical bar-eyed strains and at times that of the normal round-eyed flies.

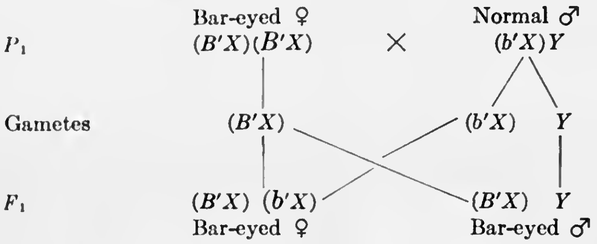


FIG. 70.—Results of mating bar-eyed ♀ with normal-eyed ♂ Drosophila.

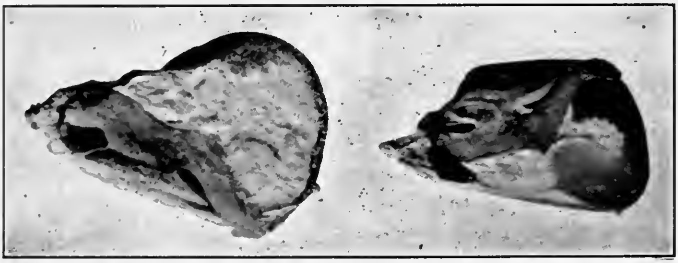


FIG. 71.—Longitudinal sections of corn grains showing differences in character of starch; left, floury; right, flinty.

An interesting case which throws considerable light on the competitive action of factors in determining character expression has been reported by Hayes and East in maize. Flint races of maize are characterized by the production of a very small amount of soft starch in the center of the seed and a large amount of hard corneous starch surrounding it. Flour corns on the other hand produce grains the endosperm of which is almost wholly made up of soft starch with occasionally a very thin layer of corneous starch at the exterior of the endosperm. These differences are shown in Fig. 71.

When a floury corn is pollinated by a flinty corn the grains which result show no effect of the flinty pollination, they are floury grains of the same character as those of a pure floury race. Similarly when a flinty corn is pollinated by a floury corn, the grains are flinty. Again they are of the same character as the maternal parent. The maternal type of grains is always produced in such reciprocal crosses. Following up this experiment, when F_1 corneous grains of the cross corneous ♀ × floury ♂ are grown and selfed, the ears produced show distinct segregation into flinty and floury corn in the ratio 1 flinty: 1 floury. F_1 floury grains from floury ♀ × flinty ♂ when grown and selfed likewise produce ears showing distinct segregation into 1 flinty : 1 floury. Evidently the F_1 grains although different phenotypically display the same genetic phenomena.

Cytological research has shown that in the fertilization of maize and other plants there is a double fertilization, one fertilization giving rise to the embryo and the other to the endosperm. In the case of the embryo, an egg nucleus unites with a nucleus from the pollen grain and from this fusion the embryo develops. In the fertilization which gives rise to the endosperm two nuclei from the female unite with one from the male, so that the cells of the endosperm contain $3x$ chromosomes rather than the duplex number characteristic of the cells of the embryo. If the flinty factor be represented by F, and the contrasted factor for floury by f, the zygote of a flinty corn is FF, but the endosperm connected with it is FFF. Correspondingly for the floury race the zygote is ff, and its endosperm fff. In the fertilization of flinty by floury corn, the egg nucleus proper, the genetic constitution of which is F, is fertilized by an f pollen grain, giving a hybrid zygote of the constitution Ff. The endosperm which surrounds this embryo, however, arises from the fusion of the two endosperm nuclei, FF, with a single nucleus from the pollen grain, giving a zygote of the constitution FFf. This endosperm is flinty because two doses of F are apparently dominant to one dose of f. On the other hand, when floury corn is pollinated by flinty, the embryo has the same genetic constitution, namely Ff, but the endosperm surrounding it arose by union of two endosperm nuclei ff with a pollen nucleus bearing the factor F. It, therefore, has the genetic constitution ffF and it is floury because the two doses of f determine the phenotypic expression to the exclusion of the single dose of F. In F_2 the hybrid flinty grains from the cross flinty ♀ × floury ♂ give exactly the same results as the hybrid floury grains from the cross floury ♀ × flinty ♂. Here the ratio is 1 flinty: 1 floury in each case, and half the members of each class are heterozygous and will reproduce the same ratios in the succeeding generation.

It would be difficult to conceive of a more beautiful illustration of the quantitative relations obtaining in the determination of dominance. Apparently the relations are about the same as those shown in the case of bar eye in Drosophila, for conceivably, if such a thing could be obtained, an endosperm arising from an *Ff* cell might show the same variation between flinty and floury that is shown in the bar-eye character of flies of the genetic constitution $(B'X)$ $(b'X)$.

Mosaic Expression of the Hybrid Character.—Another type of hybrid condition is that in which the *Aa* individuals are a mosaic of the characters of the two parents. This condition is very strikingly illustrated in Blue Andalusian fowls. Andalusian fowls are of three types: black, splashed white, and the so-called blue. Of these types the black and splashed white breed true, but the blue is a hybrid and constantly segregates in the ratio 1 black : 2 blue : 1 splashed white. When black and splashed white are mated, the progeny are all blue. The Blue Andalusian fowl of the Poultry Standard of Perfection is, therefore, a heterozygous form and for that reason all attempts to establish it as a pure breeding race have failed. The case, however, is of interest here because the Blue Andalusian is a peculiar mosaic of the characters exhibited by the black and splashed white. Its "blue" color is simply due to a fine but uneven sprinkling of black pigment through the feathers; and on some portions as for instance the feathers of the breast, the black is present as a distinct edging or lacing of the feathers.

Similar mosiac hybrids which represent a simple heterozygous condition have been reported by Nabours in grouse locusts of the genus Parattetix. Nabours found nine distinct races which bred true for particular color patterns. Hybrids, however, between any two of these species display the entire color pattern of both parents, the color patterns being merely superimposed one upon another and in such a manner that the entire pigmentation of both parents is present in the hybrid and is distributed in the same fashion. If then two races of Parattetix *A* and *B* be crossed, the hybrid *AB* will be a mosiac of the two parents, and it is possible by simple inspection of such a hybrid form to determine what races entered into it. Such a hybrid will give a population consisting of $1A:2AB:1B$, thus demonstrating that the case rests on a simple factor basis and that the mosaic pattern is simply an expression of a heterozygous condition in which both *A* and *a*, if we designate them thus, work out their full possibility in the development of the hybrid. In certain cases which did not appear to conform to this simple interpretation, a microscopic examination was resorted to. This examination demonstrated that the lack of agreement was apparent rather than real. Thus in Fig. 72 the superficial characters of the hybrid (*BI*) between *P. leuconotus* (*BB*) and *P. nigronotatus* (*II*) are for the most part those of *P. leuconotus* except for the broad black band across the pronotum which is clearly derived from *P. nigronotatus*. In the posterior part of the pronotum particularly the characters of *P. leuconotus*, appear to be dominant but the microscopic study showed clearly that this was due to differences in distribution in the two parents, and that the characters of *P. nigronotatus*, although obscured were as much present as those of *leuconotus*.

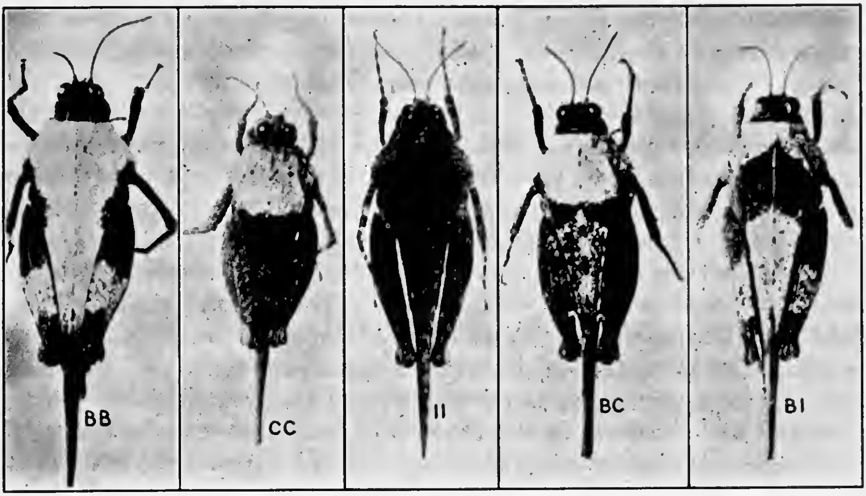


FIG. 72.—Three types of Paratettix, *BB*, *CC*, *II*, and two of the hybrids between them. (*After Nabours.*)

The Presence and Absence Hypothesis.—The foregoing accounts of the relations existing in the expression of the hybrid characters as compared with the two parental characters serves as an adequate introduction for a brief consideration of the presence and absence hypothesis. According to the presence and absence hypothesis as advanced by Bateson and Punnett, the only relations which can exist with respect to a certain factor depend on its presence or absence from the hereditary material. Thus if we consider the factor R for round shape in peas, and its allelomorph r for wrinkled shape, according to the presence and absence hypothesis the r of the genetic formula of the wrinkled pea is not itself a factor as we have assumed throughout the discussion in this text, but merely represents the absence of the factor R. The wrinkled character, therefore, is merely an expression of the action of the set of genetic factors in peas when the factor R has been taken away from the system.

In this text we have throughout assumed that the recessive symbols stand for factors just as truly as do the dominant ones, and we have regarded the difference between a recessive factor and its corresponding dominant allelomorph as dependent upon some change in a dominant factor sometimes profound and sometimes less profound so that all variations from complete dominance to a strict intermediacy may be obtained among hybrids. For cases of complete dominance, the presence and absence idea satisfies conditions very satisfactorily as far as formal relations are concerned, and intermediacy and even other conditions of the hybrid expression may be assumed to depend upon the quantitative difference in the amount of the factor present in the hybrid race as contrasted with the parent races. Difficulties, however, begin to arise when attempts are made to explain the origin of dominant mutations in terms of this hypothesis, for in such cases it is almost necessary to assume that a factor has been added to the hereditary material. It is usually considered easy enough to account for a recessive mutation as due to the dropping out of a factor from the hereditary material, but when a factor is added to that material, we must ask from whence it came, what its nature, etc. If we regard mutations as simply due to changes in a factor this difficulty vanishes for then dominance or recessiveness of the mutations depends merely on the relations between the mutated factor and its unchanged condition and there is no particular reason for assuming that all mutations should be of the nature of "loss" mutations, *i.e.*, mutations depending upon the loss of a factor from the hereditary material and resulting in the absence of some dominant character in the individuals concerned. There is no difficulty therefore, in accounting for the four or five dominant mutations which have been observed in Drosophila, if we regard mutation as a change in a locus, for these particular mutations simply happened to involve changes of such a type that the mutated locus was dominant to the unmutated condition. Obviously, also, such a view conforms more closely with the facts observed in cases of the competitive action of factors such as is seen in bar eyes in Drosophila or in the factors for flinty and floury endosperm in maize.

But there are more serious objections than these which can be raised against the presence and absence hypothesis. In Drosophila, for instance, a number of cases of return mutations have been observed, many of them in cultures so controlled that the possibility of explaining them by chance contamination is practically precluded. Thus in stock so controlled by the presence of other factors that it would practically have been impossible to have a contamination go unnoticed on account of the introduction of other factors, the bar-eyed race of Drosophila has been known to produce normal-eyed mutants (May) and eosin-eyed flies have been observed to give white-eyed flies on several occasions; while on the other hand eosin, although dominant to white, originally arose as a mutant in a stock of white-eyed flies. If we assume that the change from eosin to white involves a relatively unessential change in the *W* factor in Drosophila, in chemical terms perhaps a slight rearrangement in the molecule or a change in an end radical, then it is not difficult to imagine how a reverse mutation might arise. Reverse mutations, therefore, support the idea that the recessive member of an allelomorphic system is just as truly a factor as the dominant member. Nevertheless these considerations do not in themselves confute the argument of presence and absence, although they tend to throw the weight of evidence strongly against it. It is, however, perhaps not amiss to point out that much of the weight of authority of the presence and absence hypothesis depends on the fact that it was advanced at the psychological moment, and that, as Morgan points out, in the light of our present knowledge of the relation between factors and characters it assumes a knowledge far beyond that which we have at present attained. But the really serious objections to the hypothesis are those based on the evidence furnished by multiple allelomorphism.

Since the foregoing was written Bridges has published results of his investigation of a case of loss or inactivation of a portion of the *X*-chromosome in Drosophila. The deficient section involved the factor for bar eye. As Bridges points out this constitutes the first valid evidence upon the question of presence and absence. According to the presence and absence hypothesis the original appearance of the dominant bar character was due to the loss from the chromosome of an inhibitor, thereby allowing the normal narrowing effect of the remaining complex to assert itself. It should make no difference whether this inhibitor were lost by a special loss involving only the inhibitor or whether it were lost because of being situated in a particular section which became lost. In other words, the chromosome which is deficient for the region carrying the inhibitor should allow the occurrence of the same narrowing effect that is allowed by the simple loss of the inhibitor. In point of fact, the deficiency of the region in which the inhibitor must be hypothecated does not produce an effect like that of the mutation responsible for bar. For, the female carrying one deficient *X* and one normal *X* shows no narrowing of the eye shape, and likewise the female carrying one deficient *X* and one bar *X* is no narrower in eye shape than a normal heterozygous bar. Thus, in the only case which has a direct bearing on the presence and absence hypothesis, it is seen that the expedient of the loss of inhibitors to explain the origin of a dominant mutation is of no avail.

Multiple Allelomorphism in General.—Multiple allelomorphism is the term applied to those cases which seem to depend on a series of changes in a given factor locus. Cuenot advanced such an explanation for the inheritance of certain color patterns in mice, and Morgan has since described several cases which occur in Drosophila. Since these later cases are simpler and have been worked out in more detail they will be treated first.

Multiple Allelomorphism in Drosophila.—A typical case is that centering around the locus for eye color in Drosophila which we have called W. This locus is situated in the X-chromosome at a distance of one unit from the locus Y for body color. The first mutations in Drosophila involved a change in W such that white eyes were produced, a mutation recessive to the normal red-eyed condition. This factor is called w and its inheritance has been dealt with in previous chapters. Later some flies arose in a white-eyed culture which had eosin eyes. When a white ♂ is mated to an eosin ♀ the F_1 is eosin[1] and F_2 consists of 3 eosin:1 white. When a red-eyed ♀ is mated to an eosin-eyed ♂, F_1 is red, and F_2 segregates in the ratio 3 red:1 eosin. The facts are explainable on the assumption that the factor W has been changed in a different fashion to produce the factor for eosin which we designated as w^e. On this basis the analysis of the genetic constitutions of these different races is as follows:

$(WX)(WX)$ = red ♀ $(WX)Y$ = red ♂
$(w^eX)(w^eX)$ = eosin ♀ $(w^eX)Y$ = eosin ♂
$(wX)(wX)$ = white ♀ $(wX)Y$ = white ♂.

A change in the same locus has occurred in the mutation to white and to eosin, but the change has been different in each case. Later four other changes in this locus occurred giving eye colors which have been named cherry, tinged, blood and buff, and these fulfil the same conditions as those pointed out for eosin. The factors are designated w^c, w^t, w^b and w^{bu} respectively. These seven factors therefore display a particular type of behavior depending upon the fact that they occupy the same locus in the X-chromosome. They form together a system of septuple allelomorphs.

In Drosophila there are at least three other such systems of multiple allelomorphs. One of these centers around the Y locus in the X-chromosome which may change to y giving a yellow-bodied fly in place of the normal gray body or may change to y^s when a spot-bodied fly is produced. Another system of triple allelomorphs for eye color is located in the third chromosome; it consists of the factors for pink and peach eye color, and the normal allelomorph of these which is concerned in the production of red eyes. A fourth such series of allelomorphs is that of the factors for ebony and sooty body color and their normal allelomorph concerned in the production of gray body color. This series is also located in the third chromosome.

Assuming that more than two factors may occupy identical loci in homologous chromosomes there are several simple relations which must be fulfilled in order to establish the case experimentally. The

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[1] The F_1 ♀s actually have an intermediate eye-color, "white-eosin compound".

linkage values of such a series of allelomorphs when tested with other members of the group to which they belong should be identical. The factor for yellow body color is located at the locus 0.0 in the *X*-chromosomes, and displays definite linkage values when tested with any other factor belonging in this chromosome. The factor for spot gives exactly the same values with all factors with which it has been tested. The factors for eosin and white eye color both give one unit of crossing over

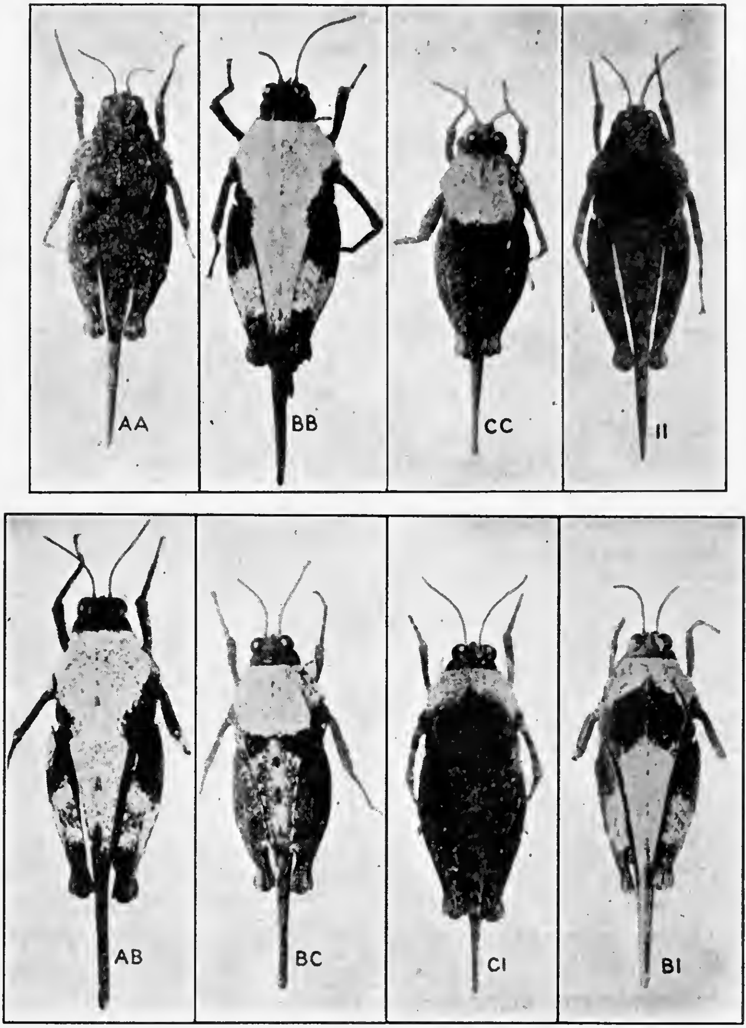

FIG. 73.—Forms and hybrids of Paratettix. *AA*, *texanus*; *BB*, *leucorotus*; *CC*, *leucothorax*; *II*, *nigro notatus*. (*After Nabours.*)

with the factor for yellow body color and they give identical linkage values with the other factors in this group. Since the factors occupy identical loci in the homologus chromosomes not more than two can occur in the same individual at the same time. This fact was demonstrated in the breeding tests applied above.

Other cases of multiple allelomorphism are known to occur in a large variety of species. In the silkworm there is apparently a series of multiple allelomorphs concerned in the production of larval patterns. As Tanaka has shown there are four larval patterns, moricaud, striped, normal, and plain. Each of these colors is allelomorphic to the other three and moreover they all apparently display the same linkage values with the pair of factors for yellow and white cocoon color. Like the multiple systems in Drosophila they give no new types by recombination when crossed.

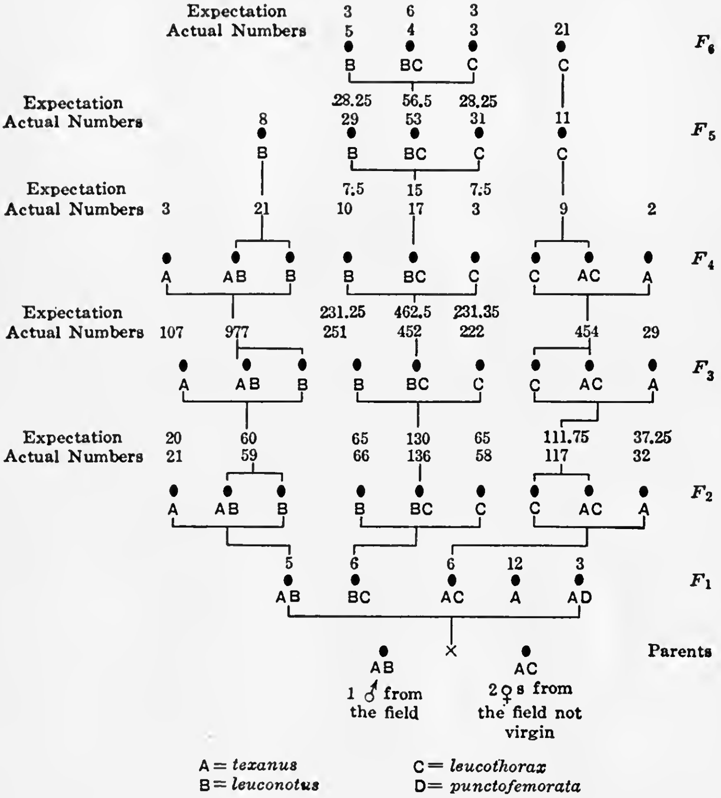

FIG. 74.—Chart showing results of a continued series of pedigree experiments with Paratettix involving types *A*, *B*, and *C*. (*After Nabours.*)

Multiple Allelomorphs in the Grouse Locust.—A very striking series of multiple allelomorphs is that concerned with color pattern in Parattetix. Nabours has investigated the inheritance of pattern in fourteen races of this insect, the grouse locust. Some of these are shown in Fig. 73 and also the hybrids between them. It was pointed out in a previous section in this chapter that these races when hybridized give intermediate forms in F_1, intermediate in the sense that they display the type patterns of both hybrids superimposed one upon the other. In F_2 they segregate into three types, the two parent types, and the hybrid form in the ratio 1:2:1.

Nabours has prepared a chart from the data of an extensive breeding experiment with some of these forms. It illustrates so admirably the type of behavior displayed by multiple allelomorphs that it is given in full in Fig. 74. In these experiments separation of B from AB and C from AC has not been attempted because the type A exerts very little influence on the color pattern of the hybrid. In this chart expected results are indicated wherever the ratio of types actually observed is of significance. The observed results show excellent agreement with expectations.

The multiple allelomorphs in Parattetix appear to affect the entire color pattern of the body and to cause different colors to develop in different parts of the body. This, however, is merely another instance of the manifold effects of single factors, and furnishes no sound argument against the conception of multiple allelomorphs. Furthermore, Nabours has discovered at least one modifying factor which can exist only with, and in addition to, any of the fourteen multiple allelomorphs or their hybrids.

Multiple Allelomorphs in Maize.—In maize there is apparently a remarkable series of multiple allelomorphs concerned in the development of red color in the husks, silk, pericarp, and cob. Practically all combinations of these are known in various different varieties of maize, so that it is possible to have varieties with red grain, silk, cob, and husk; red grain, white silk, white cob, and white husk; or any other combination whatsoever. When, however, such types are crossed the F_1 displays a superimposed set of characters, red being dominant; and in F_2 but three forms appear in the ratio 1:2:1 as with Nabours' locusts, namely the two parental types and, if it is different from either of them, the hybrid form. This indicates that the F_1 hybrids form gametes bearing factors determining only the conditions represented in the parents. This fact Emerson subjected to direct test by crossing F_1 hybrids back to varieties lacking the red color in all these parts. In one case an F_1 plant produced ears which had red cobs and variegated red grains. When such a plant was crossed back to a race having white cobs and grains, the next generation consisted only of plants which bore ears with white cobs and variegated grains and ears with red cobs and white grains. None were produced which bore ears having the F_1 combination, red cob and variegated grains, and on the other hand none were produced showing the reverse recombination, white ears and white grains.

This series of multiple allelomorphs is perhaps the most striking one known and displays just as unique relations as does that series in Parattetix. For considering only red *vs.* white alone in these characters there are sixteen possible combinations which would give pure breeding races. Besides this, however, the red, particularly of the pericarp, may be modified in many different ways with respect to shade and distribution, apparently without altering the relations of the factors involved to the allelomorphic system, so that the number of possible combinations is considerably greater. Emerson has studied the inheritance of a large number of these types and so far they all may be consistently explained on the hypothesis of multiple allelomorphs but the data are not as yet extensive enough to establish this interpretation beyond any doubt.

The general nature of multiple allelomorphism is attested to by its occurrence in widely separated species of animals and plants. Its occurrence in Drosophila, the silkworm, Parattetix, and maize has been noted above. Besides these Morgan has pointed out that cases are known in rabbits and mice among animals, and in Aquilegia, Lychnis, and the bean among plants. In rabbits the factors concerned are three, those for self-color, Himalayan pattern, and albinism. In the mouse apparently four factors make up a similar system, namely those for yellow, black, gray, and gray with white belly. In Aquilegia the system has to do with leaf color and three factors are involved, those for green, variegated, and yellow leaf color. Shull's case in Lychnis has to do with sex-determining factors. In the bean the case is somewhat like that in corn but the series is less extensive. The system there as reported by Emerson is green leaves, green pods; green leaves, yellow pods; yellow leaves, yellow pods.

Morgan has brought together the arguments in favor of multiple allelomorphism and the following discussion is based for the most part upon his presentation. This discussion will serve in a sense as a summary of the material dealing with multiple allelomorphism.

1. Systems of multiple allelomorphs appear always to affect the same character. This fact is readily apparent from a consideration of the cases which have been cited above. Beyond this the cases often give a series of diminishing intensities with respect to the character affected as for example, black, Himalayan, and white in rabbits. On this basis, Punnett has sought to disprove the validity of the hypothesis of multiple

allelomorphs as applied to the case in rabbits, for although the homozygous forms give such a series of diminishing intensity of melanic pigment, nevertheless the heterozygous forms give inconsistences. Black by agouti gives agouti-black, but black by yellow gives full black, in spite of the fact that yellow is regarded as a lower intensity of pigmentation than agouti.

The argument does not appear to be valid, however, for specific relations may still exist among the factors of a system of multiple allelomorphs. Bridges has pointed this out in the case of the eye color series red, white, cherry, eosin, tinged, blood and buff eye-color in Drosophila. He has discovered a number of factors which modify eosin, one in particular called whiting changes eosin to pure white, but does not produce any visible effect on the other members of the series. The conception of diminishing intensity as applied to multiple allelomorphs is clearly not fundamental to the hypothesis.

2. The behavior in inheritance is different from that which would be expected in case different loci in the hereditary system were involved. When different loci are involved, each of two different mutant types will contain besides its own mutant factor the normal allelomorph of the mutant factor of the contrasted type. Consequently on crossing they will unite the series of factors present in the original type and give a character expression corresponding to that of the original form. Such is normally the case in undoubted instances of mutations affecting different loci, but in the case of multiple allelomorphs one or the other of the mutant types or an intermediate is produced in F_1. When identical loci are concerned in two mutations, the hybrid between them will not reconstitute the original system, but will contain only the two mutant factors at that locus. The character expression of the hybrid therefore will depend on the interrelations existing between the mutant factors and the rest of the hereditary system rather than on the reuniting of the normal allelomorphs of the mutant factors.

3. There are difficulties in explaining the origin of some of the forms on the basis of complete linkage between factors, which disappear on the adoption of the hypothesis of multiple allelomorphism. The difficulty may be illustrated by a specific case, that of the series red, white, cherry, eosin, tinged, blood and buff eye-color in Drosophila. Considering two specific instances, cherry and white, both of which arose from red immediately, it must follow on the basis of complete linkage that one differs from red by one factor and the other by two factors. If red be $(CE)(CE)$, then cherry, which is recessive to red would be $(cE)(cE)$, and white, which is recessive to both red and cherry would be $(ce)(ce)$. This involves the assumption that white arose as a result of simultaneous mutations in two completely linked factors affecting the same character, a practically

inconceivable thing, if viewed from a purely mathematical standpoint, unless a special biological mechanism exists which favors such mutations. The same difficulties are met with in the case of other systems of multiple allelomorphs the origin of which have been observed in pedigree cultures, consequently the situation in the above system is not unique.

4. If a curve of linkage values be plotted in Drosophila for a considerable number of known factors it will be found that the frequencies of different values correspond with one another until those displaying multiple allelomorphism (or complete linkage) are met with and these are far in excess of the number normally to be expected from purely mathematical considerations. They are not, therefore, merely the extremes of ordinary cases of linkage.

5. There are no very good reasons why only one sort of change should be possible in a given locus in the hereditary material. It is true the presence and absence hypothesis does hold that the only difference with respect to a given factor is its presence in the hereditary material or its absence from it, but there are many reasons why this view at present appears untenable. A factor in the hereditary material may well be regarded as a complex chemical substance of some kind which maintains essential relations with the other factors in the system such that to lose it entirely might well disorganize the entire system. But such a complex chemical substance might well change in many relatively slight ways which would modify the particular character in which it is concerned in various directions depending upon the specific manner in which the factor has been altered.

When these arguments are considered and the type of cases to which it is applied are taken into account, it is apparent that the theory of multiple allelomorphism is a useful analytic tool in the solution of a certain class of peculiar Mendelian phenomena. Although some of the above cases may prove to be instances of extremely close linkage, nevertheless for most of them the case is firmly established experimentally, and deserves careful consideration from that standpoint.

CHAPTER IX

TYPES OF FACTOR INTERACTIONS

In the present chapter it is proposed to illustrate some of the various types of relations which exist between different pairs of factors so that the student may come to appreciate some of the more complex features of factor interaction.

The System of Aleurone Color Factors in Maize.—It has already been pointed out that some particular cases of Mendelian phenomena depend for their explanation on the presence of different factors which give similar results. These are to be considered as cases of Mendelian factor interactions as specifically as those more fully discussed in this chapter. Such a condition may be illustrated very satisfactorily by the four-factor system for aleurone color which is known to exist in maize. The factors involved in this system and their actions are as follows:

C—a factor for chromogen base. *C* is necessary for the production of any aleurone coloration in maize. Its allelomorph *c* constantly gives white grains.

R—a factor which when present with *C* gives a red aleurone color. Its allelomorph, *r*, constantly gives white.

P—a factor which when present with *C* and *R* gives purple aleurone color.

W—a dominant factor for white aleurone color. When it is present the grains will be white no matter what other factors may be present.

With this series of factors, the following homozygous races are obtainable and have the phenotypic expression here indicated:

1. *WWCCRRPP*—white.
2. *WWCCRRpp*—white.
3. *WWCCrrPP*—white.
4. *WWCCrrpp*—white.
5. *WWccRRPP*—white.
6. *WWccRRpp*—white.
7. *WWccrrPP*—white.
8. *WWccrrpp*—white.
9. *wwCCRRPP*—purple.
10. *wwCCRRpp*—red.
11. *wwCCrrPP*—white.
12. *wwCCrrpp*—white.
13. *wwccRRPP*—white.
14. *wwccRRpp*—white.
15. *wwccrrPP*—white.
16. *wwccrrpp*—white.

Of the sixteen pure breeding forms, fourteen are whites, and although indistinguishable phenotypically these whites may be separated by proper breeding tests. Some of the relations existing between the different genotypes have already been dealt with, but the student may be interested in tracing out others. Thus the presence of a factor for dominant white may be demonstrated by crossing with a purple race, in which case the grains will be white, if such a factor be present. Moreover, several of the whites when crossed give colored forms in F_1, thus 11 × 13, 11 × 14, and 12 × 13 give purple, and 12 × 14 gives red. It has already been shown how in case of the presence of the factor for dominant white, whites when crossed may give a white F_1 and white, purple, and red in various proportions in F_2. Such is the case for example in the cross 1 × 16 which will give F_1 white and F_2 in the ratio 220 white:27 purple:9 red. The complex relations here existing between only three phenotypes is a very good example of the sort of problems which must be solved by experimental genetics.

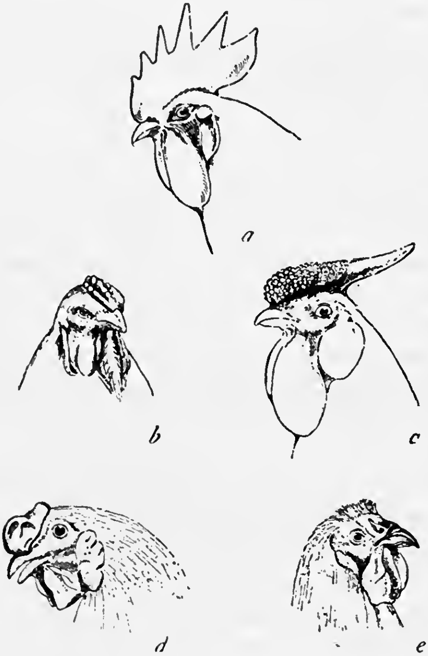

Fig. 75.—Comb types in poultry. Single, *a*; pea, *b*; rose, *c*; walnut, *d*; and breda, *e*. (*After Morgan.*)

Comb-characters in Fowls.—A variety of comb-characters are found in the domestic breeds of poultry and Bateson has made these the subject of an extensive Mendelian investigation involving the rearing of over 12,000 individuals. The comb types involved are shown in Fig. 75. In this series of characters both rose and pea comb were found to be dominant to single comb, and give in F_2 simple 3:1 ratios. These relations obviously indicate that there is a single factor difference between rose and single and pea and single, but that the pair of factors involved must be different in each case. This is again shown in crosses between walnut and rose or pea-comb fowls for such crosses give walnut in F_1 and 3:1 segregation in F_2. Accordingly taking walnut as a dominant type, rose comb may be conceived of as differing from it by the factor *r*, and pea comb by the factor *p*. Walnut comb would then contain the dominant allelomorphs *RRPP*, and rose comb would be of the genetic constitution *rrPP*, and pea comb, *RRpp*. Since single comb again differs by one factor from both rose and pea comb it must be of the genetic constitution *rrpp*. This analysis explains the experimental results which we have thus far outlined, but the critical test of the hypothesis lies in the cross rose × pea. This should give walnut, *RrPp*, in F_1 and in F_2 all four types in the proportions 9 walnut:3 rose: 3 pea:1 single as shown in the checkerboard in Fig. 76. In one series of such experiments Bateson obtained the results shown in Table XXX.

	RP	*Rp*	*rP*	*rp*
RP	*RRPP* Walnut	*RRPp* Walnut	*RrPP* Walnut	*RrPp* Walnut
Rp	*RRPp* Walnut	*RRpp* Pea	*RrPp* Walnut	*Rrpp* Pea
rP	*RrPP* Walnut	*RrPp* Walnut	*rrPP* Rose	*rrPp* Rose
rp	*RrPp* Walnut	*Rrpp* Pea	*rrPp* Rose	*rrpp* Single

Fig. 76.—Checkerboard analysis of theoretical expectations in F_2 from a cross between rose-comb fowl (*rrPP*) and pea-comb fowl (*RRpp*).

TABLE XXX.—INHERITANCE OF COMB TYPE IN FOWLS.

Cross		Walnut	Pea	Rose	Single
RrPp × *RrPp*........	Observed...	279	132	99	45
	Expected...	312	104	104	35
	Ratio	9	3	3	1
RrPp × *rrpp*.........	Observed...	664	705	664	716
	Expected...	687	687	687	687
	Ratio......	1	1	1	1

In this table the results of the back cross of F_1 walnut to single are also given. A comparison of the values given with those expected on the basis of independent segregation of the factors indicates a fairly close correspondence between the two. It may be of some significance, however, that walnut and rose are the deficient classes in both cases.

From the standpoint of factor interaction this case is of interest because it shows clearly that the character expression of a given set of factors cannot be predicted with certainty from the known character expression of some of these factors. It would have been impossible to predict from the character expressions involved that rose × pea would give walnut-comb fowls or that by recombination of the two recessive factors involved a single-comb fowl would result, for these two new comb types are totally different from the rose and pea types from which they can be derived. The obtaining of new characters of this kind by factor recombination is by no means an unusual thing in genetic experiments, and is sufficient justification in breeding work for testing factor combinations to determine what sort of character expression may result from them.

	CRVH	*CrVH*	*cRVH*	*crVH*
CRVH	*CCRRVVHH* Violet hairy	*CCRrVVHH* Violet hairy	*CcRRVVHH* Violet hairy	*CcRrVVHH* Violet hairy
CrVH	*CCRrVVHH* Violet hairy	*CCrrVVHH* Cream glabrous	*CcRrVVHH* Violet hairy	*CcrrVVHH* Cream glabrous
cRVH	*CcRRVVHH* Violet hairy	*CcRrVVHH* Violet hairy	*ccRRVVHH* White glabrous	*ccRrVVHH* White glabrous
crVH	*CcRrVVHH* Violet hairy	*CcrrVVHH* Cream glabrous	*ccRrVVHH* White glabrous	*ccrrVVHH* White glabrous

Fig. 77.—F_2 checkerboard analysis of a cross between two varieties of stocks, white glabrous (*ccRRVVHH*) and cream glabrous (*CCrrVVHH*).

Miss Saunders' Factor System in Stocks.—A more complicated case of factor interaction as related to character expression has been investigated by Miss Saunders in stocks (Matthiola) and has been interpreted in somewhat the following fashion with respect to the factors and factor relations therein concerned.

C—a factor for chromogen base which by itself gives a cream-colored flower. Its allelomorph, *c*, gives white flowers.

R—a factor for red coloration, epistatic to *C*.

V—a factor for violet coloration epistatic to *R*.

H—a factor for the production of hairs on the leaves, active only in the presence of *C* and *R*.

The complicated relations existing between these factors are well illustrated by the cross white glabrous (*ccRRVVHH*) × cream glabrous (*CCrrVVHH*). This gives in F_1 violet hairy plants (*CcRrVVHH*) which segregate in F_2 according to the analysis given in the accompanying checkerboard (Fig. 77). The proportions are 9 violet hairy:3 cream glabrous:4 white glabrous.

The peculiar feature of these relations is the fact that the factor *H* for hairiness can only act in the presence of *C* and *R*. In fact as far as the above experiment goes, the hairy condition might be considered as merely an extra effect of the interaction of *C* and *R*. However, glabrous violet plants are known and in these the factor *h* for the glabrous condition must be present. When a violet glabrous (*CCRRVVhh*) plant is crossed with white glabrous (*ccRRVVHH*) the F_1 again is violet hairy (*CcRRVVHh*), this time because the factor for hairiness is brought in by the white plant, and in F_2 the segregation is as indicated in the checkerboard in Fig. 78. The phenotypic ratio obtained this time is 9 violet hairy:3 violet glabrous: 4 white glabrous.

	CRVH	*CRVh*	*cRVH*	*cRVh*
CRVH	*CCRRVVHH* Violet hairy	*CCRRVVHh* Violet hairy	*CcRRVVHH* Violet hairy	*CcRRVVHh* Violet hairy
CRVh	*CCRRVVHh* Violet hairy	*CCRRVVhh* Violet glabrous	*CcRRVVHh* Violet hairy	*CcRRVVhh* Violet glabrous
cRVH	*CcRRVVHH* Violet hairy	*CcRRVVHh* Violet hairy	*ccRRVVHH* White glabrous	*ccRRVVHh* White glabrous
cRVh	*CcRRVVHh* Violet hairy	*CcRRVVhh* Violet glabrous	*ccRRVVHh* White glabrous	*ccRRVVhh* White glabrous

Fig. 78.—F_2 checkerboard analysis of a cross between violet glabrous (*CCRRVVhh*) and white glabrous (*ccRRVVHH*) stocks.

This analysis not only adequately accounts for the phenomena as given above, but it also accounts for the F_3 results and the various types of results that are obtained by mating other genotypes. In addition Miss Saunders found that when purple or white *incana* were mated to cream of the type above, the entire series of forms recorded for the previous white × cream mating were obtained and in addition cream hairy and cream glabrous. This at first sight appears to contradict the hypothesis that no cream or white hairy forms are possible. But closer examination has revealed the fact that white *incana*, which is itself hairy is in reality a colored form, *i.e.*, possesses the factors *C* and *R*. This is shown by the fact that a slight tinge develops in flowers of this variety on fading, and in the F_2 from a cross of this form with cream glabrous, those whites which tinge on fading are hairy and those which show no sign of coloration on fading are glabrous. The apparent difficulty is therefore merely due to the fact that some plants which possess C and R are still white on account of the action of other factors.

Altenburg and Muller's Truncate-winged Drosophila.—An even more complicated case of factor interaction is that concerned in the production of truncate wings in Drosophila (Fig. 79). The factors here involved appear to be the following:

t—a factor for truncate wings. It is a recessive factor located in the second chromosome, and without this factor the truncate wing character cannot appear.

t_1—a factor which intensifies the expression of the truncate wing character, but which is not absolutely essential. This factor is located in the first chromosome.

t_3—another factor which intensifies the expression of the truncate wing, but is not absolutely essential to it.

B'—the dominant factor for bar eyes which in addition acts as an intensifier of truncate. This is a first chromosome factor.

b—a factor for black body color located in the second chromosome. This factor has such an influence that flies of the constitution $(bT)(bt)$ or even $(Bt)(bT)$ may display the truncate wing character.

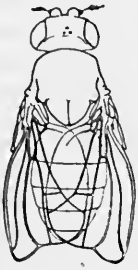

FIG. 79.—Outline drawing of a truncate-winged Drosophila. (*After Morgan.*)

The truncate wing character was particularly baffling on account of the extraordinary relations which it displayed both in hybridization and in selected strains. In hybridization instead of a 3:1 ratio of long to truncate wing the ratio was about 7:1 and in selected strains even after 100 generations of selection there were still about 5 per cent. of long winged flies. That these long winged flies were different genetically from the truncate winged flies was shown by breeding tests for in such tests they did not produce as high a percentage of truncate winged flies as did those which had truncate wings. By means of linkage relations, however, it was possible to determine the factors concerned, and their specific effects. Particularly noteworthy is the fact that the factor B' for bar eyes acts as an intensifier for truncate, thus providing an analogous case to that in stocks where the color factors are necessary for the action of the factor for hairiness. No less interesting is the affect of b, for it was found that this factor, whether homozygous or heterozygous, changed the dominance relations in the allelomorphic pair Tt, so that the truncate wing character is expressed in such individuals when heterozygous for t. Furthermore since truncate appears more readily in the female than in the male it would appear that the sex factors also act as intensifiers.

The important point involved in this case, however, is the ingenious way in which the investigators made use of the linkage relations and the known fact that crossing-over does not occur in the male in order to study these factors, particularly with reference to their constancy, since they are variable in phenotypic expression. They took a truncate male which contained the truncate factor and also the truncate intensifier of the third chromosome and mated it to a long-winged black-bodied female with pink eyes. The genetic constitution of the truncate male with respect to the factors involved was $(Bt)(Bt)(Pt_3)(Pt_3)XY$, and the contrasted black female was $(bT)(bT)(pT_3)(pT_3)XX$. A male from such a cross is of the

♂	♀ $(bT)(pT_3)X$
$(bT)(pT_3)X$	$(bT)(bT)(pT_3)XX$ black pink ♀ long
$(bT)(Pt_3)X$	$(bT)(bT)(Pt_3)(pT_3)XX$ black red ♀ long
$(Bt)(pT_3)X$	$(Bt)(bT)(Pt_3)(pT_3)XX$ Gray pink ♀ long or truncate
$(Bt)(Pt_3)X$	$(Bt)(bT)(Pt_3)(pT_3)XX$ Red gray ♀ long or truncate
$(bT)(pT_3)Y$	$(bT)(bT)(pT_3)(pT_3)XY$ Black pink ♂ long
$(bT)(Pt_3)Y$	$(bT)(bT)(Pt_3)(pT_3)XY$ Black red ♂ long
$(Bt)(pT_3)Y$	$(BT)(bT)(pT_3)(pT_3)XY$ Gray pink ♂ long or truncate
$(Bt)(Pt_3)Y$	$(Bt)(bT)(PT_3)(pT_3)XY$ Gray red ♂ long or truncate

FIG. 80.—Checkerboard analysis of F_2 generation obtained by mating an F_1 male Drosophila of the constitution $(bT)(Bt)(pT_3)(Pt_3)XY$ with a pink black long female.

genetic constitution $(bT)(Bt)(pT_3)(Pt_3)XY$, and since no crossing-over occurs in the male it produces the following series of gametes:

$(bT)(pT_3)X$ $(bT)(pT_3)Y$
$(bT)(Pt_3)X$ $(bT)(Pt_3)Y$
$(Bt)(pT_3)X$ $(Bt)(pT_3)Y$
$(Bt)(Pt_3)X$ $(Bt)(Pt_3)Y$

When, therefore, such an F_1 male is mated back to a black long pink female the results are as recorded in the checkerboard in Fig. 80. Of the male flies only the gray reds bear both the factors t and t_3. Such flies are long or truncate winged, but they should behave in the same fashion in further breeding tests unless the factors themselves are variable. Actually it was found that continued breeding back of these gray red males to black pink females gives approximately the same proportions of truncate to long in every generation. This method of taking advantage of the linkage relations and using the pink factor so that a given genotype could be determined without fail has in this series of experiments been the means of analyzing a case which otherwise would have baffled investigation, for the results clearly point to the fact that the genotypic differences which exist between the long and truncate flies of a selected culture are due to the fact that the lower vitality of truncate flies homozygous for the three factors directly concerned in the expression of this character favors the survival of heterozygous individuals, and it is, therefore, practically impossible to secure a strain of truncate winged flies which will breed true.

The Factor Explanation of Reversion.—Many phenomena included under the term reversion can be explained satisfactorily as instances of complex factor interaction. Reversion in general is a term applied to sudden return to an ancient, generally wild form, whether by hybridization or from other causes.

The Mendelian explanation of reversion is most simply illustrated in Drosophila, for in Drosophila the relation of any particular form to the wild type is known accurately. Thus for example a form of Drosophila with miniature wings arose as a mutation directly from the long-wing type. Likewise several other wing characters have arisen from the long-wing type by a single mutation, among them vestigial wings. When now a vestigial-winged female is mated to a miniature male, the progeny all have long wings. This phenomenon may be explained by the fact that in a vestigial fly, a mutation has occurred in the locus V, which changed it to v without affecting the normal allelomorph of the miniature factor. Similarly the miniature fly bears the normal allelomorph of the vestigial factor, so that when the two are mated the original series of factors of the long-winged type is reunited and consequently the characters of the original wild form are reproduced. This is the principle on which reversion in hybridization depends, and other cases differ from this one only in the number of factor differences involved.

Among the most notable cases of reversion are those which Darwin describes in pigeons and fowls. Darwin regarded these throw-backs to wild types which he obtained by crossing various breeds of pigeons as important evidence of phyletic origin, and largely on the basis of this evidence concluded that the many varied modern breeds of pigeons are monophyletic in origin, that they are all derived from a single wild species. This species is the Wild Rock Pigeon, *Columba livia*, and in the wild it has an extended range over Europe, Abyssinia, India, and Japan. Even in the wild state it is variable, but under domestication breeds have been developed which show truly remarkable differences, and Darwin has described and illustrated these with great care.

The hybridization experiments which Darwin conducted with domesticated breeds of pigeons were undertaken for the purpose of establishing relationship to the Wild Rock Pigeon. The phenomenon of throwing blue in pigeons is an exceedingly common one, but Darwin conducted experiments with breeds which had been bred for many generations and rarely, if ever, gave blue birds. Cole has summarized the results of one of his experiments about as in Fig. 81:

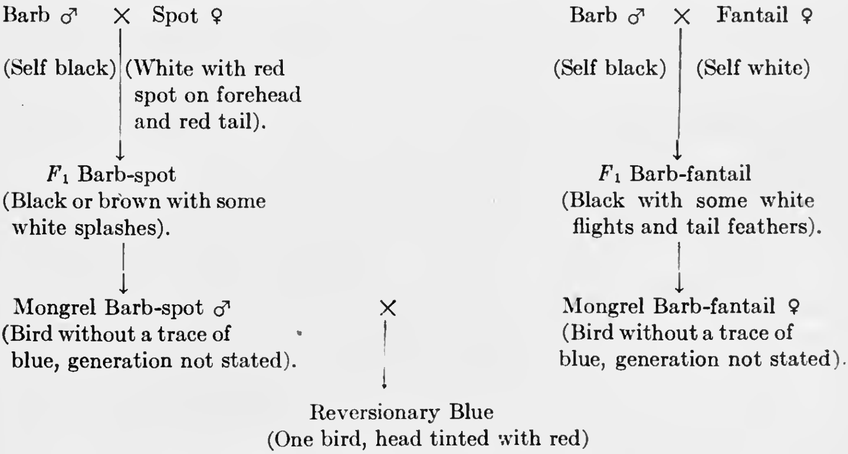

FIG. 81.—Pigeon breeding experiment resulting in reversion. (*After Cole.*)

Evidently on a factorial basis this case involves a complicated recombination of factors, and it can only be said that the Barb, Spot, and Fantail breeds which Darwin used differed from the wild pigeon in different factors and that in this experiment the original set of factors which is responsible for the blue color of the Wild Rock Pigeon was reconstituted. Darwin points out that this bird differed only in a few unimportant details from the color pattern of the Wild Rock Pigeon from the Shetland Islands.

The data which Darwin presented while giving qualitative evidence of recombination of factors do not provide quantitative data on which to base a Mendelian analysis. Staples-Browne, however, has presented a case which admits of more definite analysis. He crossed a Black-barb and a White Fantail and obtained black birds in F_1. In F_2 he obtained the results which are tabulated in Table XXXI. Cole has proposed the following factor analysis for the principal colors in pigeons:

B—a factor epistatic to the series of factors which produce red in pigeons, and giving black pigmentation. The allelomorph *b* then results in red pigmentation.

S—a factor for extension of pigment which appears to act on *B* only. *BS* gives black birds, whereas *Bs* gives birds in which the black pigment is aggregated into clumps in the barbules, the so-called blue pigeons.

T—a factor which gives black tail feathers when *B* is present. The allelomorph *b* under similar conditions gives blue tailed birds.

W—a series of factors for white pigmentation which Cole designates W_1, W_2, W_3, W_n. By W_n is designated simply an undetermined number of these white factors which may affect different portions of the plumage. Likewise by w_n is designated the recessive allelomorphs of these white factors, birds with such a genetic constitution being self-colored.

TABLE XXXI.—F_2 RESULTS FROM BLACK BARB × WHITE FANTAIL PIGEONS

Classes	Black *B*	Red *b*	Black tail *T*	Blue tail *t*	Pigmented (self)	Splashed		
						Little white	Much white	White self
5 Black (self)	5	..	5	..	5			
10 Black (white feathers)	10	..	10	..	..	10		
2 Blue (self)	2	..	..	2	2			
2 Blue (white feathers)	2	..	..	2	..	2		
5 Red (white feathers)	..	5	?	?	..	2		
2 White (black feathers)	2	..	?	?	..	..	2	
2 White (red feathers)	..	2	?	?	..	..	2	
6 White (self)	?	?	?	?	..	..	..	6
Total observed	21	7	15	4	?	14	4	6
Expected	21	7	14	5	?	?	?	?

With these factors the Black Barb would be $BBSSTTw_nw_n$ and the White Fantail $bbSSttW_nW_n$. The F_1 of such a cross, $BbSSTtW_nw_n$ would be black more or less splashed with white as were those obtained in the experiment, and in F_2, a series of forms would be obtained depending on the dihybrid nature of the *BbTt* portion of the pedigree and the number of *W* factors present. Disregarding these latter the ratio in F_2 should be 9 self black : 3 black with blue tails : 4 red, since the action of the factor *T* has not been determined in red birds. Of birds which might be classified in these categories there were actually 15 self-black : 4 black with blue tail : 5 red, a very close agreement for such small numbers. Moreover, collecting those with factors *B* and *b* which should give a 3 : 1 ratio, the numbers are 21 : 7 and similarly the numbers for black tail and blue tail are 15 : 4. The ratios, therefore, are in close agreement.

It should be noted that the above "blues" are not really the blue of the Wild Rock Pigeon but are blacks with blue tails. We can, however, understand how a blue pigeon might arise from mating black to white for it would only be necessary to employ a white of the genetic constitution $bbsstt W_n W_n$ to achieve this result. It is thus that complex cases of reversion may be explained by reconstitution of the combination of factors present in the original wild form.

CHAPTER X

FACTOR RELATIONS IN QUANTITATIVE INHERITANCE

By quantitative inheritance is meant inheritance which has to do with the size of organisms or parts of organisms, with the number of certain parts, or at times with shapes and forms as related to size. The category of quantitative inheritance is one of convenience only and is not separated sharply from other forms of inheritance. It is, however, in general notable for its complexity and difficulty of precise analysis, and these features of it have resulted in diverse interpretations, some in harmony with the Mendelian principles which have been discussed up to this time, and others which call upon auxiliary hypotheses for aid. In this discussion, we shall begin with simple cases of size inheritance and proceed from them to others more complex. Throughout the attempt will be made to develop a consistent explanation for the phenomena, and one which is in harmony with the general explanation advanced in Mendelian heredity.

Mendel's original experiments dealt with one case of size inheritance. When a tall pea is crossed with a dwarf pea, the F_1 generation consists entirely of tall peas, and in the F_2 progeny there are approximately 3 tall peas : 1 dwarf. Further tests in the F_3 generation showed that the dwarfs breed true to that character, they give only dwarf progeny. One-third of the talls, also, breed true to the tall character, but the other two-thirds give progenies which display segregation into tall and dwarf in the ratio originally obtained in the F_2 generation, namely 3 tall : 1 dwarf. The results throughout are, therefore, in harmony with the assumption that there is a single factor difference between tall and dwarf peas and that the factor for tall is completely dominant over the dwarf factor. This case we have treated in detail in Chapter V.

Results similar to this are not uncommon in studies in size inheritance involving differences between tall and dwarf races. They have been reported for tall and dwarf tomatoes, sweet peas, maize, beans, snapdragons, etc. In the case of beans, Emerson has pointed out that the differentiating factors are factors for indeterminate as opposed to a determinate habit of growth. In the dwarf or bush type of bean, illustrated by Fig. 82 (right), the axis of the plant is terminated after the formation of from four to eight nodes by an inflorescence. Pole or tall beans, as is shown on the left in Fig. 82, do not have such a terminal inflorescence and consequently continue growth until checked by unfavorable external conditions or by the drain of seed production. It is, therefore, possible in this case to state definitely upon what a size difference depends.

In sweet peas there are two distinct dwarf forms which display a simple type of inheritance when crossed with tall forms. One of these types is the Cupid sweet pea which originally arose as a mutation from Emily Henderson, a tall white variety. The Cupid sweet pea is a very dwarf procumbent type which produces no erect stems. When crossed with tall varieties it gives tall plants in F_1 and in F_2 segregation into tall and dwarf in the ratio 3 : 1. The other restricted form is the bush sweet pea. It is characterized by a profuse production of thin, wiry branches which intertwine and form a bush, sometimes three and a half feet high. Bush crossed with tall gives in F_1 tall plants and in F_2, 3 tall : 1 bush. The bush sweet pea, therefore, like the Cupid differs from the tall sweet pea in a single genetic factor, and in both cases the tall form is completely dominant.

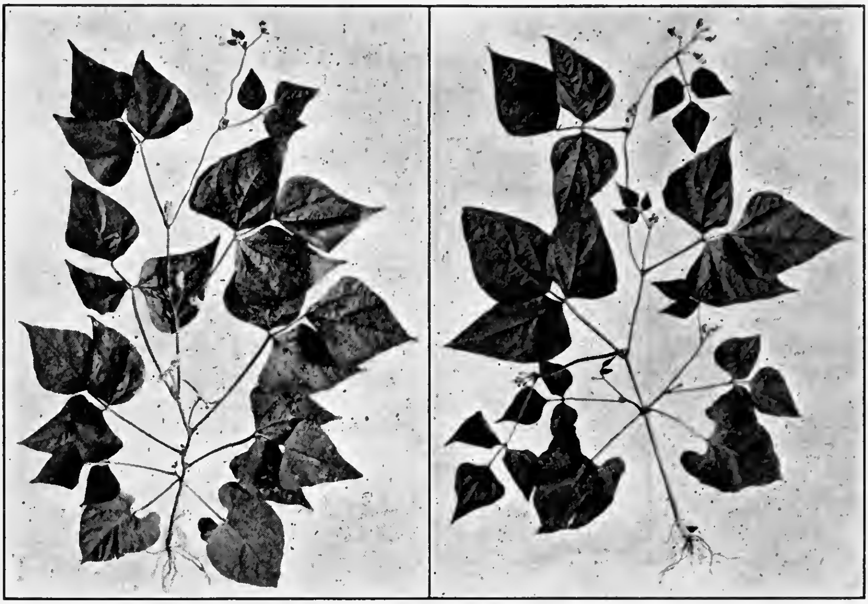

Fig. 82.—(right) Young bush bean plant showing determinate habit of growth. The axis is terminated by a flower cluster; (left) young pole bean plant showing indeterminate habit of growth. The flowers are all in the axils of the leaves. (*After Emerson.*)

An interesting situation arises when bush sweet peas are crossed with Cupid sweet peas. From our knowledge of the inheritance exhibited by these two forms when crossed with tall, we may assume as in previous cases that in the appearance of the Cupid mutation there was a change in some locus concerned in the development of height, such that a low prostrate form was produced rather than the normal tall form. We may call this locus *D* and its mutated condition in Cupid sweet peas *d* (dwarf). In the bush sweet pea a change must have occurred in some other locus concerned in the development of height such that the bush type was produced rather than the normal tall sparsely branched type. This locus in the germinal material may be called *B,* and its mutated condition responsible for the bush type of growth, *b* (bush). Considering both loci, the tall form must have the genetic constitution *DDBB,* since a change in either one of these factors results in some other type than the normal tall. The bush will then obviously be *DDbb,* since it shows only a single factor difference from tall, and likewise the Cupid sweet pea will be *ddBB.* When, therefore, bush is crossed with Cupid, the genetic formula for the F_1 is *DdBb.* Since the factor combination necessary for the production of tall plants is reconstituted in this cross, the F_1 plants are all tall. In F_2 segregation takes place in accordance with expectations based on independent distribution of the two pairs of allelomorphs as shown in the accompanying checkerboard in Fig. 83.

DDBB tall all tall	*DDBb* tall 3 tall : 1 bush	*DdBB* tall 3 tall : 1 Cupid	*DdBb* tall 9 tall : 3 bush : 3 Cupid: 1 bush-Cupid
DDBb 3 tall : 1 bush	*DDbb* all bush	*DdBb* 9 tall : 3 bush: 3 Cupid: 1 bush-Cupid	*Ddbb* 3 bush: 1 bush-Cupid
DdBB tall 3 tall : 1 Cupid	*DdBb* tall 9 tall : 3 bush: 3 Cupid: 1 bush-Cupid	*ddBB* Cupid all Cupid	*ddBb* Cupid 3 Cupid: 1 bush-Cupid
DdBb tall 3 Cupid: 1 bush-Cupid	*Ddbb* bush 3 bush: 1 bush-Cupid	*ddBb* Cupid 3 Cupid: 1 bush-Cupid	*ddbb* bush-Cupid all bush-Cupid

FIG. 83.—Checkerboard analysis of the F_2 population resulting from a cross between bush and Cupid sweet peas.

The F_2 segregation here displayed is in agreement with the usual dihybrid ratio when dominance is complete. There are 9 tall:3 bush:3 Cupid:1 bush-Cupid. In the bush-Cupid a new combination of factors is involved, and the bush-Cupid correspondingly combines the characteristics of the bush and Cupid sweet peas. Like the Cupid sweet pea it is a very dwarf form, but it is erect and much branched like the bush sweet pea. In this particular instance, therefore, the combination of recessive factors results in a combination of the characters which these factors ordinarily determine. The segregation gives four distinct types in F_2 which are easily distinguishable one from another at maturity, and which behave in characteristic manners in the following F_3 generation as is indicated by the accompanying checkerboard. The case, while more complex than those in which only one factor difference is responsible for the character differences, is still simple and readily analyzed by pedigree culture methods. Figs. 123 and 124 illustrate these forms of sweet peas.

In Drosophila there is at least one size difference dependent upon a simple factor difference. This factor belongs in the third group and bears the same relations to the other factors of the genetic system as are displayed by any other locus. The factor dwarf and the corresponding character are in every respect strictly analogous to true qualitative factors. In general the facts of heredity with regard to the simple size differences which we have noted are in agreement with the interpretation that they have arisen by some mutation in a single locus in the normal form and therefore naturally enough display simple monohybrid inheritance. In the case of Lima beans the origin of the bush type by mutation was definitely observed and similarly the Cupid sweet pea was discovered among a population of tall forms. There is no reason, therefore, for advancing any different explanations than those here given for size differences of this type.

There are other size differences which are not particularly different from those above noted except that they are in the opposite direction. A case in point is the mutation in tobacco discovered by East and Hayes. This mutation is one in which the habit of growth has been changed from the ordinary determinate type in which an inflorescence terminates the axis at a relatively invariable stage of elongation to one in which the axis continues growing and producing leaves for a considerably longer period of time. This giant type of tobacco is a recessive form, and like the size differences above noted represents a single factor difference from the normal type (see Fig. 150). In Drosophila there is a factor for giant size in the third group which gives rise to a form several times larger than the normal type, and like the factor for dwarf, which is in the same chromosome, there is no difference between it and its relation to other factors and the relation of these factors to each other. These facts like those which have been discussed above merely serve to emphasize the fact that size differences, some of them extremely wide, may depend upon simple

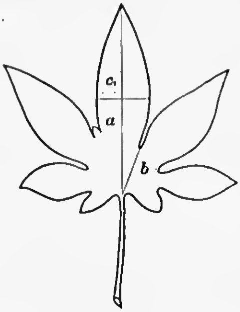

FIG. 84.—Outline diagram of a cotton leaf. The cotton-leaf factor = $\frac{a - b}{c}$. (*After Leake.*)

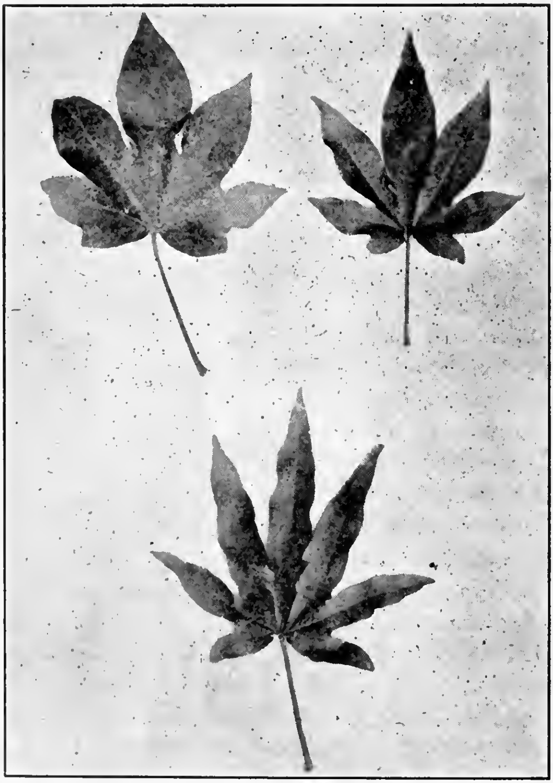

FIG. 85.—Typical cotton leaves; upper left, with leaf factor less than 2; below, with leaf factor greater than 3; upper right, with intermediate leaf factor, approximately 2.5. (*After Leake.*)

factor differences, differing, therefore, in no respect from those other Mendelian differences concerning which no question is raised.

The Cotton Leaf Factor.—Leake has investigated the inheritance of the so-called cotton leaf factor. The results of his investigations are given here in some detail because they illustrate very well the simplest expression of the most common type of quantitative inheritance. The so-called cotton leaf factor is essentially a length breadth index of the terminal lobe of the leaf. It is obtained by dividing the difference between the two measurements *a* and *b* in the accompanying diagram (Fig. 84) by the width *c* of the terminal lobe, or expressed algebraically it is the value of the expression $\frac{a-b}{c}$. Although there are variations in this value for different leaves on a single plant, Leake found that races might be obtained which were characterized by relatively constant leaf factors. Leake crossed one of these races with a mean leaf factor of 1.52 with a race the mean leaf factor of which was 3.47. The mean leaf

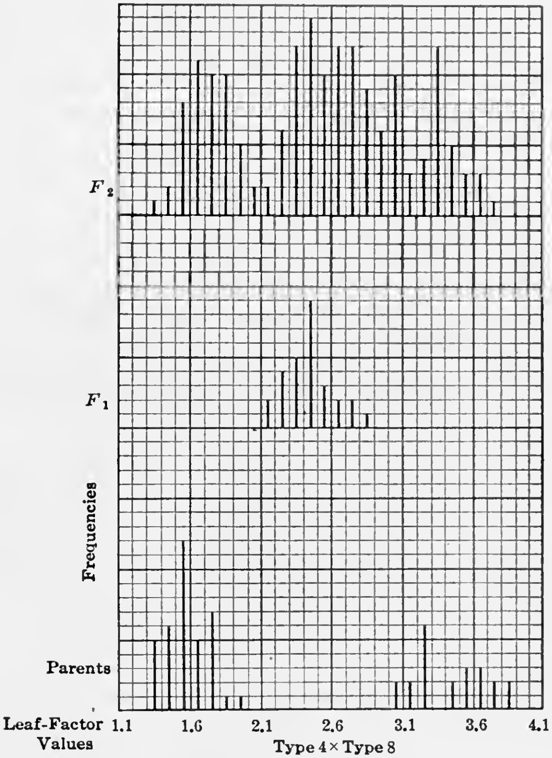

Fig. 86.—Distribution of parental, F_1, and F_2 plants with respect to leaf-factor values. (*After Leake.*)

factor of 28 F_1 plants obtained from this cross was 2.39, a value which does not differ significantly from the average leaf factor of the two parents, 2.49. Fig. 85 illustrates three leaves representing the three types concerned in this cross. From the F_1 plants of this cross 195 F_2 plants were grown, and their leaf factors were found to be distributed as shown in Fig. 86. The striking feature of this F_2 distribution is that, although practically all values for the leaf factor between the two parental extremes are represented, these frequencies of values give a trimodal distribution with modes which correspond approximately to those of the parents and the F_1. If these F_2 individuals be divided into three portions, as shown in Table XXXII corresponding to the two parents and the F_1, the mean value for the upper group is 3.42 as compared with the mean value of 3.47 for the corresponding parental type, the mean value of the mid group is 2.59 corresponding to 2.39 for the F_1, and the lower group has a mean value of 1.66 as compared with 1.52 for its corresponding parental group. In the upper group there were 46 plants, in the mid group 102, and in the lower group 47, a satisfactory agreement with a 1:2:1 ratio.

Table XXXII.—Re-appearance of Parental Values in the F_2 Offspring
(*After Leake*).

P_1		aa Parent type No. 4		AA Parent type No. 8
	Leaf factor	1.52	Mean 2.49	3.47
F_1	28 plants		Aa Mean leaf factor 2.39	
F_2	Classes	Lower	Middle	Upper
	Leaf factor	Less than 2	Greater than 2 Less than 3	Greater than 3
	No. of individuals	47	102	46
	Ratio	1aa	2.2 aA	1 AA
	Mean leaf factor	1.66	2.59	3.42

This case then gives a simple expression of the general phenomena assumed to be operative in the multiple factor theory of size inheritance. If it be assumed that a single factor difference be here operative, then the small parent might be represented as *aa* and the large parent as *AA*. Plants of the genetic constitution *aa* then fluctuate for their leaf factor around 1.52 as a mean, whereas plants of the genetic constitution *AA* fluctuate around 3.47. When these two races are crossed the F_1 is intermediate, for in quantitative inheritance in general the factors apparently do not display dominance but the phenotypic expression of Aa is approximately equal to the average of that of the two parents. If this idea be correct the F_2 should consist in this case of $1AA : 2Aa : 1aa$, which has been shown to be approximately true, if the boundaries shown in Fig. 86 be accepted. It is to be noted, however, even for as simple a case as this that the two parents and the F_1 each have their typical ranges of fluctuation. Considering the parental and F_1 distributions, the upper limits of the smaller parent run into the lower portion of the range of the F_1, and the lower limits of the larger parent run into the upper limits of the F_1. It follows that in F_2, even if there should be only a single factor difference between the two parents, the F_2 classes would overlap. Consequently some of the plants assumed to belong to the lower class and also some of those assumed to belong to the upper class really belong to the middle group, and some of those arbitrarily included in the middle class belong either to the upper or to the lower class.

The only accurate method of classifying those individuals lying near the boundaries of the classes is to test them by growing their F_3 progenies. If they belong to the upper or lower classes they should then give unimodal distributions corresponding to the parental distributions, whereas if they belong in the middle class, they should give trimodal distributions corresponding to the distribution obtained in F_2. In another case Leake has endeavored to apply this test to an entire F_3 distribution, and although the evidence indicates some discrepancies probably due to the presence of minor factor differences, nevertheless the agreement is such as to lend support to the idea of a single main factor difference.

Most size differences however are not so readily interpreted as this one, apparently because a larger number of factors is concerned in them. The general statement with regard to such size differences is that two contrasted races, each of which displays a certain characteristic amount of variability when grown in the pure line, when crossed produce an F_1 intermediate between the two parents and no more variable than either of them. The F_2 from such a hybrid when grown in large populations displays on an average an intermediate position, but some few individuals at either extreme approach the sizes of the parents, and between these extremes lies a continuous series of forms, in distribution usually approximating a normal curve. The evidence of segregation here is the increased variability in the second generation, and subsequent generations display a similar conformity to such an interpretation.

This type of inheritance may best be illustrated by a typical example, but one which has, perhaps, been more thoroughly investigated than any other, namely the inheritance of length of corolla in tobacco. East has investigated the inheritance of length of corolla in crosses between two varieties of tobacco of the species *Nicotiana longiflora.* The smaller of these two varieties has a tube length of about 40 mm., whereas the contrasted variety bears flowers the tube length of which is over twice as great, namely about 93 mm. The two varieties had been self-fertilized for a number of generations preceding hybridization, and since it can be demonstrated that continuous self-fertilization tends to reduce a variety to a homozygous condition, it is fair to conclude that the parents represented varieties homozygous for nearly, if not quite, all their factors. We are not surprised, therefore, to find that they display only a slight variability in flower size. This slight variability is to be considered merely an evidence of the influence of external conditions and of inherent variability in character expression and not of internal heterozygosity, for there is a limit below which it is apparently impossible to force the reduction in variability of any given character. In this case the accompanying table which has been reproduced from East in its entirety will serve as the material for the following discussion.

Fig. 87.—Average flowers of two varieties of *Nicotiana longiflora* with an average flower of the F_2 from a cross between them in the middle. (*After East.*)

It will be seen in Table XXXIII that when the two varieties were crossed the F_1 distribution occupied a position midway between the two parents. The number of plants grown was somewhat larger than that for the parents, consequently the range covered by the F_1 distribution is slightly greater, but calculations of the coefficient of variability show that the variability of the F_1 is only slightly and not significantly greater than that of the smaller flowered parent. When we look at the F_2 from such a cross, we find that although it, like the F_1, occupies an intermediate position, the range has been doubled and this in spite of the fact that the population contained only a few more individuals than that of the F_1. This increased variability is borne out by calculations of the coefficients of variability which are over twice as great for F_2 as for F_1. That the increased variability in F_2 is the result of genetic segregation of some sort is shown by the distributions of F_3 families. They are strikingly different from each other in their position on the range, and in the variability which they display, as is shown clearly in the table.

TABLE XXXIII.—FREQUENCY DISTRIBUTIONS FOR COROLLA LENGTH IN A CROSS BETWEEN VARIETIES OF *Nicotiana longiflora* CAV. (*After East*)

Designation No.	Year	Generation	Parent size	Class centers in millimeters																						
				34	37	40	43	46	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97	100
383	1911	....	....	..	13	80	32																			
383	1912	....	....	1	4	28	16																			
383	1913	....	....	..	4	32	1																			
330	1911	....	....																			6	22	49	11	
330	1912	....	....																			2	16	32	6	1
330	1913	....	....																			5	7	10	2	
383 × 330	1911	F_1	....								4	10	41	75	40	3										
(383 × 330)1	1912	F_2	61							1	5	16	23	18	62	37	25	16	4	2	2					
(383 × 330)2	1912	F_2	61							2	4	2	24	37	31	38	35	27	21	5	6	1				
(383 × 330)1-1	1913	F_3	72										4	20	25	59	41	19	2							
(383 × 330)1-2	1913	F_3	46				1	4	26	44	38	22	7	1												
(383 × 330)1-3	1913	F_3	50				6	20	53	49	15	4														
(383 × 330)1-4	1913	F_3	60				2	3	9	25	37	70	19	10												
(383 × 330)2-1	1913	F_3	77						1	0	1	1	1	2	16	33	43	34	20	6	1					
(383 × 330)2-3	1913	F_3	81										1	1	8	16	20	32	41	17	3	3	1			
(383 × 330)2-4	1913	F_3	80										2	8	14	21	39	39	32	10	1					
(383 × 330)2-5	1913	F_3	50					7	25	55	55	18														
(383 × 330)2-6	1913	F_3	82												3	5	12	20	40	41	30	9	2			
(383 × 330)1-2-1	1914	F_4	44			8	42	95	38	1																
(383 × 330)1-3-1	1914	F_4	43			2	23	122	41	1																
(383 × 330)2-6-1	1914	F_4	85														4	9	38	75	59	6	3	1		
(383 × 330)2-6-2	1914	F_4	87												4	5	6	11	21	33	41	29	8	5	1	
(383 × 330)1-3-1-1	1915	F_5	41	3	6	48	90	14																		
(383 × 330)2-6-2-1	1915	F_5	90														2	3	8	14	20	25	25	20	8	

That the results of experiments in size inheritance may be explained by a multiple factor hypothesis is apparent from the explanation which follows. For the sake of simplicity we will assume that two races A = 50 and B = 100 differ by five pairs of genetic factors which display an equal effect in size production. The genetic formula for Race A may be represented by *aabbccddee*; and the contrasted Race B by *AABBCCDDEE*. We assume that the factors display no dominance, that their effect is equal and cumulative, and that a dominant factor gives a character expression greater by 5 than the corresponding recessive factor. By crossing two such races an F_1 of the genetic constitution *AaBbCcDdEe* is obtained, which on the above assumptions has a size equal to 75. Selfing such a hybrid we would secure, in case these factors displayed independent segregation, the following series of phenotypes:

50	55	60	65	70	75	80	85	90	95	100
1	10	45	120	210	252	210	120	45	10	1

These values are merely the coefficients obtained by expanding the binomial $(a + b)$.^{10} If these values be plotted, they give an approximation to the usual form of normal variability curve as shown by the polygon representing expansion of this binomial in Fig. 15, and this in general is the type of curve obtained in segregation in quantitative inheritance. The increased variability in F_2 is, therefore, consistently explainable on the basis of segregation of size factors which lack dominance and which display cumulative effects.

However, in the above study of flower size inheritance the parental forms were not recovered in F_2. Elsewhere we have adopted a chromosome explanation of heredity, consequently we must inquire what chromosome conditions appear to exist in tobacco. So far as known the number of chromosomes in Nicotiana is forty-eight. With such a large number of chromosomes a duplication of the exact chromosome content of each grandparent, assuming that no crossing-over occurred, would take place only once in about 365 million millions of F_2 individuals. Consequently, if a differentiating size factor be assumed to exist in each pair of chromosomes, the reappearance of the grandparental forms on the assumptions outlined above would be practically inconceivable. It is, however, possible from the data at hand to approximate roughly the probable ratio of occurrence of the grandparental forms in F_2 populations. Assuming that the class distribution in F_2 is of the type of the normal probability curve, then the larger the number of individuals grown in F_2, the greater will be the class range over which the distribution extends. In this particular flower size problem the average mean of the smaller flowered parent is 40.54 mm., and of the larger flowered parent 93.30 mm. Half the difference between the means of the two parents, therefore, amounts to 26.38 mm. Our problem is to determine what proportion of the individuals in an F_2 population lie beyond the limits set by the value $M_{F_2} \pm 26.38$ mm., where M_{F_2} is the value of the mean for the F_2 population. The mean of one F_2 population is 67.51 mm., and its standard deviation, 5.91 mm. Now by mathematical methods it is possible when the standard deviation of a normal probability curve is known to determine what proportion of the area lying under the curve is within or outside of any assigned limits. If we apply these methods to the problem here set, we find that the part of the curve lying outside the boundaries, $\frac{26.38}{5.91} = \pm 4.46\sigma$, is equal to 0.00080 per cent. of the total area under the curve. Since a parental value might as often fall short of these modal limits as exceed them, we may fix twice this value as that marking off the parental portion of the curve. It would, therefore, be necessary to grow some 62,500 individuals in order to recover the parental forms in such an experiment as this. Considering the other F_2 population with a standard deviation of 6.79 mm., the limits in this case expressed in terms of the standard deviation are $\frac{26.38}{6.79} = 3.88\sigma$: therefore 0.010 per cent. of the curve lies outside the indicated limits. This would show that it would be necessary to grow about 5,000 individuals in order to recover the parental form. The values differ strikingly but they give a rough idea of the ratio of occurence of parental forms in F_2 populations of this kind.

East has pointed out that there are about eight mathematical requirements many of them independent which must be fulfilled in order to establish the validity of the multiple factor theory of size inheritance.

1. Crosses between individuals which from long-continued self-fertilization or other close inbreeding approach a homozygous condition should give F_1 populations comparable to the parental races in uniformity.

Continued self-fertilization tends very quickly to reduce a race to a condition in which the individuals are nearly all homozygous. The assumption, therefore, here involved is that the heterozygous condition Aa in general is no more variable than the homozygous conditions AA and aa. There are many exceptions to this rule, so that it can be said fairly that a slight increase in variability need not be taken to invalidate this first condition.

2. In all cases where the parent individuals may reasonably be presumed to approach complete homozygosis, F_2 frequency distributions arising from extreme variants of the F_1 population, should be practically identical, since in this case all F_1 variation should be due to external conditions.

This follows because all the F_1 individuals in such a case presumably belong to the same genotype. The student should compare this statement with the ideas developed in the chapter on pure lines.

3. The variability of the F_2 population from such crosses should be much greater than that of the F_1 population.

This proposition is merely a statement to the effect that segregation for size factors takes place in the same manner as segregation for other factors. Accordingly in F_2 a series of forms is obtained depending upon the recombination of size factors. Furthermore, it may be stated that with a given range, the less the number of size factors involved the greater will be the increase in variability in F_2. The maximum variability as measured by the coefficient of variability would be attained by a single factor difference. As the number of factors for the given range increases the coefficient of variability of F_2 decreases, so that with a very large number of factors the limiting value is that of the F_1 population. It is therefore possible to have size differences which give intermediate forms which appear to breed true in subsequent generations unless a large number of individuals be grown.

4. When a sufficient number of F_2 individuals are available, the grandparental types should be recovered.

Simply a restatement of the consequences of factor recombination.

In general the number of individuals necessary for recovery of the parental types depends upon the number of factors involved, so that with large numbers the expectations rapidly become very slight.

5. In certain cases individuals should be produced in F_2 that show a more extreme deviation than is found in the frequency distribution of either grandparent.

This follows from a consideration of cases like the following. If *XXAABBcc* and *XXaabbCC* be crossed, there will be obtained by recombination in F_2 individuals of the genetic constitutions *XXAABBCC* and *XXaabbcc* which would be larger and smaller respectively than the grandparental types.

6. Individuals from various points on the frequency curve of an F_2 population should give F_3 populations differing markedly in their modes and means.

This of course depends on the fact that the F_2 individuals represent a series of genotypes which give F_3 populations depending on their particular genotypic constitutions.

7. Individuals either from the same or from different points on the frequency curve of an F_2 population should give F_3 populations of diverse variabilities extending from that of the original parents to that of the F_2 population.

The variability of a population depends on the genotype of the F_2 plant selected. If this plant be heterozygous for many factors its variability obviously will exceed that of one heterozygous for but few factors. That plants occupying the same point on a frequency curve may possess different genotypes and be heterozygous for differing numbers of factors is self-evident, and is well illustrated by Nillson-Ehle's case of color of grain in wheat, which has been treated in detail in a previous chapter.

8. In generations succeeding the F_2 the variability of any family may be less but never greater than the variability of the population from which it came.

This proposition is to be taken with some reservation. Absolutely it holds only if the factors involved lie in different chromosomes. If there is any linkage between size factors then the proposition is valid only when the number of factors involved is large. In that case breaks in linkage occur as often in one direction as in the other and so would not greatly influence the result. If the number of factors be small, however, and some of them coupled, then breaks in linkage might profoundly affect the relations in recombination and thus render invalid this proposition.

Castle's Hooded Rats.—Serious objections have been raised to the multiple factor hypothesis of size inheritance particularly on the basis of results of selection experiments. The multiple factor hypothesis depends

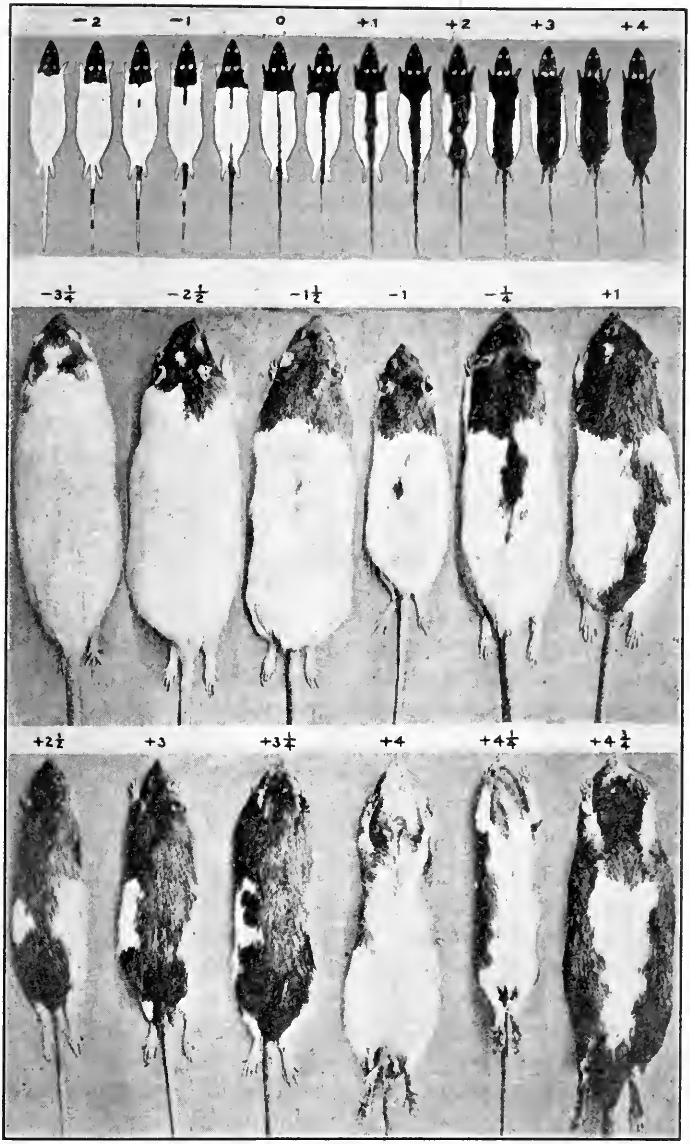

FIG. 88.—Top row, a set of arbitrary grades used in the classification of hooded rats. Middle and bottom rows, skins of rats graded as indicated by the numerals above each skin. The animals +4, +4¼, +4¾, being entirely dark above, are shown in ventral view. (*After Castle and Phillips.*)

on the acceptance of the idea of factorial constancy, which *a priori* need not necessarily be a valid hypothesis. For it is, indeed, strange, if factors are the complex chemical bodies so many have assumed them to be, that they should display such constancy in their relations with each other in spite of the intimate contact which exists between them in the cell. Castle, therefore, has pointed out that assuming that factors vary, it is possible to account for the phenomena exhibited in size inheritance without postulating the existence of so great a number of factor differences.

The case in point is that of the hooded pattern in rats. During the progress of the experiments, over 25,000 rats have been reared and the color patterns studied, so that this case has been studied as extensively perhaps as any bearing on the subject. The rats have been graded according to an arbitrary scale which is designed to express the extent of pigmentation in such a way that the results of the experiments may be analyzed statistically. The set of arbitrary standards employed together with some rats which have been classified according to it are shown in Fig. 88. As a result of these investigations, Castle has drawn a number of conclusions of which the following seem most pertinent in this connection:

1. The hooded pattern of rats behaves as a simple Mendelian character in crosses with either the Irish pattern (white belly) or the wholly pigmented condition of wild rats.

2. Though behaving as a unit, the hooded pattern fluctuates—that is, it is subject to plus and minus variations.

3. Selection, plus or minus, changes the position of the mean and mode about which variation occurs.

4. The results of such plus or minus selections are permanent, for return selection is not more effective than the original selection, and during return selection regression occurs away from the original mode, that is, toward the mode established by selection.

5. During the progress of the original selection variability as measured by the standard deviation was somewhat diminished.

6. Upon crossing the selected plus and minus races with each other, the variability was somewhat increased in F_1 and was further increased in F_2. The extreme condition (plus or minus) of the grandparents rarely, if ever, recur in this generation. Only one individual among 378 F_2 young has been recorded in a grade as extreme as either grandparent.

On the basis of these and other facts Castle argues that we must recognize three types of inheritance:

1. *Typical Mendelian Inheritance.*—Factors of allelomorphic characters may meet each other generation after generation in a common zygote, but segregate in gametogenesis without any apparent modification following their conjugation in the zygote.

2. *Typical Blending Inheritance.*—Factors of allelomorphic characters blend in the heterozygote to form factors of intermediate character. The factors of the heterozygote are as uniform as those of either parent individual.

3. *Partial Blending Inheritance.*—Factors of allelomorphic characters segregate in gametogenesis in the heterozygote, but with modification due to varying degrees of blending between the two allelomorphic factors.

The first category here set off is that of ordinary Mendelian inheritance, and includes all cases in which there is admittedly no contamination by association of the members of an allelomorphic pair in the same individual. The second category calls for an assumption of factorial alteration to such an extent that all the factors of the parents as such disappear and only a factor determining an intermediate condition remains. The case may be illustrated abstractly in this fashion. Let the difference between two races genetically be that between A and a. The races are crossed. Now according to ordinary Mendelian assumptions the factors A and a will segregate in the germ cells of the offspring and without factorial contamination. According to the assumption of typical blending inheritance, however, the two factors A and a when they meet in the hybrid immediately interact and this interaction gives an individual having the genetic constitution $A'A'$ rather than Aa, the symbol A' representing a factor intermediate in its character expression between A and a. As a consequence of this change in the factors involved such an individual, although of hybrid origin, is genetically not a hybrid and would consequently breed true. Admittedly the cases which fall into this category are not common, and it is a matter of debate whether any have thus far been found. As was pointed out in connection with the discussion of the conditions for a Mendelian interpretation of quantitative inheritance, the same relations find a consistent Mendelian explanation in those cases in which the number of factor differences is very large.

The third category assumes that a variety of conditions may arise as the result of the production of an Aa individual. The blending may be definite so that A and a become A' and a', or it may be indefinite and give rise to a series of factors $A_1, A_2, A_3, \ldots A_n$ and $a_1, a_2, a_3, \ldots a_n$, all of which may be represented in the gametes of the heterozygous individual. When definite factor contamination is assumed it may be regarded simply as an expression of the condition that the reacting system Aa reaches an equilibrium when it becomes $A'a'$, a condition for which there are many analogies in chemical reactions. In case some of the original factors still remain, such a heterozygous individual would produce gametes A, A', a', and a, which by conjugation would produce a variety of forms in its offspring. In such a case an individual AA', or Aa' might give rise to the establishment of a new equilibrium, but equally definite with respect to the factors involved. Such an assumption is obviously an hypothesis of extensive multiple allelomorphism in which the members of the system $A_1, A_2, A_3, \ldots A_n$ when in contact with each other react to form new allelomorphs. On the basis of a chemical constitution for the locus in the chromatin material, such an hypothesis would appear not improbable, for if the nucleus of this locus were identical in all the allelomorphs involving it and the changes in it were changes which took place around the fringe of the molecule, inside and end chains perhaps, then there appears to be no good reason for believing that two such similar allelomorphs when in intimate association with each other should not interact to form intermediate factors. While the very existence of the second and third categories is not generally accepted by geneticists, it must be admitted that, provided the assumptions of factorial alterability be accepted, they can explain the known facts of size inheritance.

That a factor as such may vary and that selections of variations in the expression of such a factor may permanently alter its expression in any desired direction, Castle has endeavored to show in extensive selection studies with hooded rats. The selections were made in both plus and minus directions and in each case selection did establish a permanent variation in the direction in which it was made. The condensed results of these selection experiments involving over 30,000 individuals are given in Tables XXXIV and XXXV. These results show very clearly that selection has definitely changed the mode around which the pattern fluctuates and in opposite directions in the two series. Since the hooded pattern has been shown to be a simple Mendelian recessive to self color, does this evidence prove that selection has modified the factor for hooded pattern?

Those who hold to the multiple factor idea of size inheritance contend that it does not, and for several reasons. In the first place the difference between hooded and self-colored rats, while in the main due to a single factor difference, may at the same time involve other minor differences in a number of factors which influence the *extent* of pigmentation when the factor for hooded pattern is present. According to this view selection would result in attaining a homozygous condition for certain of these modifiers and, therefore, in increasing or decreasing the area of pigmentation in the direction of selection. There may be a number of such modifiers and others may arise from time to time by mutation. It is interesting to note that Castle records the appearance of two such mutant individuals. These mutant individuals when tested with each other and the forms from which they arose, displayed a type of inheritance which indicated that their origin involved a single factor difference for extent of pigmentation from the parental group. Might not other mutations have arisen which, on account of their lesser magnitude

TABLE XXXIV.—PLUS SELECTION IN HOODED RATS

Mean grade and number of offspring produced by parents of a particular grade in each generation. The grade of the parents is indicated at the head of each column. In the body of the table is recorded the grade of the offspring (in light-faced type) and the number of offspring (in heavy-faced type) (*Adapted from Castle*).

Generation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Mean grade of parents	2.51	2.52	2.73	3.09	3.33	3.52	3.56	3.75	3.78	3.88	3.98	4.10	4.13	4.14	4.38	4.45
Mean grade of offspring	2.05	1.92	2.51	2.73	2.90	3.11	3.20	3.48	3.54	3.73	3.78	3.92	3.94	4.01	4.07	4.13
Number of offspring	**150**	**471**	**341**	**444**	**610**	**861**	**1,077**	**1,408**	**1,322**	**776**	**697**	**682**	**529**	**1,359**	**3,690**	**1,690**
Lowest grade of offspring	+1.00	−1.00	+0.75	+0.75	+0.75	+1.50	+1.50	+1.75	+1.75	+2.25	+2.75	+2.25	+2.75	+2.75	+2.50	+3.25
Highest grade of offspring	+3.00	+3.75	+4.00	+3.75	+4.25	+4.50	+4.75	+4.50	+4.50	+5.00	+5.00	+5.25	+5.25	+5.50	+5.50	+5.87
Correlation, parents-offspring	0.29	0.31	0.33	0.06	0.16	0.18	0.21	0.09	0.21	0.11	0.23	0.16	0.13	0.31	0.30	0.31

TABLE XXXV.—MINUS SELECTION IN HOODED RATS

Mean grade and number of offspring produced by parents of a particular grade in each generation. The grade of the parents is indicated at the head of each column. In the body of the table is recorded the mean grade of the offspring (in light-faced type) and the number of offspring (in heavy-faced type) (*Adapted from Castle*).

Generation	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Mean grade of parents	−1.46	−1.41	−1.56	−1.69	−1.73	−1.86	−2.01	−2.05	−2.11	−2.18	−2.30	−2.44	−2.48	−2.64	−2.65	−2.79	−2.86
Mean grade of offspring	−1.00	−1.07	−1.18	−1.28	−1.41	−1.56	−1.73	−1.80	−1.92	−2.01	−2.15	−2.23	−2.39	−2.48	−2.54	−2.63	−2.70
Number of offspring	**55**	**132**	**195**	**329**	**701**	**1,252**	**1,680**	**1,726**	**1,591**	**1,451**	**984**	**1,037**	**1,006**	**717**	**1,438**	**1,980**	**868**
Highest grade of offspring	+0.25	+0.50	0	+0.50	0	0	0	0	−0.50	−1.00	−1.00	−1.00	−1.75	−1.00	−1.75	−1.00	−1.75
Lowest grade of offspring	−2.00	−2.00	−2.00	−2.25	−2.50	−2.50	−2.75	−2.75	−2.75	−3.25	−3.50	−3.50	−3.50	−3.50	−3.50	−4.00	−4.25
Correlation, parents-offspring	......	−0.03	0.20	0.02	0.18	0.16	0.14	0.09	0.05	0.15	0.08	0.40	0.18	0.28	0.35	0.26	0.22

and intergrading with the parental forms, escaped notice as mutations but were selected for continuing the experiment? Such an assumption would render intelligible the efficacy of return selection which would be difficult of interpretation on even a multiple factor theory of heredity.

That such a system may exist in qualitative characters has been shown by Bridges for the relation between eosin eye color and its modifiers in Drosophila. One modifier called *dark* intensifies the eosin character. The other six modifiers are all diluters. Thus *cream a* changes eosin to pale yellow or cream color, *cream b* has a similar effect, but not so marked. *Whiting* changes the eosin color to white, so that eosin-whiting flies are indistinguishable from white-eyed flies in color. In these cases there is no question as to the operation of a multiple system of factors, for the specific factors have arisen singly by mutation and their linkage relations establish completely their identities. Nevertheless taken together they would give in a qualitative character a remarkably close imitation of the behavior of Castle's hooded rats.

If, however, we assume with Castle that factors like characters are variable and that allelomorphic contamination occurs, then we may offer an explanation based on a consideration of a single allelomorphic system. For such an explanation the hooded pattern may in general be represented by h, and its dominant allelomorph, the fully colored condition, by H. Self-color is dominant to hooded, but the hooded condition varies greatly in the amount of pigmentation present in the coat. These variations appear to be correlated with definite factor variations, consequently we may designate the factors determining the various degrees of pigmentation in the hooded pattern by $h_1, h_2, h_3, h_4, \ldots h_n$. This series runs from individuals which show practically no color to those which display almost a self-colored coat. If we assume that the character expression of an animal of the genetic constitution h_1h_{10} be intermediate between that of an animal of the genetic contitution h_1h_1, a very light type, and one of the constitution $h_{10}h_{10}$, a very dark type, then we may point out what would occur if selection were carried out in the progeny of such an individual. In the first place the genetic constitution h_1h_{10} of such an animal represents merely the values of the gametes that united to form the zygote. They are assumed to interact immediately, so that perhaps, in addition to the factors h_1 and h_{10}, such a zygote will produce gametes bearing for the most part the factors h_5 and h_6, representing a sort of equilibrium for the interaction of the factors h_1 and h_{10}. There would, therefore, be in the progeny of such an individual some individuals of the genetic constitution h_1h_5 which would be lighter than the parents, and some of the genetic constitution h_6h_{10} which would be considerably darker than the parents. If other products of this reaction, such as h_3, h_4, h_7, h_8, etc., were also produced, and like the original reacting factors h_1 and h_{10}

occurred in relatively infrequent numbers in the gametes, then other combinations would result. A graded series running from light to dark would then be produced, but since the mid-products, h_5 and h_6, would be by far most numerous, in small progenies most of the individuals would display a mid-condition of pigment development. On such an explanation any particular type of hooded pattern would be allelomorphic to the wholly pigmented condition or to the Irish condition, if these latter two with hooded be members of a system of triple allelomorphs. Also, the variability of the factor due to interaction with whichever other member of the allelomorphic pair it happened to be in contact would account for the variability in the expression of the hooded pattern following hybridization.

The progress of selection in such a form on the basis of a single factor as determining not only the hooded pattern, but also the extent of pigmentation in the hooded condition requires us to assume an instability in the factor even when in the pure condition. We would, therefore, assume that, in an animal of the constitution h_5h_5 with respect to the factor for hooded pattern, the instability of the factor leads at times to the production of gametes by such an animal bearing the factor h_4 on the one hand, or h_6 on the other hand. If such gametes were produced relatively infrequently, they would almost invariably mate with gametes of the genetic constitution h_5. The resulting progeny would have the genetic constitutions h_4h_5 and h_5h_6 and they would be slightly lighter and slightly darker respectively than the bulk of the animals of the genetic constitution h_5h_5. Selection of such individuals would rapidly lead to the production of races of the genetic constitutions h_4h_4 and h_6h_6. Individuals of the genetic constitution h_4h_4 on account of the variability in the factor itself would produce some gametes bearing the factor h_3 or the factor h_5, and by continuing the same process of selection a still lighter race of the genetic constitution h_3h_3 might soon be established. Assuming, therefore, that factor variability of this type occurs it is not difficult to see how a continuous process of selection such as Castle has employed should finally result in the establishment of new races differing markedly in their character expressions and possessing a different but related genotype to that of the original type from which selection has been made. Moreover, such an hypothesis accounts for the observed fact that return selection is just as efficient but no more so than the original selection in changing the mean of the races, a fact which presents some difficulties for a strict multiple factor interpretation.

It should be stated that this hypothesis of factor variability does no violence to our conception of the nature of factors, except with respect to a rather ill-established belief in factor constancy. The continuous change in a factor such as we have outlined above reminds us very forcibly of the behavior of certain chemical systems. It is a well-known fact for instance that in some systems an equilibrium is reached when a certain proportion of two substances are present in a chemical system. Thus a system consisting of *A* and *B*, two compounds mutually convertible into each other, may reach an equilibrium when say 2 parts of *A* and 1 of *B* are present in the system. If now a certain proportion of *A* is removed from the system, enough of *B* will be converted into *A* to reëstablish the old equilibrium of $2A:1B$. It is not difficult to see, therefore, that continuous removal of *A* from such a system would finally result in the conversion of all of *B* into *A*. Assuming, therefore, that our original system consisted merely of an unstable chemical compound, it might be possible by continuously removing a certain product of its instability to gradually alter the system in a given direction, much as we have outlined the case for alteration of the hooded pattern by continuous selection in rats. Since such changes are usually reversible, the efficacy of return selection is adequately accounted for.

Nevertheless, although it must be admitted that an interpretation such as we have given above may account for all the known facts of quantitative inheritance, and as the student can readily see it may be employed to interpret the entire set of eight conditions which East has outlined, we advocate the strict multiple factor hypothesis of size inheritance for the following reasons:

1. It is definitely known that large numbers of loci may be concerned in the expression of a certain character. Morgan has stated that over twenty-five factors are known to be concerned with eye color in Drosophila, and similarly a large number of factors affect body color and wing characters. The assumption of large numbers of factors as concerned with a single character does not, therefore, do violence to modern conceptions of factor and character relationships.

2. Size is a complex character depending on the coöperation and coördination of many organs, tissues, and physiological processes. Some factors may, therefore, affect one organ, some another, so from this viewpoint a large number of factor differences might be expected to be present in cases of quantitative inheritance.

3. Although factor constancy cannot yet be considered a universally established fact, those definite investigations which have been reported indicate that factors possess on the whole a high degree of stability. More definite work is needed along this line; provisionally it appears wise to consider factors for all practical purposes as constant.[1]

4. Simple factor differences are known to give size differences,

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[1] That factors are relatively stable entities is being evidenced more clearly all the time. Witness the definite arguments advanced by Bridges and Muller respectively in their recent papers on "Deficiency" and "An Oenothera-like case in Drosophila."

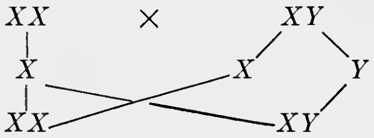
depending many times upon some definite character change in the race, for example, bush and Cupid sweet peas. It appears reasonable to refer more complex size differences merely to differences in several such definite characters.

5. Factor systems affecting a single character have been worked out definitely, which in the complexity of the interrelations they display, rival those interpretations which have been postulated for cases of quantitative inheritance. The trend of investigation seems to establish more firmly all the time the probable validity of the multiple factor interpretation of quantitative inheritance.

CHAPTER XI

INHERITANCE OF SEX AND RELATED PHENOMENA

In the description of the chromosome relations obtaining in the distribution of hereditary units, we have had occasion to show how sex in one form, *Drosophila ampelophila,* depends upon differences in the chromosome constitution. In this species three pairs of chromosomes have equal members in both sexes, but the remaining pair in the female consists of two equivalent *X*-chromosomes, in the male of one *X*-chromosome like those in the female paired to an unequal *Y*-chromosome. The distribution of sex-linked factors finds a logical explanation in their location in the *X*-chromosomes, and in Drosophila more than fifty sex-linked factors have been studied. But thus far the *Y*-chromosome has not been demonstrated to carry any of those factors which are known to be located in the *X*-chromosome. When the chromosome relations obtaining in the inheritance of sex in Drosophila are outlined they are found to be as follows:



Morgan has called this the *XY* type of sex inheritance. This type of sex inheritance is characterized by the fact that females are homozygous for the sex determiners and males are heterozygous for them. Accordingly females produce but one kind of egg with respect to the sex determiners borne by them, but the males produce two kinds of sperm in approximately equal numbers. These two kinds of sperm have been called female-producing and male-producing sperm, because normally when a female-producing sperm fertilizes an egg a female is produced and when a male-producing sperm fertilizes an egg a male is produced. The production of male and female producing sperm in approximately equal numbers and random mating with the egg cells accounts for the approximate equality of the sexes in each generation.

The *XY* type of sex inheritance is characteristic of a large number of forms. Apparently all mammals, including man, belong to this type, a number of insects, and the plants Bryonia and Lychnis. The evidence in some cases is based on the results of sex-linked experiments, in some cases on favorable cytological evidence, but in only a few cases has satisfactory evidence been secured from both sources.

In a previous chapter we have shown in detail how a sex-linked character in Drosophila is inherited. By referring to the list of factors in Drosophila it may be seen that in this insect about fifty factors are known to belong to the first chromosome, and, therefore, to display the sex-linked type of inheritance. Although cases of sex-linked inheritance are known in other animals, in none do we have as complete a body of knowledge as in Drosophila. Nevertheless, there is a sufficiency of other cases to lend strong support to the evidence derived from the Drosophila investigations. In man particularly several sex-linked factors are known, and the evidence in support of this analysis is fairly satisfactory.

A typical case in man is that of color-blindness, which is much more common in males than in females. The factor for color-blindness may be called b and its normal allelomorph B. A normal-visioned woman is then of the genetic constitution $(BX)(BX)$, and a normal man is $(BX)Y$. The corresponding abnormal forms are for women $(bX)(bX)$ and for men $(bX)Y$. Since the factor for color-blindness is recessive, a woman of the genetic constitution $(BX)(bX)$ will have normal color vision. In this we see the reason for the greater number of men that are color-blind. A man with a simplex dose of the factor is color-blind, because the Y-chromosome as in Drosophila carries no demonstrable factors. In the simplex woman, $(BX)(bX)$, on the other hand, the dominant allelomorph determines the type of color vision, so that a normal woman is produced. Simplex women are just as common as simplex men, the greater number of men displaying the color blind character is simply due to the different chromosome constitutions of the two sexes.

The relations which exist in the inheritance of color-blindness are exactly the same as those which exist in the inheritance of white eye color in *Drosophila.* A normal woman $(BX)(BX)$ mated to a color-blind man $(bX)Y$ produces in F_1 normal daughters of the genetic constitution $(BX)(bX)$ and normal sons of the genetic constitution $(BX)Y$. These F_1 normal sons are of exactly the same genetic constitution as all other normal men and, therefore, although they had a color-blind father, they can never transmit the defect. The normal F_1 women of the genetic constitution $(BX)(bX)$, however, when mated to normal men produce daughters of the formulæ $(BX)(BX)$ and $(BX)(bX)$, all of which are, therefore, normal, and sons in equal numbers of the constitution $(BX)Y$, normal, and $(bX)Y$, color-blind. A simplex woman, therefore, although she does not herself exhibit the color-blind character, when mated to a normal man, transmits that character to none of her daughters, but to half of her sons. A color-blind woman can be produced by the rare mating, simplex woman $(BX)(bX)$ by color-blind man $(bX)Y$, or by the still less frequent mating of color-blind woman $(bX)(bX)$ by color-blind man $(bX)Y$, in which latter case all the offspring whether sons or daughters are color-blind. A considerable list of other sex-linked factors demonstrate beyond question that the inheritance of sex and the distribution of sex-linked factors in man is strictly analogous to that which we have found to obtain in Drosophila.

Non-disjunction in Drosophila.—Of particular interest from the standpoint of the inheritance of sex and of the relation between factors and the chromosomes are the results which Bridges has obtained from his extensive investigations of non-disjunction in Drosophila. The investigations on non-disjunction had their origin in certain "exceptions" which appeared from time to time in cultures of Drosophila. Ordinarily in the case of sex-linked characters when a female with the recessive character is mated to a male with the dominant character all the females in F_1 exhibit the dominant sex-linked character and all the males the recessive character. The reason for this fact has been explained already, but it will be clearly apparent from a consideration of Fig. 89, which is a diagram of the results of crosses between vermilion females and red males. The vermilion factor v is borne by the sex chromosomes, and since the males from crosses between vermilion females and red males receive their only X-chromosome from the mother they should all be vermilion-eyed. The females from such a cross receive from the father an X-chromosome bearing the dominant allelomorph of v, consequently they should all be red-eyed. In the great majority of cases, this is the result actually obtained from such matings, but occasionally, about once in 1700 individuals, an exception, a vermilion female or a red male, is produced. The investigation of the "exceptional" females from such matings has provided unique evidence in support of the chromosome theory of heredity and in regard to the relations existing between the sex chromosomes and sex differentiation.

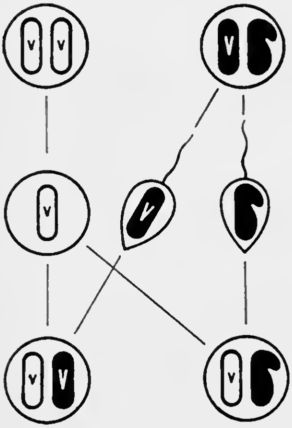


FIG. 89.—The relations of the sex chromsomes to sex production and to the inheritance of the recessive sex-linked character, vermilion eye color, in Drosophila. The straight chromosomes are the X-chromosomes, and the crooked ones the Y-chromosomes. (*Adapted from Bridges.*)

The production of exceptional individuals from matings such as we have considered above apparently results from occasional aberrant reduction divisions in the female such that the two X-chromosomes fail to disjoin from each other. As a result eggs are occasionally produced which contain two X-chromosomes instead of one as is normally the case. In Fig. 90 are illustrated in diagram the consequences of such aberrant reduction divisions in the female. If the X-chromosomes fail to disjoin in the reduction divisions, they may be included in the egg, in which case an egg with two X-chromosomes is produced, or they may both be thrown out into the polar body, in which case an egg with no X-chromosome is produced. This phenomenon Bridges calls primary non-disjunction. An egg $(vX)(vX)$ fertilized by a Y sperm gives a $(vX)(vX)Y$ zygote, and it develops into an exceptional vermilion female. An O egg (one which contains no sex chromosome) fertilized by a (VX) sperm gives a $(VX)O$ zygote, and it develops into an exceptional red male. Zygotes of the constitution $(VX)(vX)(vX)$ and YO are, also, possible as a consequence of such non-disjunction but it is certain that they die, consequently nothing definite can be determined as to their characters. The proof that non-disjunction is the correct interpretation of these exceptional cases in the transmission of sex-linked characters has been established by breeding tests and by actual cytological examination of exceptional individuals.

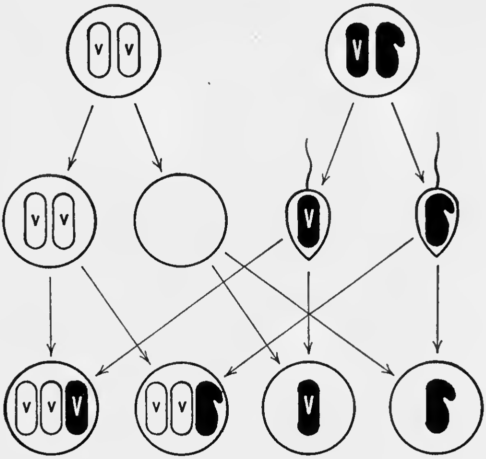


FIG. 90.—Diagram of the production of exceptional individuals, vermilion females and red males, through primary non-disjunction from matings of vermilion female by red male. (*Adapted from Bridges.*)

Assuming that homologous chromosomes pair in synapsis, in an XXY exceptional female two types of reduction divisions are possible. If the two X-chromosomes pair, then in reduction they disjoin and one goes to each pole. The free Y-chromosome then passes as often to one pole as to the other, and as a consequence, two kinds of eggs, XY and X, are produced in equal numbers. On the other hand, when the

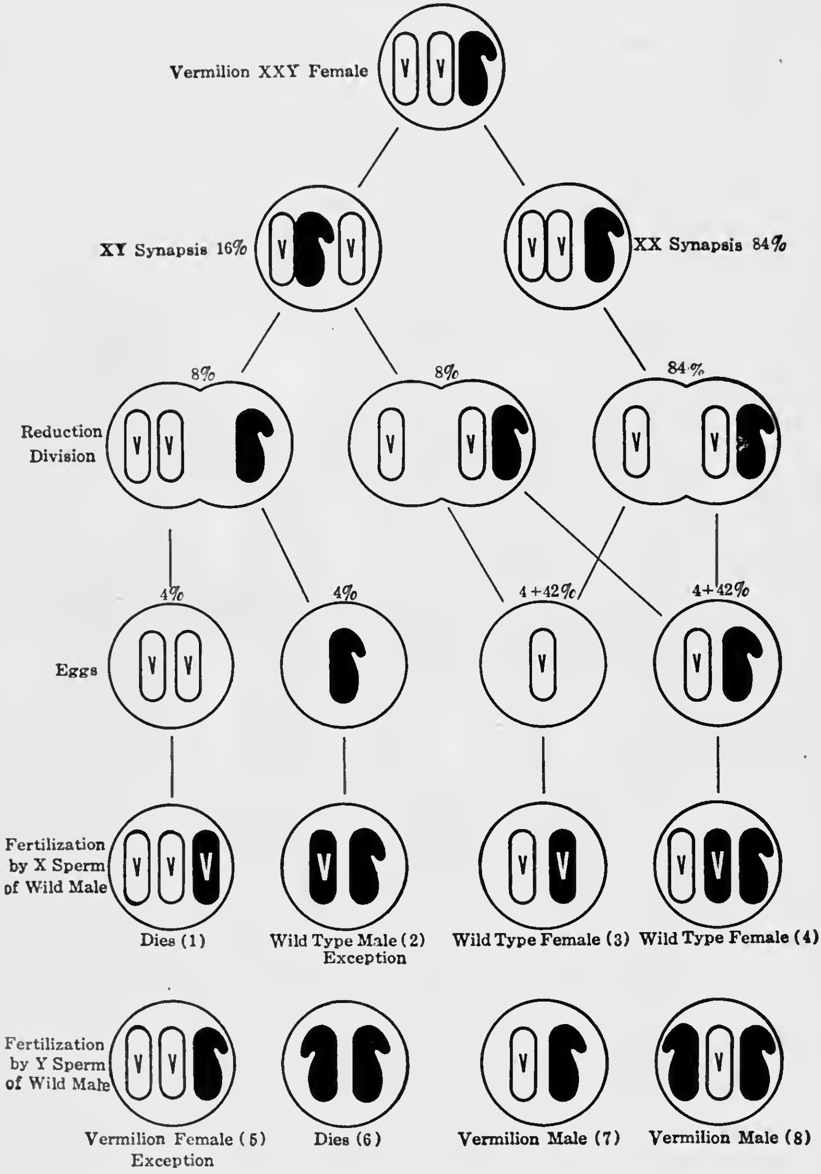


FIG. 91.—Secondary non-disjunction in the female. Diagram showing the constitution of an exceptional vermilion female, the two types of synapsis, reduction, and the four classes of eggs produced. Each kind of egg may be fertilized by either of the two (X and Y) kinds of sperm of the wild male, giving the eight classes of zygotes shown. (*After Bridges.*)

Y-chromosome pairs with an X-chromosome, the free X-chromosome then goes as often to one pole as the other and this results in the production of equal numbers of X, XX, XY, and Y eggs. This set of relations is shown in diagram in Fig. 91, which illustrates the phenomena exhibited in the production of gametes by a vermilion non-disjunctional female. From experimental evidence it has been determined that homosynapsis, *i.e.*, pairing of the two X-chromosomes, takes place in 84 per cent. of cases in non-disjunctional females and heterosynapsis, pairing of an X- with a Y-chromosome, in 16 per cent. of cases. A non-disjunctional female, therefore, will produce four types of eggs in the following proportions

$$4(vX)(vX):4Y:46(vX):46(vX)Y.$$

When a vermilion non-disjunctional female is mated to a red male, the F_1 consists of about 46 per cent. each of red females and vermilion males and about 2 per cent. each of further exceptions, vermilion females and red males. Non-disjunctional females are, therefore, characterized by the production of further exceptional offspring to the extent of about 4 per cent. This type of non-disjunction consequent upon the presence of an extra Y-chromosome is styled secondary non-disjunction. Two additional types of zygotes are produced as a result of secondary non-disjunction, those of the constitution YY which die, and those of the constitution XYY, which make up half of the males and are not exceptional with respect to their characters but which can transmit non-disjunction to a certain proportion of their offspring. It will also be noted that of the regular daughters half are of the constitution XXY. They possess the power of producing exceptions on account of the presence of the extra Y-chromosome, but they can only be distinguished from their normal sisters by breeding tests or less conveniently by cytological examination. It is evident that an F_1 population such as this from the mating of a vermilion female to a red male is very different from that which is normally obtained.

Bridges has followed out very skilfully many of the consequences of the assumption that these exceptional individuals are actually due to non-disjunction of the sex-chromosomes and consequent production of various types of abnormal chromosome constitution. Thus if we consider the exceptions produced by a non-disjunctional female, it is clear that they are a consequence of heterosynapsis in the female. Now when the X-chromosome pairs with a Y-chromosome in synapsis, it very evidently has no opportunity to exchange chromatin material with the free X-chromosome. Accordingly all the XX eggs and consequently all the exceptional daughters from such a female will belong to non-cross-over classes. A consideration of an actual experiment will make this matter clearer. Bridges took non-disjunctional females known from the type of mating involved in their production to be of the genetic constitution $(WVFb'X)(w^evfb'X)Y$ and mated them to bar-eyed males $(WVFB'X)Y$. Obviously the regular daughters of such a mating will be bar-eyed, because they receive from the father an X-chromosome bearing the dominant factor for bar eyes, but the exceptional daughters will not be bar-eyed since both their X-chromosomes are derived from the mother. The question concerning these exceptional daughters is as to whether they are invariably of the genetic constitution $(WVFb'X)(w^evfb'X)Y$ or whether they may occasionally be cross-overs, for example $(WVfb'X)(w^evFb'X)Y$ or $(Wvfb'X)(w^eVFb'X)Y$. Since the loci involved in this case are $W = 1.1$, $V = 33.0$, and $F = 56.5$, normal crossing-over should give about 50 per cent. of cross-overs. By testing the exceptional females again with bar males of the above genetic constitution, the distribution of the males into phenotypes serves as an accurate indication of the genetic constitution of the mother. In every case in tests of thirty-seven exceptional daughters, wild type males $(WVFb'X)Y$ and eosin vermilion forked males $(w^evfb'X)$ made up the largest classes. This indicated that the females were all of the genetic constitution $(WVFb'X)(w^evfb'X)Y$, and, therefore, were non-cross-overs.

The above facts are to be taken in conjunction with the fact that crossing-over actually may occur in non-disjunctional females in homosynapsis. We have pointed out in another place that crossing-over does not occur in males. Now in non-disjunctional females the occurrence of heterosynapsis might well set up a condition like that which is responsible for non-crossing-over in the male for we would have duplicated the exact type of reductional divisions which occur in the male aside from the presence of an unpaired X-chromosome in the reduction spindle. But as a matter of fact the presence of the Y-chromosome does not appear to affect crossing-over between the X-chromosomes in homosynapsis. Thus Bridges has summarized the data for crossing-over in non-disjunctional XXY cultures and compared them with the data for crossing-over in normal XX cultures with the results given in Table XXXVI. Far from resulting in no crossing-over the presence of the Y-chromosome actually appears to have increased the per cent. of crossing-over between loci in the X-chromosomes. No reason can be readily assigned for this increase in crossing-over, but it is of interest to note that the presence of a Y-chromosome does not preclude the occurrence of crossing-over.

In Fig. 91 it is shown that half of the regular sons of a non-disjunctional female are of the type XYY instead of XY as normally. The hereditary behavior of such males as determined by experiment is shown

Table XXXVI.—A Comparison of Cross-over Values from Normal and Non-Disjunctional Cultures in Drosophila (*Data from Bridges*)

Loci	*XX* cultures		*XXY* cultures		Increase	Percentage increase
	Total	Cross-over value	Total	Cross-over value		
WT..........	2,600	24.4	2,436	26.0	1.6	6.6
WV..........	15,177	29.5	12,817	33.7	4.2	14.2
WF..........	6,262	43.1	3,651	49.8	6.7	15.5
WB'..........	1,699	43.6	257	53.0	9.4	21.6
TV..........	2,600	5.6	2,436	5.9	0.3	4.6
VF..........	6,262	22.4	3,651	26.0	4.4	19.6

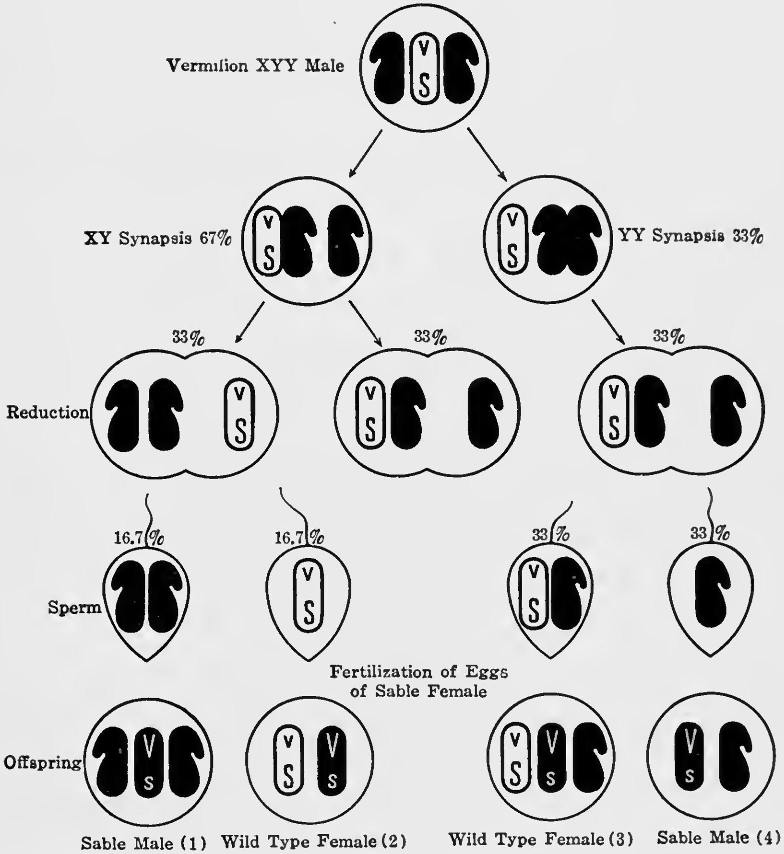


Fig. 92.—Diagram of secondary non disjunction in the male. Four kinds of sperm are produced, but none of these lead to the production of phenotypic exceptionsin F_1. (*After Bridges.*)

in diagram in Fig. 92. There are two possible types of synapsis in non-disjunctional males, the ordinary type of heterosynapsis in the male in which Y is paired with X, in which case one Y is free, or the YY type of homosynapsis in which the X-chromosome is free. Obviously, if these two forms of synapsis take place according to the laws of chance homosynapsis will occur twice as often as heterosynapsis. Assuming this to be true the gametic series of a non-disjunctional vermilion male will be as follows:

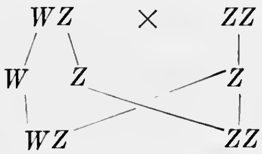
$$2(vX)Y:2Y:1(vX):1YY.$$

When such males are mated to sable females, all the males in F_1 are sable and all the females are of the wild type. No exceptions, therefore, are produced in F_1, but two-thirds of the daughters are non-disjunctional and should give exceptions in F_2. Bridges showed that among fifty-four females only fifteen gave no exceptions in F_2. Consequently 72 per cent. of the females must have been non-disjunctional, and this may be regarded as an insignificant deviation from the expected value of 67 per cent.

We cannot go into detail concerning any other of the numerous points which have been investigated with respect to non-disjunction and its attendant phenomena. That non-disjunction is not due to the presence of a sex-linked factor was proven by two lines of experimental evidence. In the first place such a factor should have shown linkage relations with the sex-linked factors and consequent crossing-over in definite percentages with different loci. An extensive series of matings showed, however, that non-disjunction was entirely independent of linkage relations. The other line of evidence related to attempts to establish pure stock of non-disjunction. These attempts failed completely, a fact readily explainable on the basis of non-disjunction, but reconciled with considerable difficulty to the factor idea. If this were not sufficient evidence, the results of cytological examination are certainly conclusive. Examination of a number of exceptional females showed them to be of the chromosome constitution XXY, and examination of regular females from non-disjunctional mothers demonstrated that about half of them were XXY, as was to be expected from theory. In brief the entire series of investigations give unique support to the chromosome theory of heredity, for throughout in this exceptional behavior of the hereditary mechanism, the factor distribution exactly parallels the unusual history of the X-chromosomes.

From the standpoint of the inheritance of sex the investigations on non-disjunction throw interesting sidelights on the relations of chromosome constitution to sex. Thus females may be of the constitutions XX or XXY or even $XXYY$. Evidently, therefore, the presence of the extra Y-chromosome has no influence on the determination of sex, although it does give rise to unusual relations in the production of gametes. Zygotes of the constitution XXX would presumably be females, but they die and consequently nothing can be determined as to their behavior. Males can be either normal XY or exceptional XYY and XO. The last, although normal males in appearance, are always sterile. The Y-chromosome, therefore, must play some definite, positive rôle in gametogenesis, although we are at present unable to state just what its function is. Along with the preceding cases of female constitutions, these different types of males indicate that the determination of sex depends upon the number of X-chromosomes present. If two be present, a female is produced and the presence of one or two supernumerary Y-chromosomes does not alter this fact. If only one X-chromosome is present a male is produced, and it is immaterial whether no Y is present or whether one or two such chromosomes are present. Throughout, the inert nature of the Y-chromosome is emphasized, the only evidence we have of its positive action being the sterility of XO males. It is important also to note that the derivation of the chromosomes, whether from the female or from the male, does not influence the sex of the offspring. Ordinarily a male is produced when a gamete from the female bearing an X-chromosome is fertilized by a gamete from a male which bears a Y-chromosome. In non-disjunctional strains, however, some males are produced from the union of a Y-bearing egg with an X-bearing sperm, exactly the reverse of the usual procedure. Also in such strains some females are produced by the union of an egg containing two X-chromosomes with a Y-bearing, or ordinarily male-producing, sperm. Non-disjunction, therefore, establishes firmly the intimate relation between chromosome constitution and sex determination.

The WZ Type of Sex-inheritance.—A method of sex-inheritance exactly the reverse of the XY type is that which Morgan has styled the WZ type of sex-inheritance. In this type of sex inheritance the females are heterozygous for a sex-determiner and the males homozygous. If we diagram the relations which exist here, they will be as follows:



The classical example of this type of sex-inheritance is *Abraxas grossulariata*, and, as in the XY type, the evidence for the relations obtaining in the inheritance of sex was given by the behavior of a sex-linked character. As it occurs in the wild, the currant moth is usually of the typical form which is characterized by dark markings on the wings which although highly variable are of characteristic shape and arranged in a definite pattern. This is the form styled *grossulariata*. Occasionally in nature, however, a female is discovered which is much lighter than the type on account of a reduction both in number and size of the black markings of the wings. This is the form styled *lacticolor*. It is of interest to note that according to Doncaster, save in one doubtful case, only females of the *lacticolor* type have been discovered in nature.

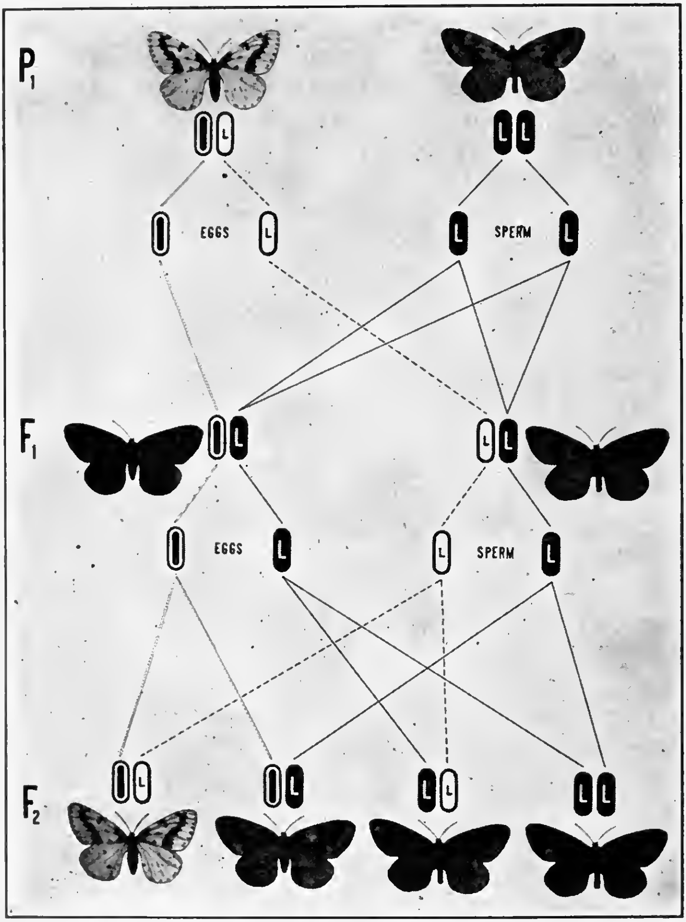


Fig. 93.—Diagram illustrating the inheritance of *lacticolor* type in Abraxas. A *lacticolor* female mated to a *grossulariata* male. (*Adapted from Morgan.*)

The inheritance of *lacticolor* type is illustrated diagrammatically in Figs. 93 and 94. In these diagrams the *W*-chromosome is represented as containing no factors, and the Z-chromosomes, as containing either the recessive factor l for *lacticolor*, or the dominant allelomorph L which conditions the development of the *grossulariata* type. When *lacticolor* females from nature are mated to *grossulariata* males, F_1 consists of *grossulariata* males and females of the genetic constitutions $W(LZ)$

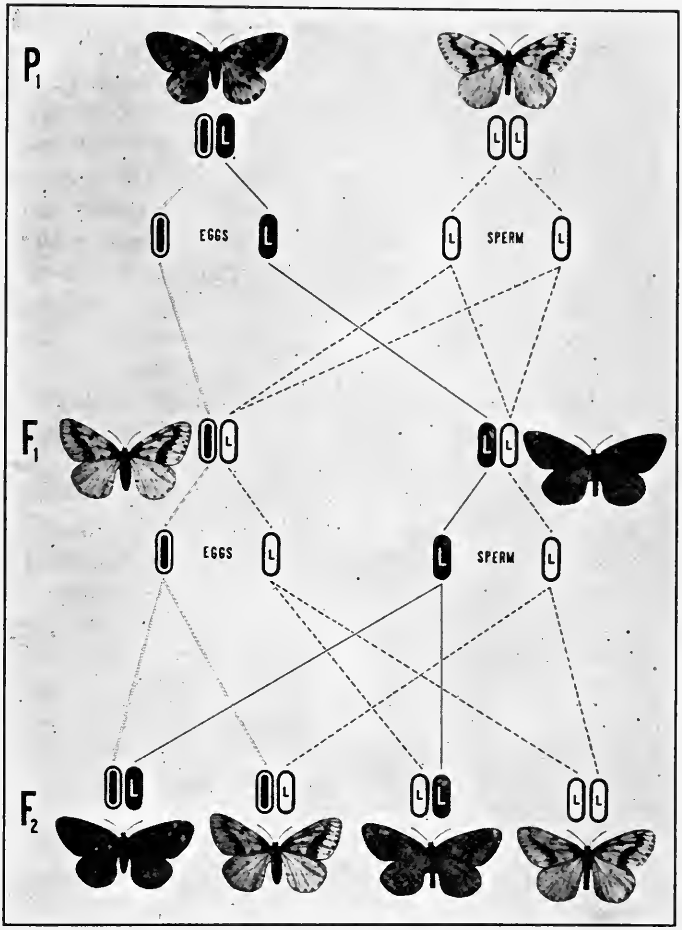


Fig. 94.—Diagram illustrating the inheritance of *lacticolor* type in Abraxas. A *grossulariata* female mated to a *lacticolor* male, the reciprocal cross of that represented in Fig. 93. (*Adapted from Morgan.*)

and $(LZ)(lZ)$ respectively. The females are genetically the same as those of a pure race of *grossulariata*. Abundant experimental evidence demonstrates conclusively that not only are they themselves *grossulariata*, but they cannot transmit anything but the *grossulariata* character to their offspring. The F_2 consists of *grossulariata* males half of which are homozygous for *grossulariata*, therefore $(LZ)(LZ)$, and half heterozygous $(LZ)(lZ)$. Of the females half are *grossulariata* $W(LZ)$ and half *lacticolor* $W(lZ)$. No *lacticolor* males are produced in this generation, but they may be obtained from matings of heterozygous *grossulariata* males $(LZ)(lZ)$ with *lacticolor* females $W(lZ)$. The reciprocal cross requires no special explanation, since it is perfectly clear from the diagram just how the *lacticolor* factor is transmitted in such cases. Throughout, the whole set of experimental evidence duplicates exactly the relations found to exist for the inheritance of white eye color in Drosophila except that the sex relations are reversed.

The cytological relations in Abraxas do not appear to rest upon as firm a basis as those in Drosophila. Apparently there are normally 56 chromosomes in both the male and female, and no pair are obviously unequal in either sex. Apparently then the W-chromosome in the female is about the same size as the homologous Z-chromosome, but like the Y in Drosophila it is a neutral chromosome, *i.e.*, it carries none of the dominant sex-linked factors.

Some additional cytological evidence is provided by examination of lines giving aberrant sex ratios. Doncaster discovered certain strains in which some of the females gave only female offspring, others only a few sons, and still others the normal 1:1 ratio. In these strains the males had 56 chromosomes, but the females only 55. As Bridges points out, if 56 is the normal chromosome number for the females of Abraxas, then those females having 55 chromosomes may be regarded as of the ZO type, corresponding to the XO males in non-disjunctional strains of Drosophila. Such females produce eggs some with 27 and others with 28 chromosomes. If as Doncaster's early observations seemed to show, the odd chromosome ordinarily is included in the polar body, then the eggs would contain mostly 27 chromosomes, and these on fertilization would give 55 chromosome zygotes, presumably females of the ZO type. Later observations of Doncaster's, however, do not confirm the conclusion that 27 chromosome eggs are more frequent than those containing 28 chromosomes. Moreover, although this is perhaps not a very weighty argument, it is not clear why ZO females in Abraxas, if such exist, should not be sterile like their counterparts, the XO males in Drosophila.

It is of considerable interest that exceptions in the transmission of the sex-linked character *lacticolor* occur in Abraxas just as they do in Drosophila. The mating *grossulariata* female by *lacticolor* male should give only *lacticolor* females and *grossulariata* males. However, Doncaster found among 611 females, the offspring of 27 such matings, three *grossulariata* females and two of these were in the same brood. Assuming that the two which were in one brood represented cases of secondary non-disjunction, it would appear that primary non-disjunction in Abraxas is not certainly more frequent than in Drosophila. There appears at present to be good reason for accepting the explanation of non-disjunction for these exceptional cases, although Doncaster has advanced the suggestion that, if the sex-differentiator be assumed to occupy a definite locus in the *Z*-chromosome, then, if the *Z*-chromosome divides in such a way that the factor *l* is separated from the sex factor, exceptions will be produced. This case has not yet been worked out as carefully as has that in Drosophila, but it presents so many close analogies that the possible interpretation is fairly clear.

Of forms showing the *WZ* type of sex inheritance a number are known. Moths and butterflies appear to exhibit this type universally, and such birds as have been investigated are all of the *WZ* type. A familiar example is that displayed by the barred pattern factor in poultry. When black hens are mated to barred cocks, F_1 consists of barred hens and barred cocks and F_2 of 2 barred cocks : 1 barred hen : 1 black hen. The reciprocal cross barred hen by black cock gives in F_1 black hens and barred cocks, and in F_2 1 barred cock : 1 black cock : 1 barred hen : 1 black hen. These are the relations which Pearl and Surface have demonstrated for crosses between the Plymouth Rock fowl and the Cornish Indian Game. The relations are exactly like those in the crosses of *grossulariata* and *lacticolor*, to diagram them it is merely necessary to substitute barred for *grossulariata* and black for *lacticolor*. A number of other characters in birds display the *WZ* type of sex-linked inheritance. Red-eye color in canaries behaves like *lacticolor* in Abraxas when contrasted with black-eye color, but exceptions seem to be unusually numerous. In pigeons a number of factors are known to be sex-linked. Thus in turtledoves normal color is sex-linked when contrasted with white; and in the domestic pigeon the factor for intense coloration is sex-linked. In the fowl Bateson and Punnett have shown that an inhibiting factor for silky pigmentation is sex-linked, and Pearl has demonstrated the existence of a sex-linked factor for high egg production. The latter case because of its economical importance will be given full treatment in another place. Besides these there are many other suspected cases, but they all occur either in moths and butterflies or in birds.

Finally it remains to call attention to another analogy between the *XY* and *WZ* types of sex-inheritance. It is a fact firmly established by abundant experimentation that no crossing-over takes place in the male of Drosophila. Not enough evidence has yet been obtained in other forms to indicate whether the lack of crossing-over is a general phenomenon in males that display the *XY* type of sex-inheritance, but it is highly probable that such is the case. In the silkworm moth which may be assumed to follow the *WZ* type of sex-inheritance, Tanaka has studied very thoroughly the linkage relations exhibited by a system of quadruple allelomorphs, the factors for striped, moricaud, normal, and plain larval pattern, and a pair of factors for yellow and white cocoon color. Sturtevant has pointed out that the experimental results are explicable if there is no crossing-over in the female, the sex-heterozygote in this case. Typical results are given by crosses involving striped, P_s, and plain, p, larval patterns and yellow, Y, and white, y, cocoon colors. Thus striped yellow $(P_sY)(P_sY)$ crossed with plain white $(py)(py)$ gives in F_1 striped yellow individuals of the constitution $(P_sY)(py)$ in both sexes. When F_1 males were crossed back to plain white females, there were obtained 2907 individuals of which 865 were striped white and plain yellow, which are the cross-over classes. This gives a value of 29.8 per cent. for crossing-over in the male. Similarly striped yellow males of the genetic constitution $(P_sy)(pY)$ crossed back to plain[1] whites gave 488 individuals of which 151 were striped yellow and plain white, which are the cross-over classes in this case. The value for crossing-over in this latter case is 30.9 per cent., substantially in agreement with the previous calculation. These results are to be compared with those obtained by crossing back striped yellow females of the genetic constitution $(P_sY)(py)$ to plain white males. From such crosses 1183 offspring were reared all of which were either striped yellow or plain white, consequently non-cross-overs. In both types of sex-inheritance, therefore, no crossing-over occurs in the sex-heterozygote. However, in plants which have the male and female organs in the same individual, crossing-over takes place both in the formation of pollen grains and ovules.

The relations exhibited in sex-determination in some insects are extremely complex and present many differences from the simple types which have been described above. Much painstaking cytological investigation has been done in determining these intricate relations with results which for the most part confirm our general observation as to the essential rôle played by the chromosomes. One of the simplest cases is that of the honey bee. As is well known there are three forms of the honey bee; the queens, the drones, and the workers. Worker bees are females with their sex organs undeveloped as a result of the kind of food furnished them during the larval state. Queen bees lay fertilized or unfertilized eggs. From the former, worker bees and queen bees develop according as to whether they are provided with royal jelly in the larval stage. Unfertilized eggs on the other hand always give drones. Along with these observations it should be noted that under exceptional conditions worker bees lay eggs and these always develop into drones. From a chromosome standpoint, therefore, queen bees and worker bees

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[1] This cross as reported by Tanaka actually involved moricaud larval pattern not plain larval pattern, but, as previously stated, it has been proved that the factor for moricaud occupies the same locus as the factor for plain.

possess the diploid number of chromosomes and drones the haploid number. By means of experimental investigations on the sex ratio A. F. Shull has recently shown that sex-determination in the mullein thrips, *Anthothrips verbasci*, is accomplished by the same method as in the honey bee, *i.e.*, females have the diploid number and males the haploid number of chromosomes.

Morgan has worked out in detail the complex type of chromosome relations obtaining in the inheritance of sex in the hickory phylloxeran, *Phylloxera caryæcaulis.* The life cycle of this insect with respect to the chromosome cycles is shown in diagram in Fig. 95. There are eight chromosomes in this phylloxeran and of these four appear to be connected with the determination of sex. They are the only ones illustrated in the diagram. Beginning with the stem mothers at the top of the diagram, these emerge in the spring from fertilized eggs. They immediately attach themselves to the hickory leaves, thereby causing a gall to be formed around them, and in this gall they lay their eggs. As

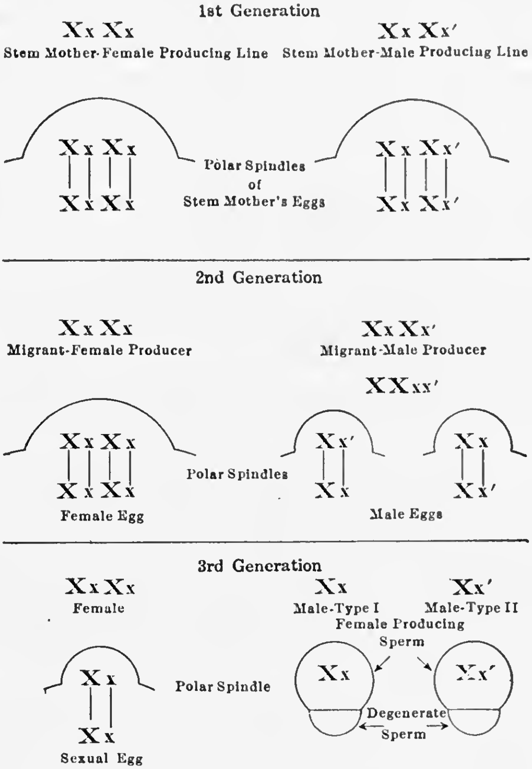


Fig. 95.—Diagram to illustrate the chromosomal cycle of *Phylloxera caryæcaulis.* (*After Morgan.*)

shown in the diagram, these eggs extrude a polar body, but the division is not reductional for the eggs all have four sex-chromosomes, the same number as the mother. These eggs hatch without fertilization into the winged migrant females. Of these there are two kinds, those which lay large eggs and those which lay small eggs, and, moreover, all which come from the same gall and, therefore, from the same stem mother lay the same kind of eggs. Accordingly the stem mothers are of two kinds with respect to their chromosome content as illustrated in the diagram. The female producing stem mothers are $XxXx$ and the male producing stem mothers are $XxXx'$, and the migrant females have the same chromosome content as the stem mother from which they were derived. The migrant female of the type $XxXx$ produces large eggs which throw off a polar body, but do not undergo reduction. The resulting egg develops without fertilization into a minute sexual female. The other type of migrant females, however, lays small eggs in which, prior to extrusion of the polar body, the large X's and the small x's conjugate. One of each of these pairs then passes out into the polar body, so that two types of eggs are produced Xx and Xx' and these develop without fertilization into the minute males. In the sexual females a true reduction division takes place so that her single egg is of the chromosome constitution Xx. The males on the other hand produce sperm cells half of which are Xx or Xx' according to the type of male and half of which have none of the sex-chromosomes. Sperms of this latter type degenerate, so that only female producing sperm remain. When these fertilize the sexual egg the resulting eggs are either $XxXx$ or $XxXx'$, and give rise to the corresponding type of stem mother. This completes the complicated life cycle in this form, and illustrates again the close dependence of sex-determination on chromosome content.

In plants only a few cases of sex-inheritance have been studied and these for the most part inadequately. Two of these, namely *Bryonia* and *Lychnis*, appear to display the XY type of sex-inheritance, but in a somewhat modified form. Thus Correns crossed *Bryonia alba*, which is monœcious, with *Bryonia dioica*, which is diœcious. The former species as a rule bears male and female blossoms on the same inflorescence, the female above and the male below, whereas the latter species constantly bears all male or all female blossoms on the same stem. Correns summarizes his results under four heads as follows:

1. Female plants of *Bryonia dioica* pollinated by male plants of the same species give approximately equal numbers of male and female plants.

2. Female plants of *Bryonia dioica* pollinated by *Bryonia alba* give only female offspring.

3. *Bryonia alba* pollinated by male plants of *Bryonia dioica* gives approximately equal numbers of male and female plants.

4. *Bryonia alba* self-pollinated gives only monœcious plants.

If we assume that all the pollen grains and ovules of *Bryonia alba* are of one kind which is indicated by the fact that it breeds true to the monœcious condition, then there is no escape from the conclusion that female plants of *Bryonia dioica* produce only one type of ovule but male plants produce two types of pollen grains. Unfortunately as is often the case in interspecific hybrids, the F_1 of this cross is sterile and consequently the analysis cannot be carried further.

Shull, however, has studied the inheritance of sex in *Lychnis dioica* which is normally diœcious but occasionally produces hermaphroditic plants. Although this case has not yet been fully analyzed, the results thus far indicate clearly that the male is heterozygous with respect to a sex-determiner, and the female homozygous. The results of Shull's investigations may be stated under several definite heads as follows:

1. Females with pollen from males give substantially equal numbers of male and female offspring.
2. Females with pollen from genetic hermaphrodites give equal numbers of hermaphrodite and female offspring.
3. Females with pollen from somatic hermaphrodites give equal numbers of male and female offspring.
4. Genetic hermaphrodites selfed give equal numbers of hermaphrodite and female offspring.
5. Genetic hermaphrodites with males give equal numbers of male and female offspring.
6. Females from whatever source are genetically identical. Thus females from the cross female × hermaphrodite transmit the same sex-determiners as females from the cross female × male.
7. In crosses between female and hermaphrodite a small percentage of mutant males always appears and in crosses between female and male approximately the same percentage of mutant hermaphrodites appears.

In the above résumé of the experimental evidence on sex-determination in Lychnis, the equality of sexes was only approximate, in fact females usually occurred in excess, and sometimes in considerable excess.

Shull has interpreted this evidence to indicate that in Lychnis the hermaphroditic condition results from a modification of the male condition, and that this modification is reversible as shown by the evidence in 7, above. Interpreted in terms of the XY type of sex-inheritance then, females are XX; males, XY; and hermaphrodites, XY'; and the change from Y to Y' is reversible. Clearly the results indicate that males and hermaphrodites are heterozygous with respect to the sex-determiner, and females homozygous, although later investigations which have not yet been fully interpreted indicate that some disturbing factors are at work, at least in certain cases.

Shull's conclusions are further supported by evidence from the inheritance of a sex-linked character in Lychnis, the only sex-linked character thus far known in plants. The character in question is that of narrow rosette leaves as distinguished from the normal broad type of leaf, and there are other associated character differences (Fig. 96). The narrow-leaved form, called *angustifolia,* was discovered by Baur as a single male mutant individual, a significant fact when taken in connection with its subsequent behavior. The factors in this case are B for the broad-leaved condition and b for the narrow-leaved condition. Crosses between *typica* females $(BX)(BX)$, and *angustifolia* males $(bX)Y$ gave in F_1 all broad-leaved plants $(BX)(bX)$ females and $(BX)Y$ males. Heterozygous broad-leaved females $(BX)(bX)$ mated to broad-leaved males $(BX)Y$ gave all broad-leaved females, and approximately equal numbers of broad-leaved and narrow-leaved males. Hermaphrodites were also found to behave the same way with respect to the factor B as did the males, which confirms the hypothetical relation supposed to exist between hermaphrodites and females. The evidence clearly indicates the existence of sex-linkage of the kind called for on the assumption that Lychnis exhibits the XY type of sex-inheritance.

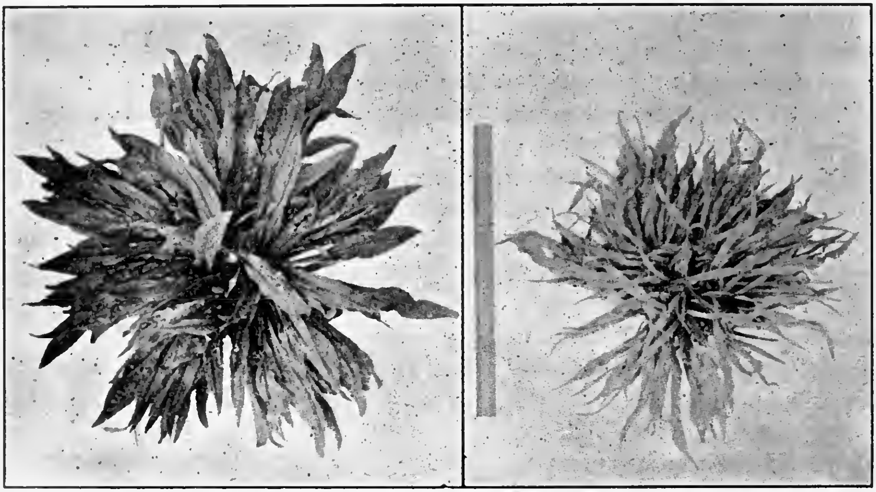


FIG. 96.—Adult rosettes of *Lychnis dioica*; on the left a plant of the normal form, *typica*; on the right a plant of the narrow-leaved form, *angustifolia*. (*After Shull.*)

Secondary Sexual Characters.—Secondary sexual characters are those which appear as an invariable or almost invariable accompaniment of a particular sex in most animal forms. They include many diverse things, such as the antlers in male deer, the horns of the males of some breeds of sheep, the mane of the lion, the power of song of many birds, and various fantastic, ornamental, and combative characters, usually confined to the male. Much historical interest attaches to secondary sexual characters because of the attention directed to them by Darwin's theory of sexual selection. With that we have no particular concern in the present chapter, but shall only consider the inheritance of them in one form as it is related to the inheritance of sex.

In the foregoing discussion no particular reference has been made to sex-factors, because after all so little is known concerning them. In some cases we have found sex accompanied by differences in chromosome content, one sex containing an equal pair of chromosomes which are represented in the opposite sex by an unequal pair, in another case the difference in sex appears to depend upon whether the individual possesses the haploid or diploid number of chromosomes. We have also noted that there are two different types of sex-inheritance, one in which the male is heterozygous and the other in which the female is heterozygous. It is only fair to conclude, therefore, that until more light is thrown upon these matters, the assumption that sex-determination depends upon a sex-factor rests on a rather slender basis. The experimental evidence, it is true, is strictly analogous to certain types of Mendelian inheritance, and an interpretation of the sex-factor may be given which does no violence to our ideas of the complexity of sex-differences. Thus it has been shown by ample evidence that the color of eyes in Drosophila depends upon the coöperation of a number of different factors; we cannot say definitely how many, but mutational changes have indicated that over twenty-five different loci have something to do with the reactions concerned in pigment production in the eye. Yet in spite of this fact the presence of a single factor may make all the difference between a red eye and a white eye. Similarly the sex-factor may act in conjunction with a whole series of other factors, yet the difference dependent upon its presence in the homozygous or heterozygous condition may make all the difference between the two sexes. At least in one form, however, we have even more definite evidence of the presence of a definite sex-factor. Shull has shown in Lychnis that where males are expected, hermaphrodite mutants occasionally appear. If we offer the same explanation for the occurrence of these mutants as we have offered for the occurrence of mutations in Drosophila, a change in a single locus in the hereditary system, then the appearance of these hermaphrodites might be offered as almost conclusive evidence of the sex-determining action of a single sex-factor in this particular case. The evidence here becomes even stronger when we consider the fact that this particular type of change is reversible. Some additional light may be thrown upon this question by the consideration of secondary sexual characters as related to the inheritance of sex, although thus far the evidence has not admitted of an entirely satisfactory interpretation. We shall consider one case, that which Goldschmidt has investigated in Lymantria as an example of the results obtained by investigations of this kind.

Goldschmidt's investigations are concerned with *Lymantria dispar*, the European gypsy moth, and *L. japonica*, its Japanese form. As may be seen from Fig. 97, Lymantria is strongly sexually dimorphic, the females are much lighter in color and larger than the males; *japonica* is somewhat larger than *dispar*, but otherwise in general agrees with it. Goldschmidt's investigations deal with the production of intersexual forms in crosses between these two species. He has shown that with proper combinations of different races of these two species, intersexes may be produced which occupy all possible intermediate positions in a continuous series in which maleness and femaleness are the two extremes. Thus female intersexes, *i.e.*, individuals which are of the chromosome constitution *WZ*, may be obtained which range from those that show only a very slight development of male characters in the feathering of the antennæ to those which are so nearly males that they show only a faint trace of their female origin in a few minor characters. On the other hand, male intersexes of the chromosome constitution *ZZ* may be produced ranging from those which exhibit a few white flecks on the wings up to those which

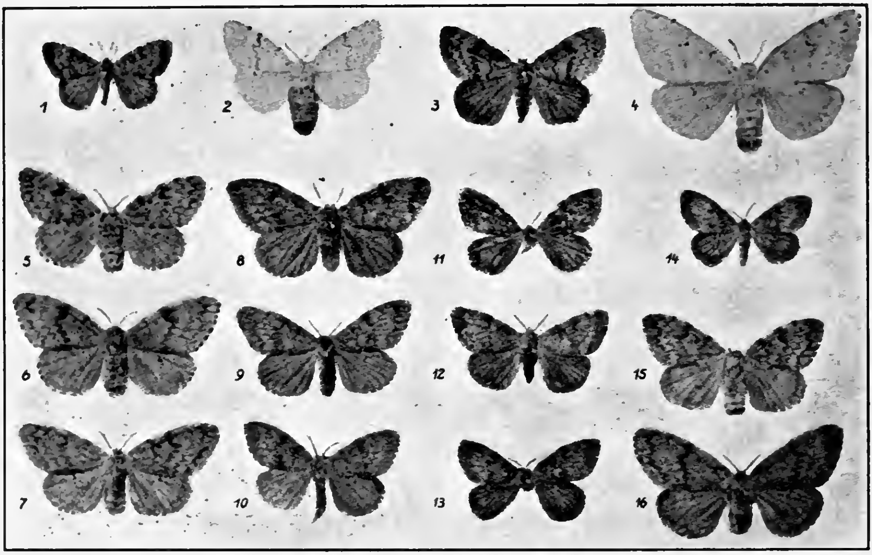


Fig. 97.—Typical forms and hybrids of *Lymantria*; 1 and 2, male and female of *L. dispar*; 3 and 4, male and female of *L. japonica*; 5–16, hybrids combining male and female characters. (*After Goldschmidt.*)

have gone about three-fourths of the way toward the assumption of the entire set of female characters.

Goldschmidt ascribes these results to differences in potency of the sex-factors. The European gypsy moth was found in all races to possess sex-factors of low potency, whereas in the Japanese races the potency was in general higher, but ranged from the lowest to the highest condition. Thus males of a moderately strong Japanese race mated to females of a Japanese race of slightly less potency give in F_1 very low-grade female intersexes. When mated to a somewhat less potent Japanese race a higher grade of female intersexualism results, and when mated to the weakest European race nothing but high-grade female intersexes are produced. The highest grade of female intersexualism, the transformation of those individuals which are genetically females entirely into males, results from matings of females of European races of the lowest potency to males of Japanese races of the highest potency. Now if the development of sexual characters depends upon the sex-factors acting in conjunction with other elements in the genotype, the existence of sex-factors or rather of systems of factors might operate in somewhat the following fashion. In the female the sex-factor in a heterozygous condition acts in conjunction with a set of factors some of which are perhaps sex-linked, although the number of chromosomes, 62 in this case, would indicate that perhaps most of them were located in other chromosomes. In a heterozygous condition then a certain sex-factor with those factors with which it acts produces a female with the female set of secondary sexual characters. In the homozygous duplex condition the same sex-factor, presumably acting in conjunction with the same set of factors as in the female, produces a male with the male set of secondary sexual characters. If now there should be variations in the potency of a sex-factor, as Goldschmidt assumes, then a strong sex-factor, or a sex-factor which would interact more effectively in a given genetic environment would have a tendency in the heterozygous condition to throw the reaction more in the direction of that formerly conditioned by the existence of the normal sex-factor in the homozygous condition. Such relations would result in the formation of female intersexes, individuals genetically females so far as the chromosome constitution is concerned, but developing male characters in a degree corresponding to the greater potency of the introduced sex-factor as compared with the sex-factor normal for the race in question. In case the introduced sex-factor, along with the factors with which it normally interacts and which must never be disregarded, equals in sex-determining power that of the normal sex-factor in the duplex condition, then we might expect to get males of the chromosome constitution WZ. This appears actually to be the case in certain of the experiments. Similarly a weaker potency of the sex-factor might be conceived to result in the production of male intersexes, *i.e.*, individuals of the chromosome constitution ZZ which display female characters, because the weaker potency simply means a more or less close approach to the potency of the normal factor in the heterozygous condition and a consequent approach of the individual to the characters of the male. Goldschmidt's results are intensely interesting and promise much for an elucidation of the problems connected with sex-determination.

We cannot refrain from drawing a comparison between these results and some which have been secured in species crosses in Nicotiana. Thus a definite factor for calycine flower in *Nicotiana tabacum* causes the flowers to develop a petaloid calyx and a split corolla, a striking teratological form. The character is a simple recessive to the normal form in variety crosses but when crossed with *N. sylvestris*, a different species, the normal flower factor in *N. sylvestris* appears to possess a lower potency than that of normal flowered varieties of *N. tabacum*. Consequently the hybrids are intermediate with respect to the flower character expression, all of the flowers on a given plant exhibiting some development of the calycine flower character. We interpret this to indicate that the normal flower factor of *N. sylvestris* does not interact normally with the set of factors which interact to determine the floral character expression in the hybrid, but that the calycine flower factor is able to interact normally and to its full extent with these factors. As a consequence the flowers of the F_1 hybrid are strongly calycine. This interpretation is further supported by the fact which we have previously set forth in some detail that practically the entire set of characters are determined by the *N. tabacum* parent. It is conceivable that crosses with other species would show the same character of variability in potency as has been found for the sex-factors of Lymantria. At any rate a close analogy here exists between the behavior of sex as a character and the behavior of a character known to depend upon a simple factor difference.

The evidence which has been presented with reference to the determination of sex lends strong support throughout to the idea that sex-determination depends on the genotypic constitution of the individual. This does not, it must be clearly understood, mean that other external factors may not act to disturb the usual relations just as they occasionally do with other factors; but as in such cases these external factors must act in conjunction with the genotypic sex-factors. To assume that changes occur willy-nilly in the case of sex-factors is no more warrantable than to assume that other factors change frequently in response to environmental conditions, an assumption that does violence to the high degree of stability which has been observed to obtain for factors in general.

CHAPTER XII

SPECIES HYBRIDIZATION

In the preceding chapters an attempt has been made to show how character differences in a large number of plants and animals may be interpreted on the basis of differences in the unit factors which are distributed to the germ cells during gametogenesis. The character differences, however, which were analyzed, although often seemingly complex, were really rather simple, for rarely were more than four or five factor differences taken into account. In a few species of plants and animals the number of factors which have been investigated is considerable, but when compared with the number of factors which must constitute the entire hereditary material of a species it is an insignificant fraction of the total. The analyses which have been presented, therefore, are for forms which possess an enormous number of factors in common. The differences which they display are mostly unessential alterations in scattered loci in these systems.

With the taxonomic question as to what constitutes a species difference, we are not greatly concerned. It is clearly apparent that species as they have been named represent widely divergent differences with respect to the extent of separation from related species. It must be clear to the geneticist, therefore, that specific difference is a variable thing, sometimes meaning one thing, sometimes another. If we look at the question from the standpoint of the number of factors involved, we see clearly that races of plants and animals may differ in one or many genetic factors. Just where the line should be drawn which distinguishes varieties, forms, species, etc., would therefore appear to be almost wholly an arbitrary matter, usually to be decided from considerations of convenience. Whatever it is, however, the distinction cannot well be viewed from the genetic standpoint, for ordinarily the systematist works with plants and animals which have not been investigated in such a fashion, and, in the case of the more widely separated forms, with those which cannot be so investigated.

A genetic investigation of the difference between two species depends upon the possibility of crossing the species in question, and further upon the possibility of securing offspring from the progeny of such a cross. Not infrequently this latter condition is not fulfilled, for it often follows as a result of species hybridization that the individuals thus produced, although vigorous and normally developed, are totally sterile. The mule is a familiar example, many others could be given, but they will be considered elsewhere along with the problem of sterility in species hybrids. For the present we shall consider one of the simpler cases in which the species hybridized, although differing very markedly in morphological characters, produce hybrids which appear to be fully fertile.

Species Hybrids in Antirrhinum.—Baur crossed the wild *Antirrhinum molle* with the common garden snapdragon, *Antirrhinum majus*, and Baur and Lotsy have made extensive studies of the progenies obtained in successive generations of this cross and of other species hybrids in Antirrhinum. *Antirrhinum majus* and *A. molle* differ strikingly in a large number of morphological characters. The size proportions and general characteristics of the common snapdragon of the garden are familiar to everyone. It is a strong growing erect herbaceous plant, about three feet high producing spikes of large zygomorphic flowers. Under the careful attention of commercial seedsmen it has produced a very large number of varieties which differ in the form and color of the flowers, in height and in other characteristics. *Antirrhinum molle* on the other hand is a low growing prostrate plant which is profusely branched and produces flowers about one-third as large as those of *majus*, but very like them in form and general appearance. The species differs from *majus* also in being apparently totally self-sterile, so that with respect to their genetic constitution plants of *molle* are normally heterozygous to some extent. Since *molle* occurs in nature in a number of slightly different forms its self-sterility must not be lost sight of in interpreting the results of hybridization between it and *majus*. F_1 of the reciprocal crosses *molle* × *majus* and *majus* × *molle* are completely self-fertile, and identical in every respect. Minor differences did occur but they were of such a nature that they could be accounted for as a result of the slight degree of heterozygosis of the particular plant of *molle* which was used as a parent.

Baur employed a peloric *majus* for crossing with *molle* in order that he might follow a known factor difference throughout the investigation. The F_1 plants in this experiment bore zygomorphic flowers, a fact which indicated a corresponding behavior as regards dominance for the factor for zygomorphic flowers in *molle* and *majus*. Six F_1 plants differing slightly in their characters were selected as parents for the F_2 generation. Lotsy grew the progeny of five of these, obtaining from them 624 F_2 plants. The general conclusions which Baur and Lotsy have drawn from a study of these F_2 plants is that the extreme range of forms displayed, so great that no two plants resembled each other in all their characters, is a result of Mendelian segregation and recombination of characters. The diversity, however, was so great as to preclude the application of any exact factor analysis to the case.

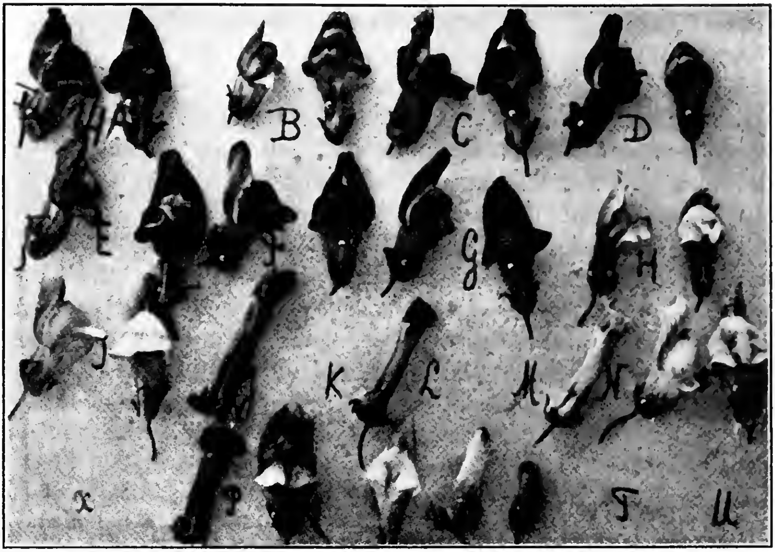


FIG. 98.—Flower types obtained in F_2 of a cross between *Antirrhinum majus* (peloric) and *A. molle.* (*After Lotsy.*)

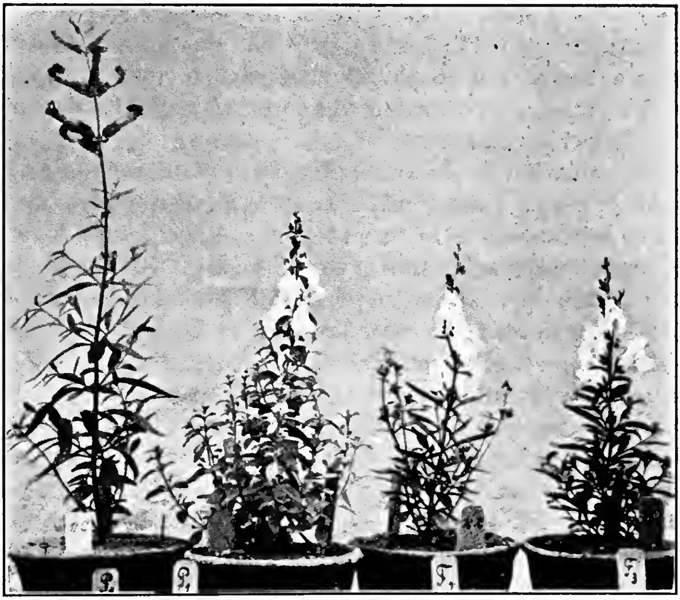


FIG. 99.—Beginning at the left, a peloric *majus* of the type used in crosses with *molle*; a plant of *molle*; a plant much resembling *molle* obtained in F_2; and on the extreme right the F_3 progeny of such a plant. (*After Lotsy.*)

In one F_2 population of 255 plants Lotsy was able to distinguish about twenty-five different flower types as shown in Fig. 98. The flower types were not distinct, but represented merely different steps in an almost continuous series, save for the discontinuity incident upon the sharp segregation of a group of plants which bore peloric flowers. Moreover, within any of these flower types the plants differed greatly in a number of other characters, such as size, color of flower, form of leaf, habit of growth, etc. As regards fertility there was segregation into self-fertile and self-sterile plants, the former being in the majority. Of the 255 plants, 135 produced zygomorphic flowers, 119 peloric flowers, and one plant produced both zygomorphic and peloric flowers. In color the flowers on different plants ranged from the deep red of the *majus* parent to the pale color of *molle.*

Lotsy also grew several F_3 populations. One of these from an F_2 plant bearing hooded zygomorphic flowers consisted of 209 plants all of which were different, indicating again an extreme condition of heterozygosity. Not a single plant produced flowers displaying the hooded character of the parent plant. There was again a vast array of flower forms, twenty-three different types being represented. With respect to the peloric condition, 113 plants bore peloric flowers only, 94 zygomorphic flowers, and 2 bore both types. Although several different colors were represented, Lotsy was able to arrange them in two classes; the first consisting of 153 plants approximating the red color of *majus,* and the second group of 56 plants of about the color of the pale *molle* parent. There was, therefore, a fair indication of Mendelian segregation for color in this generation.

In this population as shown in Fig. 99 a plant was obtained which very closely resembled the type of *A. molle* in all its characters, and reproduced these characters in its progeny. Other plants were obtained which strongly resembled *majus* in certain of their characters, but not so completely throughout. The important feature here is the fact that even in F_2 segregation and recombination of factors have produced a plant which is practically identical with one of the parents.

Other F_3 populations were grown from F_2 plants displaying different sets of characters. One of these from a zygomorphic F_2 plant produced a population segregating for color and form (zygomorphic *vs.* peloric) of flower. Another population from a peloric F_2 plant consisted entirely of peloric flowering plants, but in this population there were many different color classes. An F_2 plant of the pale color of *molle* gave an F_3 population consisting entirely of pale-flowering plants but showing segregation in form and for the peloric character.

Obviously if results such as these are to be explained on a Mendelian basis, it must be assumed that a relatively large number of factor differences exist between the two species under consideration. When we observe the number of differences in habit, form, size, etc., which are known to obtain between the two species, this assumption does not appear to do violence to actual facts in the case. Baur has sought by systematic hybridization investigations to determine which of the known factors of the hereditary material of *A. majus* are also contained in that of *A. molle*. From these investigations he concludes that *A. molle* certainly possesses the factors indicated by the incomplete formula *BBDDEEFFll*, in which *B* represents a factor for yellow flower color; *D*, a factor for extension of pigment to the tube of the corolla; *E*, the factor for zygomorphic flowers; *F*, a base factor for red flower coloration which is epistatic to *B*; and *l*, a recessive factor which determines a low intensity of flower coloration. His success in determining the presence of these factors in the hereditary material of *A. molle* has led Baur to conclude that it is entirely within the range of possibility to analyze completely the differences which exist between these two undoubted species. All the unusual flower forms, therefore, which are obtained by crossing them are to be regarded as the results of peculiar factor interactions. We have pointed out in previous chapters that it is not always possible to predict the character expression of a given set of factors from a knowledge of their known expression in certain combinations. That this condition is here operative is borne out in part by the fact that certain flower types which appeared in F_2 did not reappear even among fairly large numbers in the F_3 generation from such F_2 plants. We consequently can state with assurance in spite of unsatisfactory ratios and peculiar character expressions that the results obtained in this species cross may reasonably be interpreted in harmony with Mendelian doctrine.

Detlefsen's Cavy Hybrids.—A similar line of investigation in animals has led Detlefsen to similar conclusions. He crossed the tame guinea-pig, *Cavia porcellus*, of which many different races have been produced under domestication, with the wild *C. rufescens*. The latter differs from the tame guinea-pig in a number of respects. It is very much smaller, weighing about half as much as the tame guinea-pig, and in skeletal measurements and other characters it is definitely set off as a distinct species from *C. porcellus*. In color it is of the agouti type common to all wild rodents, but the agouti differed from that of the tame guinea-pig in having less power to exclude black and brown from the hair than has the agouti of the tame animals, consequently individuals of the wild *C. rufescens* have darker coats than those of the tame *porcellus*.

By crossing *C. rufescens* and its hybrids with *porcellus* with various races of *porcellus*, Detlefsen was able to study the inheritance of the following factors in this species cross:

A—the agouti factor, which operates by restricting the black or brown pigment in the hairs thus producing the gray or agouti pattern. There are variations in the regional distribution of the restrictive action. The allelomorphic condition *a* gives self-colored individuals.

B—the factor for black. The allelomorph *b* conditions a brown coloration instead of black.

C—the basic color factor in rodents. The allelomorphic condition represented by *c* gives albinos.

E—a factor conditioning the extended type of pigmentation of self-black or brown animals. The allelomorph *e* gives the black-eyed or brown-eyed red or yellow coat.

R—the factor for rough or rosetted coat, as distinguished from the smooth coat determined by the allelomorph *r*.

The work of a host of investigators has demonstrated beyond question the Mendelian inheritance of these factors in races of the tame guinea-pig. Castle in particular has demonstrated how these factors behave in Mendelian fashion, one among the first investigations establishing the general validity of Mendelian principles. Moreover, these conclusions have been abundantly confirmed by investigations with other rodents, which appear to possess a closely analogous series of color factors.

Detlefsen's experiments were conducted by crossing tame female guinea-pigs to wild males, and then mating back the hybrid females to tame male guinea-pigs. This was necessary because the male hybrids were sterile until back crosses to the tame guinea-pigs had been made for two or three generations. Crossing back to the wild species was impossible on account of the scarcity of wild animals and their failure to breed freely under domestication. The investigations were carried through eight generations, during which many types of matings were made, and a total of 1160 hybrids were reared and studied.

As a result of these investigations Detlefsen concludes that the wild *rufescens* is of the constitution *AABBCCEErr* with respect to the factors noted above. Moreover, the relation of these factors as respects dominance and segregation was throughout identical with the relations displayed in intervarietal crosses in the tame guinea-pig. Recombinations of factors occurred in the normal fashion so that it was possible to secure hybrids showing any type of coloration found in the tame guinea-pig. The conclusion, therefore, that interspecific crosses between *C. porcellus* and *C. rufescens* display complex Mendelian inheritance appears to be established by these investigations.

It may be pertinent, however, to enquire whether homologous factors normal for the two species are really identical. If we assume that the two species possess similar genetic constitutions, *i.e.*, have similar sets of chromosomes bearing the factors in like arrangement, it is entirely conceivable that, although the formal arrangement of factors in the hereditary material might be the same for the two species, the actual factors themselves might differ in certain respects, for example in the exact type of character expression and in their power to react with a given set of factors. If the differences be relatively slight, the factors might still be able to interact with each other approximately in the normal fashion, and to display allelomorphic relations dependent upon their position in the hereditary material. On this point Detlefsen contributes very important data which we shall consider somewhat in detail.

The first set of observations relates to the differences between the agouti factors of *C. porcellus* and *C. rufescens*. It is a common observation that the agouti pattern in rodents in general is a variable one. Some of this variability is unquestionably due to the presence of modifying factors, but not all such variations can be interpreted in this fashion. Elsewhere we have pointed out that in mice a system of quadruple allelomorphs includes the factors for yellow, black, gray, and gray with white belly. In the rabbit, Punnett's results may be interpreted as establishing the existence of a triple system of multiple allelomorphs consisting of the factors for yellow, agouti, and black. Similarly in the tame guinea-pig there are apparently allelomorphic variations which affect the agouti pattern, but Detlefsen finds, nevertheless, that these never condition the type of agouti presented in *C. rufescens*. Detlefsen points out that agoutis in common restrict black or brown in the sub-apical band of individual hairs so that the dorsal hairs present a barred appearance. More powerful restriction is shown in the hairs of the belly, but there is always a close correlation between the amount of restriction in dorsal and ventral regions, for the darker the dorsal region, the darker is the pigmentation of the ventral surface. The wild agouti factor was distinguished by its weak restricting power, so that ordinarily the yellow sub-apical band in the hairs of these animals was distinctly narrower than in some agouti guinea-pigs. In some cases the lack of restriction was so marked that only a slight sprinkling of agouti hairs in the adult gave evidence of the existence of the agouti factor. Moreover, in some cases the wild agouti pattern carried with it a ticked belly, a condition apparently unknown in the tame guinea-pig. Some variation was observed in the agouti patterns of the original individuals of *C. rufescens* and this must not be forgotten in interpreting Detlefsen's results. Dark agoutis produced by constantly mating wild agouti hybrids to tame non-agouti guinea-pigs, were mated to tame agouti animals. We may represent the factor for wild agouti by A', that for tame agouti by A, and that for the allelomorphic condition in the tame guinea-pig by a. Following this formula, then those dark agoutis produced by mating wild hybrid agoutis to tame non-agoutis must have been of the genetic constitution $A'a$. When such animals are mated to tame agoutis two types of animals are produced, those of the genetic constitutions AA' and Aa respectively. Phenotypically these two classes of individuals are exactly alike for the powerful tame agouti factor is alike dominant to the wild agouti factor A' and to the tame non-agouti factor a. When the individuals of this population were bred to tame non-agouti animals of the genetic constitution aa the existence of the two above-mentioned genotypes was clearly demonstrated, for half the individuals gave progenies exhibiting sharp segregation into light tame agoutis and dark wild agoutis in approximately equal numbers and the other half gave progenies consisting of approximately equal numbers of light tame agoutis and non-agoutis. Other tests satisfactorily supported this analysis so that it may be concluded that the agouti factor of the wild *C. rufescens* is different from the agouti factor of the tame *C. porcellus*, but that they are allelomorphic to each other. If we consistently follow up the hypothesis which we have developed as to the constitution of the hereditary material and the operation of the chromosome mechanism, this can only mean that the factors for agouti, although different, occupy corresponding loci in the hereditary system of these two species. Aside from certain observations indicating differences between the rough factor of wild and tame guinea-pigs we have no evidence as to whether or not those other factors, the inheritance of which was investigated, are different, but we may safely conclude that factors of corresponding behavior occurred at exactly the same loci in the hereditary system of the wild *C. rufescens*.

Evidence as to the difference between the two agouti factors is also provided by the irregular behavior of the wild agouti factor in the hybrids. Although the first hybrids between the wild agouti and tame non-agouti guinea-pigs are mostly of the dark wild type with ticked bellies in subsequent generations there appear agoutis which are so light as to approach closely the light agouti type of the tame parent and others are so dark that the individuals show only a slight sprinkling of agouti hairs. Individuals displaying such modifications of the wild agouti pattern show no very regular type of behavior, for dark individuals sometimes produce some light individuals and the light individuals sometimes produce some dark ones. The dark modification, however, is most common and often becomes more pronounced upon successive dilutions with tame blood. An interpretation of such phenomena cannot be made satisfactorily unless we consider the agouti factor as a member of a complex system of factors which together operate to give the agouti type of coloration. From this standpoint it is not at all strange that the wild agouti factor acting in conjunction with a corresponding system of factors mostly derived from the tame guinea-pig should exhibit the full power of its customary restrictive action because of a failure to set up wholly harmonious relations with these factors. This modifying of the wild agouti pattern, therefore, lends additional support to the conclusion that these two agouti factors, although occupying homologous loci in the hereditary systems of the two species are different from each other.

The Forms of Species Hybrids.—Thus far we have dealt with two species crosses which have given satisfactory indications of behavior essentially in accord with generally accepted Mendelian principles. The remainder of the chapter will be devoted to general considerations respecting species hybrids and to particular cases which do not give entirely satisfactory evidence of Mendelian behavior. In common with most variety hybrids, species hybrids display marked uniformity in the first generation and equality of reciprocal crosses. Exceptions, however, occur to both these conditions and these we shall take up later in the discussion.

With respect to the characters which they display species hybrids usually represent an intermediate condition as compared with the parents. We may refer this condition to a mixture of dominant factors derived from both parents and in some cases to actual intermediate expression of contrasted allelomorphs, as is not uncommon in variety hybrids. The intermediacy of F_1 in species crosses is a well-known phenomenon and is so common that it may be regarded as the rule. This condition was well known to the older hybridists, such as Kölreuter, Gärtner, Naudin, and Focke, all of whom investigated extensive series of species hybrids with respect to the characters both of the immediate hybrid and of its progeny. The intermediate condition however, is not universal, for examples are known of all conditions from that of strict intermediacy to a condition so nearly resembling one parent in certain cases that only slight character differences or sterility establish the existence of an actual cross.

Intermediate species hybrids are so common that it seems superfluous to call especial attention to them, nevertheless this will be done in order to point out the relation of the intermediate condition to other characteristic features of species hybridization. In the first place the intermediate condition is not associated with any particular degree of fertility in the hybrids. Partial sterility is a common characteristic of wide crosses, and in fact this sterility in some cases appears to be complete. The Antirrhinum species hybrids are intermediate in practically all characters, but they are apparently completely fertile. Such cases are, however, uncommon in species hybridization, but nevertheless a few others have been studied. Baur and Lotsy have reported other species hybrids in Antirrhinum which give fertile intermediate hybrids.

Some species hybrids in Nicotiana are known to be very nearly completely fertile. East has reported investigations of a cross between *N. alata* and *N. langsdorffii*. *N. alata* has flowers the corolla length of which averages about 82 mm., whereas the corolla length of flowers of *N. langsdorffii* averages not over 22 mm., so that *N. alata* flowers are nearly four times as large as those of *N. langsdorffii*. In addition to these differences there are other distinct differences between the two species. Nevertheless examination indicated that there was little, if any, diminution in fertility in F_1. A few other species hybrids in this group of Nicotiana give highly fertile F_1 hybrids, for example *N. alata* × *N. sanderæ* and *N. langsdorffii* × *N. sanderæ*. There appears to be little reason for not regarding these as species hybrids, although it should be stated that some investigators feel inclined to restrict the species concept to forms which display a certain degree of partial sterility in F_1. Such a line of separation must, however, be purely arbitrary since it can be shown that fertile species hybrids merely represent one of the extremes in a continuous series extending from complete fertility to complete sterility.

Since partial sterility is such a characteristic feature of species hybridization, it is not surprising to find that diminution in fertility is not associated with any particular kind of character expression in the hybrids. Intermediate hybrids as well as those which more or less resemble one of the parents usually, therefore, display a considerably diminished fertility. Not much has been done with such hybrids for aside from exceptional instances sterility presents at once a bar to their further analysis and to their use for economical purposes. A familiar example, the mule, a cross between *Equus caballus* and *E. asinus*, has given no authentic case of the production of offspring, although produced for many centuries under domestication and in vast numbers. Among plants so many examples occur that it is of no advantage whatever to attempt an enumeration of them here. The student who is particularly interested in such matters will find that excellent compilations of species hybrids in plants have been made by Gärtner and Focke; and Ackermann, Przibram, and Rörig have performed a similar service for the animal kingdom.

In tobacco a large number of species hybrids occur which give partially sterile intermediate hybrids. The genus Nicotiana had been much employed in hybridization investigations providing as it did the first instance of hybridization in the plant kingdom when in 1760 Kölreuter crossed *N. rustica* and *N. paniculata*. The hybrid thus obtained was intermediate in its characters and was only slightly fertile. Varying comments have been made as to the exact expression of the characters of this hybrid as compared with those of its parents, but apparently careful scrutiny reveals the influence of both parents in practically every character, although to varying extents in different characters. All, however, have found it relatively infertile, although among some hundreds Lotsy, in one experiment, discovered one plant which possessed a rather unusual degree of fruitfulness.

Although the condition of intermediate character expression includes by far the majority of species hybrids, there are some notable exceptions which very closely duplicate the set of characters of one parent almost to the exclusion of those of the other. This fact was recognized even by the older investigators, for Gärtner states that any condition may be obtained from that of strict intermediacy to a condition so closely resembling one parent as to be distinguished from it only by increased vigor and partial sterility. Gärtner found examples of dominance of one parent particularly striking in some Nicotiana crosses. Thus *N. paniculata* × *N. langsdorffii* is reported to give a hybrid form almost indistinguishable from *N. langsdorffii* and *N. suaveolens* × *N. macrophylla* is predominantly *N. macrophylla* in its character expression. Later in this chapter we shall describe crosses between *N. sylvestris* and a series of varieties of *N. tabacum* which constantly yield hybrids resembling the particular *tabacum* variety used in crossing. Curious instances of such predominance of one type are reported for triple hybrids. Thus *N. rustica* × *N. paniculata* pollinated with *N. angustifola* gives plants closely resembling *N. angustifola;* if the same hybrid is pollinated with *N. glutinosa* it produces plants closely resembling *N. glutinosa.*

There are authentic instances of species crosses which do not give equivalent results in reciprocal crosses. It is a common observation that some species crosses may be made in one way only. Crosses between wheat and rye are sometimes successful when wheat is the female parent, but the reciprocal cross has never been obtained. But usually when a cross is possible in both directions the reciprocal hybrids are practically indistinguishable. Among exceptions to this rule are crosses between *Digitalis purpurea* and *D. lutea,* strikingly different species, which constantly give hybrids resembling the female parent. In Oenothera such results are particularly common, and de Vries and others have investigated a number of such cases. A typical case is that of *O. biennis* and *O. muricata* which give strongly patroclinous hybrids in reciprocal crosses. The fact, however, that these hybrids breed true in further generations introduces a complication which places us on our guard against the operation of some as yet undiscovered factors. We can understand why reciprocal crosses should give different results, when there are differences in chromosome number or content in the two sexes as is generally the case among animals, but in plants it is more difficult to assign a reason for this type of behavior aside from a few cases in which apogamy is known to occur. It is, therefore, necessary for us to accept these cases with some reservations, looking to the future for experimental investigations which will provide us with a satisfactory explanation for them.

The Vigor of Species Hybrids.—The increased vigor displayed by species hybrids has been frequently commented upon by investigators from the time of Kölreuter down to the present. In 1849 Gärtner in his general treatment of this subject in species crosses especially notes that the luxuriance of hybrids frequently expresses itself in an unusual development of practically all plant parts. He also cites a considerable number of the earlier hybridists who have noted this increased vigor, among them Kölreuter, Sageret, Berthollet, Herbert, Mauz, and Lecoq. Hybrids which up to that time had been particularly noted for this sort of vigor represented such a large number of different families that there could be no question as to the generality of the phenomenon. For increase in length of stem Gärtner notes especially *Verbascum lychnites* × *V. thapsus* which grows to a height as great as 15 feet; *Althæa cannabina* × *A. officinalis* which sometimes attains a height of 12 feet; *Malva mauritiana* × *M. sylvestris* which attains a height of 11 feet; *Digitalis purpurea* × *D. ochroleuca* which grows to a height of 10 feet; and finally *Petunia nyctaginiflora* × *P. phœnicea* and *Lobelia cardinalis* × *L. syphylitica* which attain a height of 3 to 4 feet, a significant increase as compared with their low-growing parents. Often the vigor is expressed in a general increase in size throughout as appears to be particularly true of hybrids between different species in the genera Mirabilis and Datura. In Nicotiana a number of hybrids such as *N. suaveolens* × *N. macrophylla*, *N. rustica* × *N. marylandica*, and many others display such general hybrid vigor sometimes to a very marked extent. *Tropæolum majus* × *T. minus*, a hybrid of the tall and dwarf nasturtiums of the garden is another notable instance of hybrid development. Gärtner also records many interesting ways in which this hybrid vigor expresses itself. Thus certain hybrids in Dianthus, Lavatera, Lobelia, Lychnis, Geum, and Penstemon while not displaying notable increases in vegetative vigor lend themselves much more readily to vegetative propagation than do their parents. In some cases the hybrids show an unusual tendency to produce side branches and suckers, and in other cases still other outlets of this hybrid vigor are found.

Not all species hybrids, however, display hybrid vigor, and many indeed show a strikingly weakened condition accompanied by much lessened vegetative vigor. In tobacco several species hybrids show lessened vegetative vigor, as for example, *Nicotiana grandiflora* × *N. glutinosa*, *N. glutinosa* × *N. quadrivalvis*, *N. rustica* × *N. suaveolens*, and *N. suaveolens* × *N. quadrivalvis*. Similarly *Verbascum blattaria* × *V. lychnitis* gives weakened hybrids. Consequently within the same genus some species hybrids show marked increases in vegetative vigor, whereas others show just as marked decreases.

Investigations since Gärtner's time have simply extended observations on the comparative vigor of parents and hybrids in species hybrids as well as in the less violent variety hybrids. Thus Focke who investigated large numbers of species hybrids found many that were abnormally weak, but these usually represented rather wide crosses. Crosses between more closely related species, however, generally showed an increased vegetative vigor. The increased vegetative vigor, he regards as merely an extension of the same condition which Darwin had investigated in variety crosses, namely that crossbreeding is advantageous from the standpoint of the general growth of the forms involved. The idea that sterility may be the cause of this increased vigor is refuted on the one hand by the fact that some of the most vigorous species hybrids are also highly fertile, and on the other hand by the fact that most of the weak hybrid forms are nearly or quite sterile.

East and Hayes have attempted to offer an explanation for these phenomena on the basis of heterozygosis. They have reached this conclusion from extensive investigations of the effect of self-fertilization in maize and of cross-fertilization in tobacco. In corn they have found, as we shall describe more in detail later, that continued self-fertilization results in the isolation of races which are very uniform as respects their character development, but which almost constantly show considerably decreased vigor of growth. This decrease in vigor is most rapid in the first generations and becomes less rapid as the races become more constant in their characters. Since the approach to constancy in characters may be regarded as evidence of approach to a homozygous condition in this a normally highly heterozygous species, East and Hayes argue that the normal vigor of maize is largely an expression of its heterozygous condition and that the decrease in vigor is a consequence of reduction to a homozygous condition. This conclusion is in part confirmed by the evidence from crossing such homozygous strains of maize. The F_1 of such crosses usually exhibits an immediate return to the vigor of the population from which the strains were isolated. However, it is not entirely clear why this behavior cannot be ascribed to the isolation of races possessing fewer dominant factors than most of the plants in the original population. When such races are crossed the original set of dominant factors would be reunited, and in consequence the normal vigor of the original population would be exhibited.

Since the foregoing was written D. F. Jones has published an explanation of increased vegetative vigor of hybrids or "heterosis," as it has been termed by Shull, which he has summarized as follows:

1. The phenomenon of increased growth derived from crossing both plants and animals has long been known but never accounted for in a comprehensible manner by any hypothesis free from serious objections.

2. The conception of dominance, as outlined by Keeble and Pellew in 1910 and illustrated by them in height of peas, has had two objections which were: *a*. If heterosis were due to dominance of factors it was thought possible to recombine in generations subsequent to the F_2 all of the dominant characters in some individuals and all of the recessive characters in others in a homozygous condition. These individuals could not be changed by inbreeding. *b*. If dominance were concerned it was considered that the F_2 population would show an asymmetrical distribution.

3. All hypotheses attempting to account for heterosis have failed to take into consideration the fact of linkage.

4. It is shown that, on account of linked factors, the complete dominant or complete recessive can never or rarely be obtained, and why the distributions in F_2 are symmetrical.

5. From the fact that partial dominance of qualitative characters is a universal phenomenon and that abnormalities are nearly always recessive to the normal conditions, it is possible to account for the increased growth in F_1 because the greatest number of different factors are combined at that time.

6. It is not necessary to assume perfect dominance. It is only necessary to accept the conclusion that many factors in the $1n$ condition have more than one-half the effect that they have in the $2n$ condition.

7. This view of dominance of linked factors as a means of accounting for heterosis makes it easier to understand: *a*, why heterozygosis should have a stimulating rather than a depressing or neutral effect; and *b*, why the effects of heterozygosis should operate throughout the lifetime of the individual, even through many generations of asexual propagation.

In order to extend their investigations to normally self-fertilized species, East and Hayes made numerous crosses between different species of Nicotiana. As a result they found, as indeed had previous investigators on this the favorite genus for hybridization studies, that the vigor of hybrids varied all the way from a condition so weak as to give embryos incapable of germination to a condition greatly exceeding in vigor that exhibited by either parent. Thus *Nicotiana tabacum,* the commonly cultivated tobacco, when crossed with *N. sylvestris* gives hybrids which exceed by 35 per cent. the average height of the parents and are estimated to be 20 per cent. more vigorous. Similarly *N. tabacum,* when crossed with *N. rustica,* gives hybrids exceeding by 80 per cent. the average height of the parents, but when crossed with *N. alata grandiflora,* the hybrids are only about 10 per cent. of the average of the parents, both in height and vigor. About fifty species crosses within the genus were made by these investigators with results in respect to vigor which bore out those already known for various specific crosses.

It is obvious from these results that stimulation in the hybrid is a result of certain specific interactions. East and Hayes regard those hybrids which show decreased vigor as evidence of such great differences between parents that normal cell division is impossible. When on the other hand the differences are not great enough to obstruct normal cell division, the degree of stimulation is held to increase directly with the amount or kind of heterozygosis present.

These conclusions, however, do not appear to be very firmly established on the experimental side for by no means the only explanation has been offered. When we consider the recent work with Drosophila it is clear that many factor differences are known which in addition to resulting in some definite character distinction display a rather ill-defined effect in decreasing vigor. Thus the factor for white eye color in addition to determining white eyes has such an effect on the viability of the white-eyed phenotype that in segregation this class never comes up to Mendelian expectations. Similarly other factors have definitely a weakening effect in vigor, in sterility, and in other characteristics. This effect, also, is apparently cumulative, so that in Drosophila strains containing many recessive factors almost invariably must be carried on in a heterozygous condition on account of their low viability. Here very evidently the increased vigor of the heterozygous strains is to be attributed to a recombination of the dominant factors normal to the wild type, for the heterozygous forms display the characters of the normal wild type and a size and vigor approximating that of the homozygous wild type. Similarly in corn the occurrence of open pollination makes it possible for a relatively large number of such factors which lower vigor to exist in a variety. These show their effects in marked degree only on self-fertilization for such self-fertilization automatically results in a rather rapid reduction of strains to a homozygous condition. If the number of recessive factors affecting vigor is fairly large then it is evident that the mathematical probability of isolating some of them in continued self-fertilization is relatively great, but the chances that the same ones will be isolated in different pure strains is relatively slight. It follows that usually pure strains resulting from continued self-fertilization will display lessened vigor and productiveness, and that different strains isolated in this fashion will give hybrids approximating the normal condition of fertility and productiveness. The increased or even decreased vigor of species hybrids of the wider type appears, therefore, to belong to a distinctly different category for which we are not yet fully prepared to provide an explanation. To suggest that the increased stimulation depends on the specific interactions which occur between two different contrasted hereditary systems is, confessedly, falling back on a less definite explanation, but one which does not appear improbable when viewed in the light of our knowledge of the unexpected relations which certain factor combinations display when brought together.

Sterility in Species Hybrids.—A common phenomenon of species hybridization is the marked degree of sterility which is exhibited. This fact of sterility in speices hybrids has led certain investigators, particularly Jeffrey, to lay great stress upon partial sterility as an evidence of hybrid character. This contention may be valid for a majority of cases, but obviously it would not follow even if all species hybrids displayed partial sterility, that all cases of sterility are to be referred to hybridity. Specifically many instances are known for which simpler and more satisfactory explanations suffice. Thus Bateson has recorded a case of contabescence in the anthers of sweet peas which is strictly due to the presence of a definite factor for contabescence. The ratios obtained are approximately 3:1 ratios, contabescence being recessive, and moreover, the factor for contabescence is definitely linked with other factors, so that in every respect the factor analysis of this case of sterility is wholly satisfactory. In Drosophila similarly some cases of sterility are definitely referable to the action of specific factors which sometimes have effects so marked that strains homozygous for the factors in question cannot be maintained. This condition is well illustrated by flies which are homozygous for the factor for rudimentary wings. Such flies are practically never fertile. Many other instances are known where slight effects on fertility result from factors which are intimately concerned in the expression of other characters. A somewhat different type of sterility, but one which is also definitely established, is that which Bridges has reported for the males of *Drosophila ampelophila* which lack the *Y*-chromosome. The evidence upon which this case of sterility is based appears to be conclusive, and to demonstrate that while the male Drosophila lacking the *Y*-chromosome may develop a normal soma, it cannot produce functional germ cells. The sterility of wide crosses, however, appears to belong to a distinct category, an explanation for which we shall endeavor to give later on in this chapter. At this point we shall only take up some of the types of sterility displayed in such crosses.

At the outset it may be well to note that the degree of sterility displayed by hybrids varies from complete fertility to complete sterility. It is, therefore, readily apparent that sterility in hybridization as a means of species differentiation gives no natural divisions, but that arbitrary ones must be erected depending upon the degree of sterility displayed. Moreover, other factors such as those noted above complicate matters and render it extremely difficult to decide where to draw the line. Here again, therefore, the search for a universal species indicator has met with failure. From a genetic standpoint this is as it should be for it merely indicates that races of plants and animals display all degrees of genetic differences from simple differences in isolated factors to complex differences in entire series of factors.

Sterility in crosses between apparently good species may be at times almost completely lacking. Thus the crosses between *Antirrhinum majus* and *A. molle* and some other crosses made by Baur within the genus Antirrhinum proved fully fertile. The same condition has been found in other species crosses. Thus *Nicotiana alata grandiflora* and *N. langsdorffii*, although they differ strikingly in their characters, give hybrids which are about as fertile as the parents. Certain orchid crosses are also reputed to display a high degree of fertility, but on the whole crosses between good species very rarely show even an approximation to the full degree of fertility, and this is true of both plant and animal hybrids.

The sterility displayed by species hybrids may not always be equivalent in both sexes. Thus one of Baur's Antirrhinum crosses, that of *A. majus* × *A. siculum* proved completely sterile as far as the production of good ovules is concerned, but some good pollen grains are produced which can be used in back crosses to the parents. In the case of *Cavia porcellus* × *C. rufescens*, we have already noted that the males are sterile and the females fertile. Detlefsen attempted to follow out the inheritance of fertility in this case, and attacked the problem from many angles. The fertility of the females appears to be complete, since the F_1 females produce litters of approximately the average number of young of those of the two parent species. The offspring of the hybrid females when crossed back to the tame guinea-pig again produce fertile females and sterile males. With each successive back cross to the tame guinea-pig the percentage of fertile males rises in a fairly regular fashion as is shown in Table XXXVII. Detlefsen points out for this case that the assumption that the wild species carries eight disturbing dominant factors gives a very close agreement with the observed re-

TABLE XXXVII.—PERCENTAGES OF HYBRID OFFSPRING WITH MANY MOBILE SPERM IN MATINGS OF FEMALE HYBRIDS WITH TAME GUINEA-PIGS, AND FEMALE HYBRIDS WITH FERTILE MALE HYBRIDS (*After Detlefsen*)

Generation of females	Offspring of female hybrids and guinea-pigs		Offspring of female hybrids and fertile male hybrids		Calculated for eight factors
	Number	Percentage with many mobile sperm	Number	Percentage with many mobile sperm	
F_1	1	00.0	1	00.0	00.0
F_2	8	00.0	2	00.0	00.4
F_3	49	14.3	7	14.3	10.0
F_4	99	33.3	17	58.8	34.4
F_5	150	60.7	11	63.6	59.7
F_6	49	69.4	..	.....	77.6
F_7	15	73.3	1	100.0	88.2

sults. The F_1 hybrids would then be of the genetic constitution *AaBbCcDdEeFfGgHh*. Such individuals produce gametes of the constitution *abcdefgh* only once in 256 times, so that when crossed back to tame guinea-pigs which produce only gametes bearing the recessive factors, 0.4 per cent. of the males should be fertile. The percentage of fertile males in successive generations of back crossing should then increase progressively as shown in the last column of Table XXXVII. As Detlefsen himself, however, points out the close agreement of these calculated figures with those actually observed is misleading as an indication of the significance of the analysis, for it is doubtful whether simple segregation of Mendelian factors provides an explanation of the entire phenomena. It is rather strange in fact that only the males display this sterility, and it is of interest to note, as Detlefsen points out, that several other analogous instances of male sterility in animal species hybrids are known. The yak, *Bibos grunniens*, crossed with the domestic cow, *Bos taurus*, gives fertile female and sterile male offspring. Similarly the gayal, *Bibos frontalis*, the gaur, *Bibos gaurus*, and the American bison, *Bison americanus*, have been crossed with domestic cattle and have given fertile female and sterile male hybrids. There is strong evidence that hybrids of the banteng, *Bibos sondaicus*, and the zebu, *Bos indicus*, display similar relations. When we consider the physiological relations between factors and particularly the significant fact that probably no crossing-over occurs in the males of this species, we feel inclined to attribute the male sterility to other causes than to a mere sorting of factors having to do with fertility.

Partially Sterile Hybrids of Wheat and Rye.—Thus far cases have been considered in detail in which the species hybrids display a considerable degree of fertility. At the other extreme stands a series of hybrids which display sterility which is nearly but not quite complete. Such are the hybrids between wheat and rye which Jesenko has subjected to thorough experimental study. There can be no question that wheat and rye are distinct species, in fact they have been universally assigned to different genera. They seem to represent about the extreme limitations of effective hybridization. Jesenko and others have been able to obtain hybrids between wheat and rye only when wheat is used as the female parent, consequently we are unable to compare the results of reciprocal hybridization in this case. Even pollination of wheat with rye is successful only about six times in one thousand as Jesenko found in over six thousand trials with different species and varieties. The F_1 hybrids were intermediate in general characters, although the relations of dominance displayed in variety crosses was preserved in the species crosses. In Fig. 100 is illustrated one of these hybrids and its two parents. The increased size of the spike as compared with those of either parent is particularly striking. These F_1 hybrids are completely sterile with their own pollen. However, it was possible by pollinating the hybrids either with pollen from wheat or rye to obtain a few viable seeds. For wheat pollination the ratio of success was about 3 in one thousand; for rye only one plant was secured from nearly five thousand trials. The pollen grains of the hybrids were apparently completely non-functional, and cytological examination indicated prevailingly irregular divisions and behavior in their production.

The product of back-crossing the F_1 hybrids to wheat gave plants very similar to wheat. This is illustrated in Fig. 101. Although all these plants resembled wheat in their general characters, they nevertheless showed wide differences from one another, not only in morphological characters but in physiological ones such as fertility as well. A few of the plants were totally sterile, but some of them were more or less fertile and in general those were most fertile which most closely resembled the wheat parent. In the next following generation, the progeny of those plants which were most fertile consisted of plants which were apparently pure wheat and completely fertile and plants which were less like wheat and showed lessened fertility as the resemblance to wheat decreased.

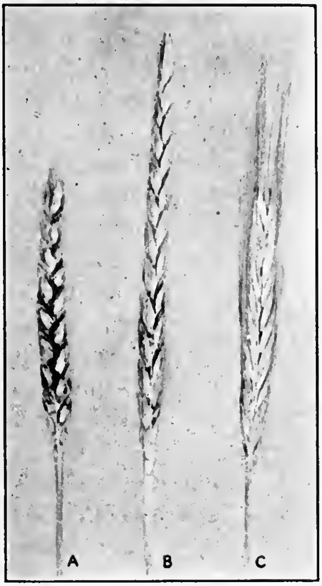


Fig. 100.—Sterile hybrids between wheat and rye, *A*, the wheat parent; *C*, the rye parent, and *B*, the F_1 hybrid between them. (*After Jesenko.*)

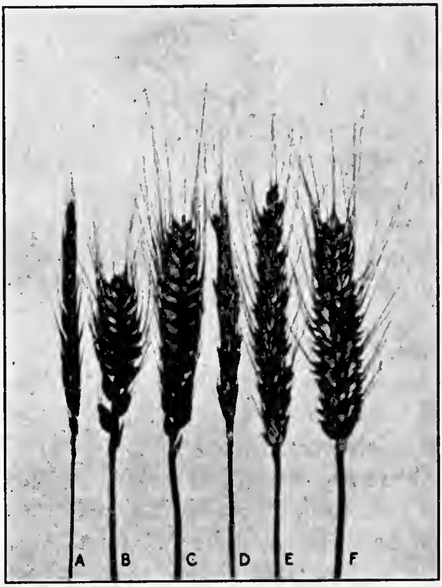


Fig. 101.—Sesqui-hybrids from the F_1 wheat × rye crossed back to wheat. (*After Jesenko.*)

For a few particular characters, Jesenko was able to establish close approximation to a Mendelian analysis, so that it can scarcely be doubted that in the sorting out of the factors to establish the constant races of further generations, the phenomena displayed were such as to indicate clearly the operation of a Mendelian mechanism.

But when we consider the phenomena in the light of the characters involved, then it may be seen that the results obtained are truly remarkable. Wheat and rye differ strikingly in their characters and the recovery of approximately the parental form so often in these back-crosses is out of the question from a strict Mendelian viewpoint, if all combinations are assumed to survive.

As an explanation of these phenomena, Jesenko calls attention to the fact that there are eight chromosomes in the germ cells of rye and wheat, so that in the formation of gametes in the F_1 some will possess eight wheat chromosomes, others seven wheat and one rye, and so on. When back-crossed to wheat, therefore, union with those gametes which contain only wheat chromosomes or at most two or three rye chromosomes results in wheat-like plants which are fertile, whereas greater proportions of rye chromosomes results in plants which are less like wheat and sterile. Similarly, as Jesenko in fact found, pollination with rye results in plants resembling rye, because of the union of the rye pollen with gametes which contain all or nearly all rye chromosomes. The sterility in these hybrids, therefore, Jesenko regards as the consequence of the inharmonious action of a "plasma" built up of large proportions of both rye and wheat elements.

Partially Sterile Hybrids in Nicotiana.—A similar state of affairs has been found to exist in hybrids between various varieties of *Nicotiana tabacum*, the commercial tobacco, and *N. sylvestris*, a very different species. *N. tabacum* occurs in a very large number of distinct varieties some of which are so different that they could justly lay claim to recognition as distinct species. Goodspeed and Clausen have studied the hybrids of a number of *N. tabacum* varieties with *N. sylvestris* and have found that in all cases the F_1 hybrid duplicates very closely the total set of characters of the particular *tabacum* variety used in the hybrid save on a very much enlarged scale, for these hybrids are conspicuous for the increased vigor due to hybrid stimulation. In Fig. 102 is illustrated a typical plant of *N. sylvestris*. *N. sylvestris* is a monotypic species and has been grown under cultivation for over thirty years without producing any distinct varieties. It is a strikingly beautiful plant with its stout, erect growth; stiff, broad ascending leaves; and its star cluster of long pure white flowers. Nothing even approximating its flower characters occurs in the numerous varieties of *N. tabacum,* in fact it belongs to a totally distinct section of the genus Nicotiana. In spite of its distinct characters, however, it crosses freely with members of the *tabacum* group, and yields reciprocal hybrids which are equivalent throughout. In Fig. 103 on the right is illustrated a plant of *N. tabacum angustifolia* and beside it the F_1 hybrid with *N. sylvestris*. The figure shows clearly how faithfully the characters of the *N. tabacum* parent are reproduced in the hybrid. The leaves are long, narrow and petioled, the upper ones strap-like and pendant, the flowers are narrow and have narrow, sharply pointed lobes—these and the general habit of growth are all characters clearly referable to the *N. tabacum* parent. A very different variety of *tabacum*, such as the variety known in the University of California Botanical Garden cultures as *N. tabacum* "Cuba" gives corresponding results. This variety is tall and bears white flowers many of which are quadrimerous instead of pentamerous as is normally the case in Nicotiana. These characters are faithfully reproduced in the hybrid with *sylvestris* as is shown in Fig. 104. *N. tabacum* "Cuba" is peculiar among the tabacum varieties in its ability to develop seed capsules in the absence of fertilization, and these may sometimes contain a few viable seeds. This is appa-

Fig. 102.—Typical plant of *Nicotiana sylvestris*.

rently a recessive character in crosses with *N. tabacum* varieties which display a normal behavior in this respect, but it is manifested in the F_1 hybrids with *N. sylvestris* in the remarkable way in which this hybrid retains its seed capsules, although there are very few or no seeds in them. Since all the other F_1 hybrids of *tabacum* varieties and *sylvestris* shed their flowers, often before the corolla has withered, this feature has very conspicuously characterized the F_1 hybrids of *N. tabacum* "Cuba" and *sylvestris.*

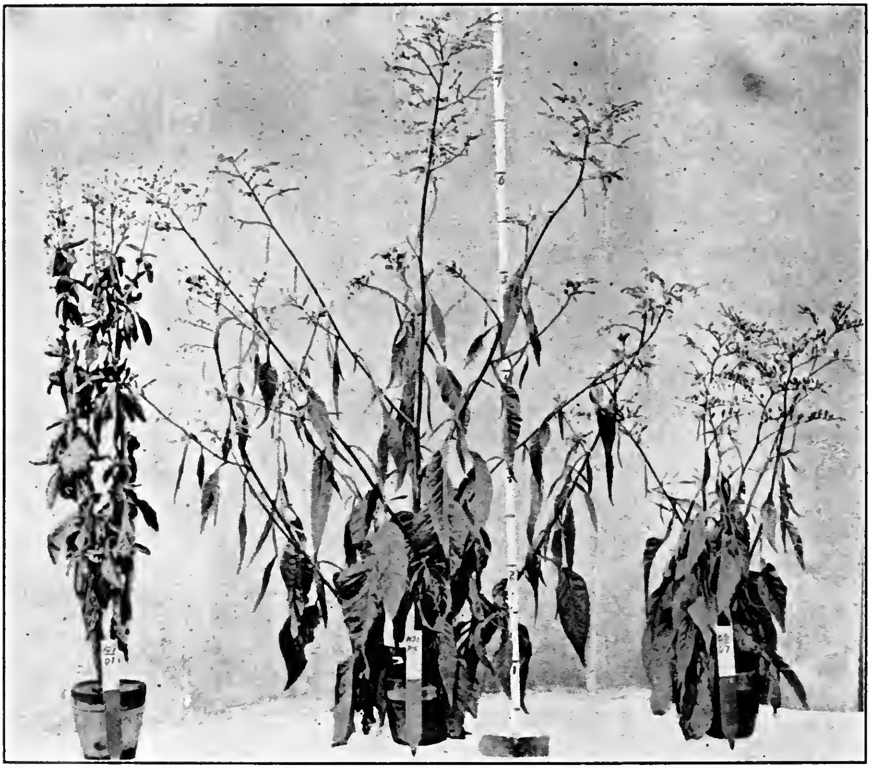


FIG. 103.—*Nicotiana sylvestris* (left), *N. tabacum angustifolia* (right) and the F_1 hybrid (center). (*After Goodspeed and Clausen.*)

The significant feature of these hybrids, however, is the hereditary behavior which they display. They are almost completely sterile, but if the plants are grown under reduced conditions of culture and the flowers are hand pollinated with pollen from either of the parent species, a few seeds are set, but not more than about 1 per cent. of the number ordinarily produced by the parents. If *N. sylvestris* pollen is used to pollinate the F_1, the sesqui-hybrids thus obtained are of diverse types, most of them abnormal, but about 10 per cent. closely approximate *N.*

sylvestris in all their characters. These latter plants are fertile and in succeeding generations give offspring which to all indications are pure *sylvestris* individuals. Similarly when pollen of the *N. tabacum* parent is used, the sesqui-hybrids are of a variety of forms, but all approximate the *N. tabacum* parent in their characters and no one could determine by studying them that they were only once removed from *N. sylvestris*. Those which most closely approximated the *N. tabacum* parent in morphological characters are also most fertile and give rise to fertile races which do not differ significantly from the *N. tabacum* parent.

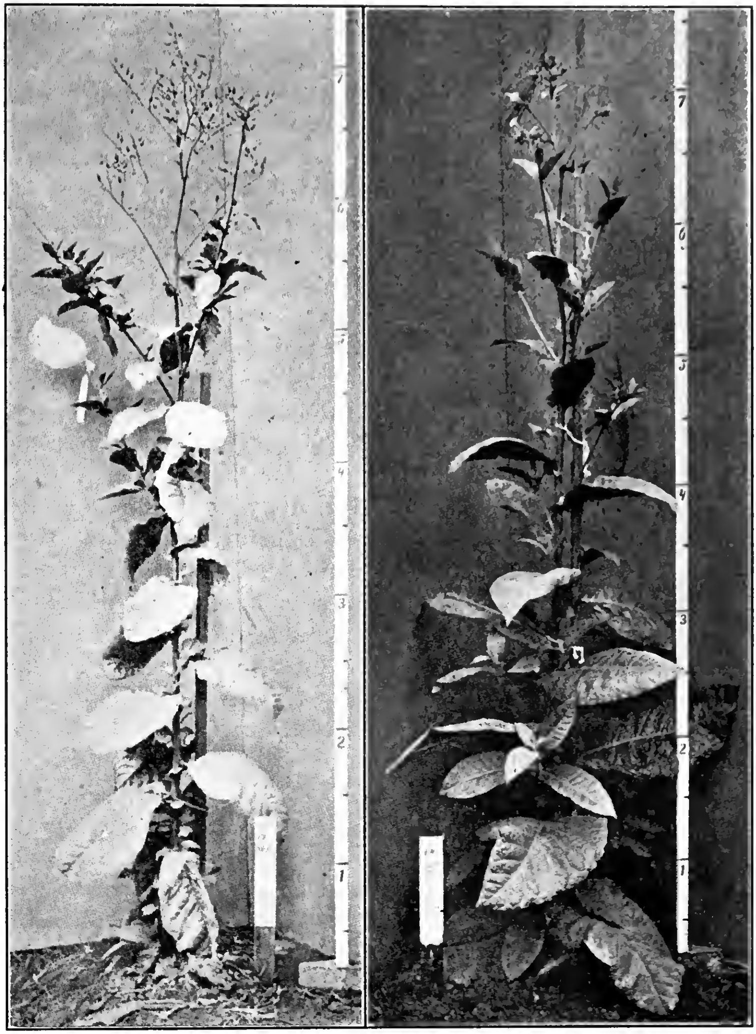


FIG 104.—*Nicotiana tabacum* "Cuba" (left) and its F_1 hybrid with *N. sylvestris* (right). (*After Goodspeed and Clausen.*)

The behavior is truly remarkable when viewed in the light of modern Mendelian conceptions. The number of character differences between the two forms is very considerable, and the recovery of the parental forms with almost unimpared fertility is so frequent that subsidiary assumptions must be made to account for them on a Mendelian basis. Goodspeed and Clausen, therefore, have developed the conception of Mendelian reaction systems for an explanation of these phenomena. According to this conception the normal functioning of a gametic or zygotic set of factors depends upon the harmonious interrelations which the factors maintain with one another. The uniform resemblance of the F_1 hybrids of *N. tabacum* varieties with *N. sylvestris* to the *N. tabacum* varieties is held in these cases to indicate that the *N. tabacum* set of factors is dominant as a Mendelian reaction system to the set of factors contributed by *N. sylvestris.* The fact that these hybrids so completely resemble the *N. tabacum* parent indicates that the elements of the *N. sylvestris* system are throughout unable to interact normally with those in the opposed *N. tabacum* system. It is for this reason that a recessive factor which is practically completely swamped in F_1 intervariety crosses in *N. tabacum,* expresses itself so strongly in the F_1 hybrids with *N. sylvestris* for, if the corresponding element of the *N. sylvestris* system were unable to interact with the elements of the dominant reaction system, then it is clear that although the factor is dominant, the corresponding character cannot possibly express itself in the individual.

The haploid number of chromosomes in these Nicotiana species and varieties is probably twenty-four. Consequently the recombination series is given by the expansion of the expression $(1 + 1)^{24}$. Only one gamete in 16,777,316 would carry only *N. tabacum* chromosomes and the same proportion would hold for gametes carrying only *N. sylvestris* chromosomes. This is on the assumption that no crossing-over occurs in the formation of gametes in the F_1 hybrid. If crossing-over should occur normally the proportion of pure *N. sylvestris* or *N. tabacum* gametes would then be correspondingly reduced. The further assumption is also tacitly made that there are some factor differences between *N. tabacum* and *N. sylvestris* in every chromosome, which is in all probability correct when we consider the striking differences between the two species. Accordingly the results of the back-cross with *N. sylvestris* which gives a relatively high percentage of what are apparently pure *N. sylvestris* plants are exceedingly significant. Developing the reaction system hypothesis, it would appear that, if the *N. tabacum* and *N. sylvestris* systems display a high degree of mutual incompatibility, any gamete containing elements derived from both systems would give a reaction system subject to profound disturbances incident upon the inharmonious relations set up between the *N. tabacum* and *N. sylvestris* elements. If the admixture be relatively slight, the inharmonious elements may not greatly affect the workings of the reaction system, and there would result individuals showing practically the entire set of characters of one or the other parent, and such individuals would be fully fertile. A slightly greater proportion of inharmonious elements in the reaction system would result in such profound disturbances in its functioning as to produce the abnormal individuals of various kinds which make up so large a proportion of the progeny from such parentage. When the proportions of inharmonious elements in the gametes becomes still greater, they fail to function at all. It is upon the formation of such non-functional gametes or the attempt to produce them, that the partial sterility of the hybrid depends, and since in this particular case these form by far the greater proportion of gametes, the hybrid is very nearly completely sterile.

The relations may be illustrated by Table XXXVIII which represents

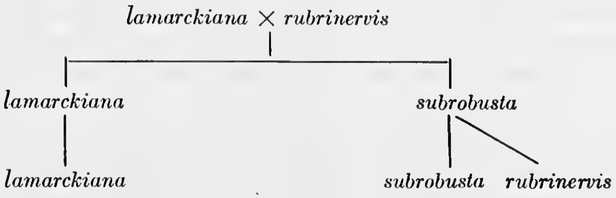
TABLE XXXVIII.—RECOMBINATION SERIES IN GAMETES OF F_1 OF *N. tabacum* × *N. sylvestris*

Condition of gametes	Tabacum: sylvestris chromosomes	Proportionate number of gametes	Progeny when pollinated with *N. tabacum*	Progeny when pollinated with *N. sylvestris*
Functional......	24:0	1	Plants resembling the *N. tabacum* parent and of various degrees of fertility	Plants resembling the F_1 and abnormal plants but all nearly completely sterile
	23:1	24		
	22:2	276		
	21:3	2,024		
	20:4	10,626		
	19:5	42,504		
Non-functional .	18:6	134,596	No viable seeds	No viable seeds
	17:7	346,504		
	16:8	236,321		
	15:9	1,307,504		
	14:10	1,961,256		
	13:11	2,496,144		
	12:12	2,705,456		
	11:13	2,496,144		
	10:14	1,961,256		
	9:15	1,307,504		
	8:16	736,321		
	7:17	346,504		
	6:18	134,596		
Functional......	5:19	42,504	Plants resembling the F_1 hybrid and nearly completely sterile	Abnormal, infertile plants and fertile plants closely resembling *N. sylvestris*
	4:20	10,626		
	3:21	2,024		
	2:22	276		
	1:23	24		
	0:24	1		

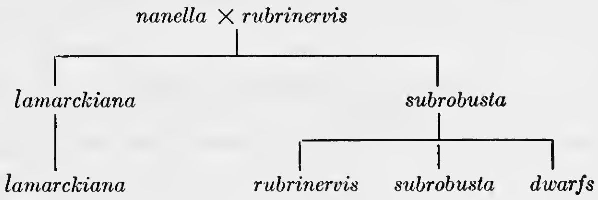
the recombination series obtained in the F_1 hybrid on the assumption that the chromosome mechanism is operating normally and there is no crossing-over. Neither of these assumptions is correct, but the table will show the principles involved in the production of the progeny by back-crossing. If it be assumed that the presence of not more than five *N. sylvestris* chromosomes in a system containing mostly *N. tabacum* chromosomes or correspondingly not more than five *N. tabacum* chromosomes in a system containing mostly *N. sylvestris* chromosomes will not completely disturb the relations within the systems to the point of failure to function at all, then about 0.7 per cent. of the gametes will be functional and 99.3 per cent. non-functional. This accounts for the high degree of sterility displayed by F_1. Pollinated by *N. tabacum* those gametes at the *N. tabacum* end of the series produce some plants which closely resemble the *N. tabacum* parent and are fertile, and others less fertile and resembling the *N. tabacum* parent somewhat less. Conceivably some of these give abnormal forms such as have been observed in the cultures. The *N. sylvestris* end of the recombination series pollinated with *N. tabacum* gives sterile hybrids approximating the F_1 in their characters and some of these might likewise be abnormal. On the other hand when the *N. tabacum* end of the series is fertilized by *N. sylvestris*, sterile individuals result which resemble the F_1 and perhaps where there is any missing link in the chain of *tabacum* chromosomes, the resulting individuals are abnormal. The *N. sylvestris* end of the series, however, gives fertile individuals closely resembling *N. sylvestris* and perhaps abnormal individuals which have a tendency to resemble *N. sylvestris*. The high proportion of fertile individuals resembling the parents in either case depends on the selective elimination of the greater proportion of the gametes which contain elements derived from both parents. The conception then that recombination gametes must form harmonious reaction systems in order to function accounts in these nearly sterile hybrids for the high degree of sterility, for the quick recovery of either parent by back-crossing, and for the recovery of full fertility in subsequent generations upon return to the parental type. It is a curious consequence of these phenomena that it is easier to recover the exact parental types from hybrids of *N. sylvestris* and *N. tabacum* than from intervarietal hybrids of *N. tabacum*, which are fully fertile and display all manner of recombinations.

Species Hybridization in Œnothera.—Curious results have been obtained in Œnothera in which genus considerable attention has been given to the results of hybridization of a large number of different species. Since these results have often been cited as evidence of non-Mendelian behavior, it is well to consider some of them in detail. De Vries particularly has made a thorough study of almost every conceivable combination of species within the genus, and also of the mutants of *O. lamarckiana* with the parent species, with one another, and with other species.

As an example of the type of behavior displayed by these hybrids we shall take the results of intercrossing *lamarckiana* and its two mutant derivatives *rubrinervis* and *nanella*. When *lamarckiana* is crossed with *rubrinervis*, the phenomena are as outlined below:



The F_1 consists of two forms in about equal proportions, *lamarckiana* and *subrobusta*, the latter a form intermediate between *lamarckiana* and *rubrinervis*. In subsequent generations, the *lamarckiana* individuals breed true, but the *subrobusta* individuals produce both *subrobusta* and *rubrinervis*, the latter breeding true. To these results we may add those obtained by crossing *lamarckiana* and *nanella*, the dwarf mutant of *lamarckiana*. This cross gives in F_1 approximately equal numbers of *lamarckiana* and *nanella* and both forms breed true in subsequent generations. Finally to complete the triangle we may consider the results of hybridization of *rubrinervis* and *nanella* which are given below in the form of a diagram.



The percentage of *subrobusta* individuals in the F_1 of this cross is usually considerably below 50 per cent. In subsequent generations the *subrobusta* individuals segregate in the same fashion as those of the F_1. The dwarfs obtained in this experiment unite the characters of *rubrinervis* and *nanella* and are consequently designated *rubrinervis nanella* to distinguish them form the true *nanella*. Like the *lamarckiana* and *rubrinervis* individuals, they breed true in subsequent generations. The actual results of this series of experiments are given in Table XXXIX, from which data on those forms which bred true is omitted. It is at once ap-

TABLE XXXIX.—RESULTS OF VARIOUS MATINGS OF *rubrinervis* (*R.*) AND *nanella* (*N.*) AND THE FORMS PRODUCED FROM SUCH MATINGS (*compiled from de Vries, "Gruppenweise Artbildung"*)

Parentage	Number of plants	*Lamarckiana*	*Rubrinervis*	*Subrobusta*	*Nanella*	*Rubrinervis nanella*
		Per cent.	Per cent.	Per cent.	Per cent.	
Nanella × *rubrinervis*	105	73	..	27		
Nanella × *rubrinervis*	79	59	..	41		
Rubrinervis × *nanella*	70	59	..	41		
(*N.* × *R.*) *subrobusta*	160	..	10	80	..	10
(*R.* × *N.*) *subrobusta*	160	..	3	85	..	12
(*R.* × *N.*) *subrobusta*	56	..	34	52	..	14
(*N.* × *R.*) *subrobusta*	230	..	21	70	..	9
(*R.* × *N.*) *subrobusta*	234	..	15	73	..	12
Lamarckiana × *R. nanella*	152	3	..	77	20	
R. nanella × *lamarckiana*	152	25	..	32	43	
(*N.* × *R.*) *lamarckiana* × *nanella*	266	86	..	..	14	
(*N.* × *R.*) *lamarckiana* × *nanella*	70	80	..	..	20	
(*R.* × *N.*) *lamarckiana* × *nanella*	112	76	..	..	24	
Nanella × (*R.* × *N.*) *lamarckiana*	68	62	..	..	38	
Nanella × (*N.* × *R.*) *lamarckiana*	27	55	..	..	45	
(*R.* × *N.*) *lamarckiana* × *R. nanella*	84	3	87	..	9	1
Nanella × (*N.* × *R.*) *subrobusta*	45	33	16	..	51	
R. nanella × (*R.* × *N.*) *subrobusta*	204	..	33	..	67	
(*N.* × *R.*) *subrobusta* × *nanella*	138	51	20	..	29	
(*N.* × *R.*) *subrobusta* × *R. nanella*	246	..	75	..	25	
(*N.* × *R.*) *subrobusta* × *R. nanella*	214	..	72	..	28	
(*R.* × *N.*) *subrobusta* × *R. nanella*	289	..	72	..	28	

parent that the phenomena exhibited, although complex, are very orderly; but no very consistent Mendelian interpretation has been advanced to account for all of them.

The hypothesis of de Vries while ingenious does violence to many of our most cherished conceptions of the general nature of hereditary phenomena. De Vries assumes that pangens exist in three forms; active, labile, and inactive. Two pangens are concerned in the above series of forms, the *rubrinervis* pangen for strengthening of the vascular bundles and the *nanella* pangen for stature. These pangens exist in *lamarckiana* in the labile condition in which they occasionally change to the inactive condition and thus produce the corresponding mutations *rubrinervis* and *nanella.* Labile pangen × inactive pangen then gives according to de Vries in F_1 the ascendency of either one or the other condition to the complete exclusion of the other form in later generations. Accordingly *lamarckiana* × *nanella* gives in F_1 *lamarckiana* and *nanella* which breed true in further generations. Similarly when *lamarckiana* is crossed with *rubrinervis*, the *rubrinervis* pangen in *lamarckiana* is in the labile condition, but in *rubrinervis* it is in the inactive condition. Here, however, a difficulty is introduced by the fact that the form corresponding to *rubrinervis* in F_1 is intermediate between *rubrinervis* and *lamarckiana*, it is the form which de Vries calls *subrobusta*. Must we assume a fourth condition for the pangens in this form? An additional difficulty is introduced when we consider crosses of *rubrinervis* and *nanella*. *Rubrinervis* has arisen from *lamarckiana* by mutation, by a change of the labile *rubrinervis* pangen in *lamarckiana* into the inactive condition. But when *rubrinervis* is crossed with *nanella*, F_1 consists entirely of *lamarckiana* and *subrobusta* plants. As we pointed out, crosses of *nanella* with *lamarckiana* show that the *nanella* pangen

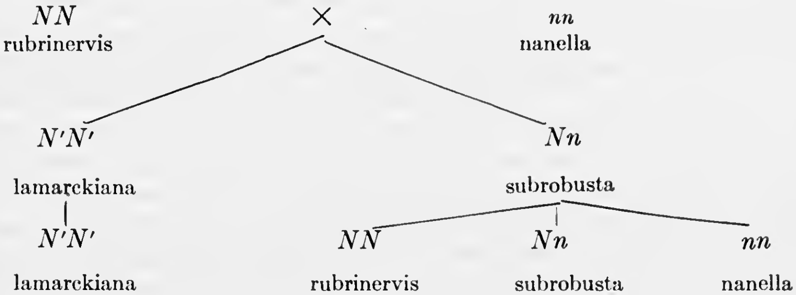


Fig. 105.—Results of crossing two "mutants" of Œnothera lamarckiana.

in *lamarckiana* is in the labile condition. How, then, should this pangen have become inactive in *rubrinervis* which was supposedly derived from *lamarckiana* by a change in the *rubrinervis* pangen? For according to de Vries the behavior of the *nanella* pangen in such an experiment is illustrated in Fig. 105 in which the active pangen is designated by N, the labile pangen by N', and the inactive pangen by n.

Those who have attempted to apply a rigid Mendelian analysis to the Œnothera phenomena have failed to do so without making assumptions which thus far remain beyond the limits of experimental verification. Nevertheless the work of such investigators as Heribert-Nilsson, Renner, Davis, and others demonstrates that Mendelian analyses may be applied to particular cases and that when the difficulties which occur in Œnothera are considered, the facts thus far discovered do not preclude an explanation on an essentially Mendelian basis. Davis in particular has pointed out that thus far no species of Œnothera has been found which will stand trial as of strict genetic purity. In all species apparently 50 per cent. or more of the pollen grains are abortive and similar proportions of the ovules are non-functional. To this category of facts must be added the high percentage of seed sterility which is common in the genus. If any of this pollen, ovule, and seed sterility is selective, then obviously it will be impossible to analyze the progeny successfully, unless the exact nature of the non-functional gametes and zygotes may be determined. The importance of this point has been indicated in the explanation of the frequent occurrence of parental forms among the sesqui-hybrids of rye and wheat and of *Nicotiana tabacum* with *N. sylvestris,* and it has been definitely established for many cases of albinism in plants and for peculiar sex ratios and consequent disturbances of Mendelian ratios in Drosophila. Until, therefore, a satisfactory account can be given of the difficulties which have been enumerated above it will be impossible on the one hand to offer a satisfactory Mendelian interpretation of the Œnothera investigations and illogical on the other hand to advance the results of these investigations as evidence of non-Mendelian inheritance.

Moreover, considerable success has attended the efforts to produce by species hybridization strains of Œnothera which behave like *lamarckiana.* It is not without significance that Davis has been able to produce forms by crossing *O. biennis* and *O. franciscana* so much like *lamarckiana* as to be indistinguishable from it taxonomically. Tower also has taken pure species of Leptinotarsa, the Colorado potato beetle, and by mating them has produced strains which breed approximately true, but which under the stress of unusual conditions may throw off small percentages of aberrant forms. In his species crosses in Antirrhinum, Lotsy has reported the occurrence of races which give small proportions of aberrant forms. Since at present we have no certain knowledge that *lamarckiana* is not a form of hybrid origin and that its so-called mutants are not really segregants from a race possessing a peculiar hybrid constitution, these analogous cases assume considerable importance as an indication of the line of attack which may be followed for an explanation of the Œnothera phenomena.

Conclusions.—If we attempt to outline the present status of our knowledge of the phenomena of species hybridization, we see thus far no clear evidence of non-conformance to an explanation which is essentially Mendelian. The strict Mendelian explanation must be modified to take into account the peculiar relations which obtain in species hybridization. For an explanation of such relations the reaction system conception has been advanced. According to this conception the total set of factors in any species forms a reaction system in which the factors display harmonious interrelations with one another. Variety hybridization, since it is concerned only with isolated differences in systems which are fundamentally identical, usually produces no disturbances in the reaction system relations. Consequently strict Mendelian analyses may be applied to such phenomena, and the reaction system relations need not be considered. But when species are crossed we must look to reaction system relations to account for the fact that not every set of factors which can be obtained by recombination is capable of establishing the harmonious interrelations which are necessary for normal functioning in a reaction system. As a consequence species hybrids exhibit a peculiar set of phenomena including sterility, whether partial or complete, production of abnormal forms, and apparent lack of conformance to established principles of hybridization. Underlying all these surface phenomena, however, is a behavior essentially Mendelian, if we take Mendelism to include all those phenomena consequent upon the shuffling and recombination of factors which possess at least a relatively high degree of stability. Since any irregularities in the distribution of factors or chromosomes, which may be occasioned by the inharmonious relations within the hybrid reaction systems acting upon the chromosome mechanism, can hardly be considered to give rise to results which should not be included under the term Mendelism, it is very evident that simple assumptions such as we have outlined above will account for a considerable array of phenomena.

CHAPTER XIII

PURE LINES

For half a century succeeding Darwin, it was assumed that by selecting a certain type of individual for propagation, the species or variety would be continually transformed in the direction of the selection. Such a conception was a natural result of the widespread acceptance of Darwin's theory of the method of evolution and later of Galton's "law of inheritance" as applied to selection. Experience seemed to bear out this idea also, inasmuch as continual selection of the best plants for seed and the best animals for mating was found to be profitable. But it was not until Johannsen decided to test the power of selection by keeping the pedigrees of individual plants and their descendants that the truth concerning the composition of varieties of cultivated plants became known. Heterogeneity within single botanical species had already been discovered, but that horticultural varieties were also heterogeneous but with respect to less easily distinguishable characters had not been realized. Definite knowledge concerning the composition of horticultural varieties threw light on the problem of selection by explaining why continuous selection *within a variety* is necessary in some crops while it has little or no effect in the case of certain other crops. This discovery was of tremendous significance to genetics, particularly to breeding. For this reason the following account of Johannsen's classical experiments is based directly upon his own presentation of the matter.

Discovery of Pure Lines.—Johannsen chose a certain brown variety of the common garden bean (*Phaseolus vulgaris nana*) known as the Princess bean. In 1901 he harvested 287 plants which had grown from selected seeds of very different sizes and of known weights. The harvested beans from each plant were weighed separately. They were then divided into classes with an interval of 10 cg., the class center values ranging from 30 to 80 cg. Next he determined the mean weights of all the beans from the plants grown from mother beans falling in the first class (25–35 cg.) and similarly for the progeny of each of the groups of the mother beans. The result is shown in the following table.

Weight of mother beans...............	30	40	50	60	70	80
Mean weight of progeny...............	37.1	38.8	40.0	43.4	44.6	45.7

These two series may be expressed in terms of percentage by multiplying each series by a factor that will change the value of the middle class to 100. The mean weight of all the mother beans was very nearly 50 cg. while that of the progeny is approximately 40 cg. Thus the first series is multiplied by 2 and the second by 2.5 giving the following result.

Weight of mother beans...........	60	80	100	120	140	160
Mean weight of progeny...........	93	97	100	108	111	114

Now the deviation of each progeny class can be compared directly with the deviation of the mother class.

Deviation of mother beans.............	−40	−20	0	20	40	60
Deviation of mean weights of progeny..	−7	−3	0	8	11	14

Thus the ratios of the minus deviations of the progeny classes to the minus deviations of the mother classes are $\frac{7}{40}$ and $\frac{3}{20}$, the mean of which is $\frac{13}{80}$ or 0.163. Similarly for the plus deviations, $\frac{8}{20}, \frac{11}{40}, \frac{14}{60} \times \frac{1}{3}$, 0.303. The average of these two values is 0.233 which is about $\frac{1}{4}$ as compared with Galton's observation of $\frac{2}{3}$ inheritance in size of seed in the sweet pea and stature in man.

During these preliminary experiments, however, Johannsen noticed that plants grown from similar sized beans produced beans of very different sizes. Thus, for example, the plants grown from the largest mother beans (about 80 cg. in weight) yielded seeds of strikingly different sizes. The average weight of the seeds of these individual plants varied between 35 and 60 cg. and when the weights of all the individual beans of this series were arranged in a frequency distribution it produced a series that differed considerably from the normal frequency distribution. The distribution of 598 seeds, all progeny of beans about 80 cg. in weight, when arranged in classes of 5-cg. intervals, was as follows:

Classes......................	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80
Number of seeds............			5	18	46	**144**	127	70	70	63	28	15	8	4	
Theoretical numbers...........	1	3	11	26	53	85	109	**112**	91	59	30	13	4	1	

$$M = 45.44 \pm 0.43 \text{ cg.}; \quad \sigma = 10.40 \text{ cg.}$$

Clearly this distribution if plotted would produce a skew polygon with the mode to the left of the theoretical mode. This observation caused Johannsen to have serious doubt regarding the biological justification of Galton's law. For such a distribution did not appear to be the expression of only one "type"; on the contrary, it seemed more likely that the material was mixed.

This state of affairs was the starting point of further critical study. In order to take account of the effect of selection supposedly in the opposite direction, he next examined the progeny of the smallest mother beans (about 30 cg.) and found that they displayed no such striking irregularity as did the progeny of the largest beans. (Possibly this was due to the fact that about 20 plants were grown from the smallest beans while the progeny of the largest beans came from only 11 plants.) The progeny seeds from the smallest mother beans were weighed individually and the data put in the form of a frequency table as in the former case.

Classes	15	20	25	30	35	40	45	50	55	60	65
Number of seeds		8	18	71	156	**172**	127	35	15	3	6
Theoretical numbers	1	6	27	77	139	**162**	121	57	17	3	1

$M = 36.68 \pm 0.30$ cg.; $\sigma = 7.33$ cg.

This distribution does not indicate a mixture. Instead it suggests that a single original "weight type" of bean was set apart by selection in the minus direction. The general result of this preliminary study was certainly a sort of confirmation of Galtonian regression; but at the same time the doubt was aroused whether the original population was not a heterogeneous mixture from which selection simply sorted out already existing "types". Hence came the question: Will selection of plus or minus variants within pure lines bring about the isolation of types and cause Galtonian regression?

This question was answered the following year (1902). A series of 19 pure lines was used for this investigation. Each of these pure lines originated from a single bean from the crop of 1900. In the fall of 1901 each line was represented by the seeds of one plant. In 1902 he planted 524 seeds. Every seed was given a number and each plant was harvested separately. Each pure line, each plant and every single bean was separately numbered. Thus each individual could be compared with every other individual. Johannsen first compared his material as a whole with the results of his preliminary study. Having recorded the weight of each bean, he arranged the data in groups corresponding to the classes of mother beans as in the previous year.

Weight of mother beans	20	30	40	50	60	70
Mean weight of progeny	44.0	44.3	46.1	49.0	51.9	56.1
Number of progeny seeds	180	835	2,238	1,138	609	494

Again he found about ¼ inheritance and ¾ regression of progeny on mother beans. He next divided each of these six groups of progeny beans into classes according to weight as shown in Table XL.

TABLE XL.—SHOWING VARIATION WITHIN CLASSES IN A POPULATION COMPOSED OF PURE LINES. (*From Johannsen*)

Classes of mother beans, cg.	Classes of progeny seeds in cg.										*n*	*M*	*σ*
	5	15	25	35	45	55	65	75	85	95			
15–25		1	15	90	63	11					180	43.78±0.56	7.47
25–35		15	95	322	310	91	2				835	44.47±0.31	9.03
35–45	5	17	175	776	956	282	24	3			2,238	46.17±0.19	8.93
45–55		4	57	305	521	196	51	4			1,138	48.94±0.28	9.34
55–65		1	23	130	230	168	46	11			609	51.87±0.42	10.42
65–75			5	53	175	180	64	15	2		494	56.03±0.45	10.02
Total 15–75 cg..	5	38	370	1,676	2,255	928	187	33	2		5,494	47.92±0.13	9.87

It is true that each of the six progeny series corresponds closely to the normal frequency distribution. There is no distortion such as would be expected from mixed material. Nevertheless it becomes evident that the material is heterogeneous as soon as the data are arranged by pure lines as shown in Table XLI.

TABLE XLI.—SURVEY OF THE EFFECT OF SELECTION IN PURE LINES

(The dark-faced figures indicate mean weights in cg.; the light-face figures designate respective numbers of seeds.) (*From Johannsen*)

The pure lines	Weight in cg. of the mother beans												Mean weights of the lines	
	20		30		40		50		60		70			
I	....	....	....	....	....	...	....	...	**63.1**	....	**64.9**	91	**64.2**	145
II	....	....	....	....	**57.2**	86	**54.9**	195	**56.5**	120	**55.5**	74	**55.8**	475
III	....	....	....	....	....	...	**56.4**	144	**56.6**	40	**54.4**	98	**55.4**	282
IV	....	....	....	....	....	...	**54.2**	32	**53.6**	163	**56.6**	112	**54.8**	307
V	....	....	....	....	**52.8**	107	**49.2**	29	....	....	**50.2**	119	**51.2**	255
VI	....	....	**53.5**	20	**50.8**	111	....	...	**42.5**	10	....	...	**50.6**	141
VII	**45.9**	16	....	....	**49.5**	262	....	...	**48.2**	27	....	...	**49.2**	305
VIII	....	..	**49.0**	20	**49.1**	119	**47.5**	20	....	....	....	...	**48.9**	159
IX	....	....	**48.5**	117	....	...	**47.9**	124	....	....	....	...	**48.2**	241
X	....	..	**42.1**	28	**46.7**	412	**46.9**	93	....	....	....	...	**46.5**	533
XI	....	....	**45.2**	114	**45.4**	217	**46.2**	87	....	....	....	...	**45.5**	418
XII	**49.6**	14	....	....	....	...	**45.1**	42	**44.0**	27	....	...	**45.5**	83
XIII	....	....	**47.5**	93	**45.0**	219	**45.1**	205	**45.8**	95	....	...	**45.4**	712
XIV	....	....	**45.4**	21	**46.9**	51	....	...	**42.8**	34	....	...	**45.3**	106
XV	**46.9**	18	....	....	....	...	**44.6**	131	**45.0**	39	....	...	**45.0**	188
XVI	....	....	**45.9**	147	**44.1**	90	**41.0**	36	....	....	....	...	**44.6**	273
XVII	**44.0**	78	....	....	**42.4**	217	....	...	....	....	....	...	**42.8**	295
XVIII	**41.0**	54	**40.7**	203	**40.8**	100	....	...	....	....	....	...	**40.8**	357
XIX	....	....	**35.8**	72	**34.8**	147	....	...	....	....	....	...	**35.1**	219
I–XIX	**44.0**	180	**44.3**	835	**46.1**	2238	**49.0**	1138	**51.9**	609	**56.1**	494	**47.9**	5494

The above analysis not only demonstrates that Johannsen's material was a mixture of different "weight types" but it also gives striking proof that selection within a single pure line has no effect. Johannsen points out that in certain lines (*I, X, XI*) there seems to be a slight effect but that in others (*VI, IX, XII*, etc.,) an opposite tendency appears; while still others (*II, III, VIII*) are irregular. Generally speaking then no effect of selection is seen for there is no significant difference between the means of the several groups in each pure line. The apparent indications of selection effects are merely fortuitous variations. In each of these lines, therefore, the offspring of plus and minus variants exhibit complete regression to the mean of the particular line. In short, individual variations were not inherited, only the characteristic modifiability of the particular line was inherited.

Johannsen did not rest here but continued to test his pure lines of beans during successive years. He found a certain amount of seasonal fluctuation in the range of variation and in the variation constants, yet each pure line maintained its own individuality as indicated by the variation in weight of beans produced. And this maintenance of entity was accomplished in spite of repeated selections of smallest and largest beans so that each year every pure line was represented by two lots of plants, a "plus strain" grown from the largest beans and a "minus strain" grown from the smallest beans. Complete failure of such repeated selection to cause significant change in the mean weight of either strain was observed in each pure line. As illustrations the data on Lines I and XIX are presented in Tables XLII and XLIII.

From these data it is evident that six years of selection of plus and minus strains within Line I produced no permanent departure in either direction. In fact the last column (*B–A*) actually shows an inverse effect during three of the six years. Moreover, if the average of the means for the six years in both strains be compared this conclusion is verified.

TABLE XLII.—SELECTION-EFFECT DURING SIX GENERATIONS IN LINE I OF THE PRINCESS BEANS. (*From Johannsen*)

Harvest years	Total number of beans	Mean weight of mother beans of the select strains		Difference $b - a$	Mean weight of progeny seeds of select strains		Difference $B - A$
		a–minus	*b*–plus		*A*–minus	*B*–plus	
1902	145	60	70	10	63.15±1.02	64.85±0.76	+1.70±1.27
1903	252	55	80	25	75.19±1.01	70.88±0.89	−4.31±1.35
1904	711	50	87	37	54.59±0.44	56.68±0.36	+2.09±0.57
1905	654	43	73	40	63.55±0.56	63.64±0.41	+0.09±0.69
1906	384	46	84	38	74.38±0.81	73.00±0.72	−1.38±1.08
1907	379	56	81	25	69.07±0.79	67.66±0.75	−1.41±1.09

Table XLIII.—Selection-effect During Six Generations of Line XIX of the Princess Beans. (*From Johannsen*)

Harvest years	Total number of beans	Mean weight of mother beans of the select strains		Difference $b - a$	Mean weight of progeny seeds of select strains		Difference $B - A$
		a–minus	*b*–plus		*A*–minus	*B*–plus	
1902	219	30	40	10	35.83±0.44	34.78±0.38	−1.05±0.58
1903	200	25	42	17	40.21±0.65	41.02±0.43	+0.81±0.78
1904	590	31	43	12	31.39±0.29	32.64±0.21	+1.25±0.36
1905	1,657	27	39	12	38.26±0.16	39.15±0.17	+0.89±0.23
1906	1,367	30	46	16	37.92±0.22	39.87±0.16	+1.95±0.27
1907	594	24	47	23	37.36±0.30	36.95±0.21	−0.41±0.37

The mean for the progeny of the plus strain is 66.12±0.28 and for the progeny of the minus strain, 66.66±0.33. The difference is −0.54±0.43 (the probable error of the difference in all cases being found by taking the square root of the sum of the squares of the two probable errors). In Line I, therefore, there is no positive effect of selection; on the contrary there would appear to be a slight inverse effect!

Line XIX was characterized by beans of the least weight. The data for the results of six years of selection in plus and minus directions, particularly the difference between the progeny means (*B–A*), reveal somewhat larger fluctuations in the plus direction than in Line I but it will be noted that the probable errors of the differences are smaller, hence the validity is the more certain. Comparing the means of the means of the progeny seeds as before, for the plus strain we have 37.40±0.11 and for the minus strain, 38.83±0.15, the difference being +0.57±0.19, which is certainly small although in the plus direction. Now, if we compare the summaries of the data from these experiments, −0.54 and +0.57, we are forced to conclude that selection was without effect in these pure lines.

Finally Johannsen conducted similar experiments with the Princess beans, using the characters, length and breadth. He came to the same general conclusion, to wit, that he found no trace whatever of selection effect within pure lines and that the variations in pure line individuals are merely fortuitous modifications and are not inherited.

Conditions Necessary for the Existence of Pure Lines.—Johannsen defined a pure line as *the progeny of a single self-fertilized individual of homogeneous factorial composition.* Unless mutation takes place none of the descendants of such an individual can differ from the parent in their genetic factors. Two important conditions are imposed by this definition, viz., homozygosity and self-fertilization. The latter of these is the more fundamental inasmuch as it is mathematically demonstrable that self-fertilization, if continued generation after generation, leads rapidly toward a homozygous condition in all descendants. Thus, Jennings shows that in the case of the original cross, AA by aa giving all Aa, if thereafter all breeding is by self-fertilization, then, after n generations, the proportions of different genotypes in the population may be calculated by the following formulæ:

$$AA = \frac{2^n - 1}{2^{n+1}};$$

$$Aa = \frac{1}{2^n};$$

$$aa = \frac{2^n - 1}{2^{n+1}}.$$

Therefore, within six self-fertilized generations after a cross involving a single pair of factors, the proportion of homozygous individuals in the population for one or the other of the two factors will be 98.4 per cent. Hence it is clear that, even though many genetic factors are concerned, as is undoubtedly the case in any crop plant or domestic animal, yet in those species where self-fertilization is the method of reproduction, the fundamental condition necessary to the existence of pure lines is met. Although by definition every pure line is a genotype, yet every genotype is not a pure line, for any heterozygote belongs to some genotype whereas a pure line is necessarily homozygous. Upon the basis of Johannsen's definition, it would be impossible to obtain pure lines from obligatory allogamous species, to which class belong all domestic animals and certain cultivated plants. However, it is clear that continual inbreeding in such organisms would tend to produce a homozygous genetic composition.

Isolation of Pure Lines from Mixed Populations.—In order to obtain pure lines from mixed populations the method employed will depend upon the method of reproduction of the organism. In autogamous species the method adopted by Johannsen in working with beans is adequate. The individual plant being capable of reproducing the species through self-fertilization and incapable of natural cross-fertilization, it is only necessary to isolate the progeny of single individuals to establish pure lines. However, in supposedly autogamous species natural hybrids sometimes occur. Hence in critical work it is always advisable to protect the flowers even of autogamous plants. In dealing with allogamous species, in which it is necessary to mate two individuals, when starting with a mixed population of unknown genetic factors the original selections must be made on the basis of phenotypic similarity. With domestic animals the repetition of such selection for a large number of generations has produced the "pure" or pedigreed breeds, which approximate more or less closely to pure lines and hence should be expected to breed fairly true to type. With plants the method of procedure depends upon the details of reproduction in the species under consideration. For example, corn is naturally cross-fertilized but is also self-fertile, while the common sunflower is self-sterile and so must always be cross-fertilized. With such plants as the sunflower, then, the procedure will be as with animals and the length of time required to produce approximately pure lines will depend upon three things: (1) the number of genetic factors for which each of the selected individuals is heterozygous; (2) the number of genetic factors with respect to which the two selected individuals differ; (3) the number of chromosomes in the species. The specific chromsome number is an important consideration because of its direct relation to the number of linked character groups or in other words to the possible number of freely assorting pairs of factors. Sufficient has been said concerning the comparative ease of isolating pure lines from populations of autogamous species and the relative difficulty of obtaining pure lines from allogamous species to make it clear that the material under consideration is of the highest importance in all critical discussions of the effect of selection within pure lines. Finally, it is to be noted that a vegetatively propagated phenotype may or may not be a pure line according to its genetic constitution. A group of individuals thus propagated is known as a *clone*. In strictly allogamous species a clone would hardly ever be homozygous.

The Effect of Selection Within Pure Lines.—There is now considerable evidence in support of the theory that selection within a pure line is without effect. This evidence comes from the results of practical breeding as well as scientific investigations of certain autogamous species of plants, such as wheat, oats and barley; also from thoroughgoing research on a few allogamous species, especially on certain insects and protozoa, particularly paramecia. The constant maintenance of head type in wheat is strikingly portrayed in Fig. 106, which shows two heads from each of four varieties which were first isolated by Louis de Vilmorin between 1836 and 1856. The plants according to Vilmorin were found to be identical in all respects "although separated by an interval of 50 years during which annual selection had been continued. This fixity is shown not only in the characters of the ear but also in all the other characters of the plant even that of precocity, which would appear to be most dependent on climate." The use of this case as evidence in support of the pure-line theory has been criticised upon the ground that the selection practised had for its purpose the preservation rather than the alteration of the type. But from the experience of many investigators and breeders we may safely conclude that within true pure lines selection is without effect on the type unless mutations occur. After subjecting a variety of barley known as Glorup to plus and minus selection for eight generations, the character under observation being degree of mealiness of the kernel (Schartigkeit), Johannsen concluded that the selection had produced no effect. Moreover the Swedish plant-breeding station at Svalöf has been guided for years by the knowledge that their pedigree cultures, *i.e.*, pure lines, were not changed by selection. A similar conclusion was reached by Tower after four to ten generations of rigorous selection of albinic individuals in three different attempts to establish an albinic race from a stable race (pedigree material) of the Colorado potato beetle (*Leptinotarsa decemlineata*). The history of these three experiments are shown at *A*, *B* and *C* in Fig. 107. The small black polygons show for each generation the individuals selected to become the parents of the next generation. It will be noted that neither the range nor the mode of the population is permanently shifted in the direction of the selection. Thus we find that in races or varieties which are constant (homozygous) selection has no effect unless mutations occur. Various evidence has been brought forward to show that the principle does not hold for all organisms. But in all such cases among sexually propagated species we may assume that the material used was heterozygous for certain factors. Such has been shown already to be a satisfactory explanation of Castle's results in selecting for plus and minus strains in the hooded rats which is one of the cases originally advanced as evidence against the pure line theory.

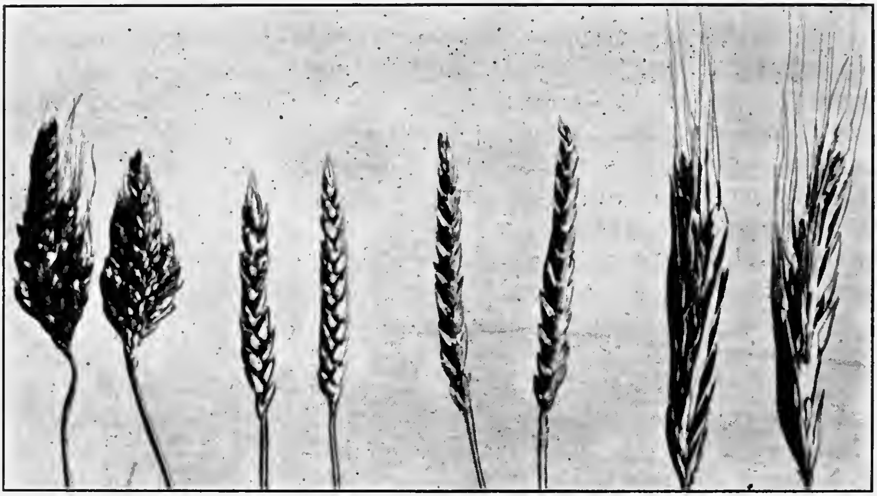


Fig. 106.—Four pure lines of wheat which have been grown by Vilmorin for 50 years. The original specimen in the seed museum is shown on the left in each case. The close similarity of the pairs of heads indicates that pure lines remain constant indefinitely. (*After Hagedoorn.*)

Significance of the Pure Line Theory in Breeding.—The question thus arises: How does the pure line theory explain the fact that man has wrought profound changes in domesticated animals and plants by selection? It is well known that as a rule a mixed population consists of a number (probably quite large) of distinct biotypes and that in autogamous species these biotypes are pure lines to begin with, while in allogamous species it is only by continued intensive selection that existing

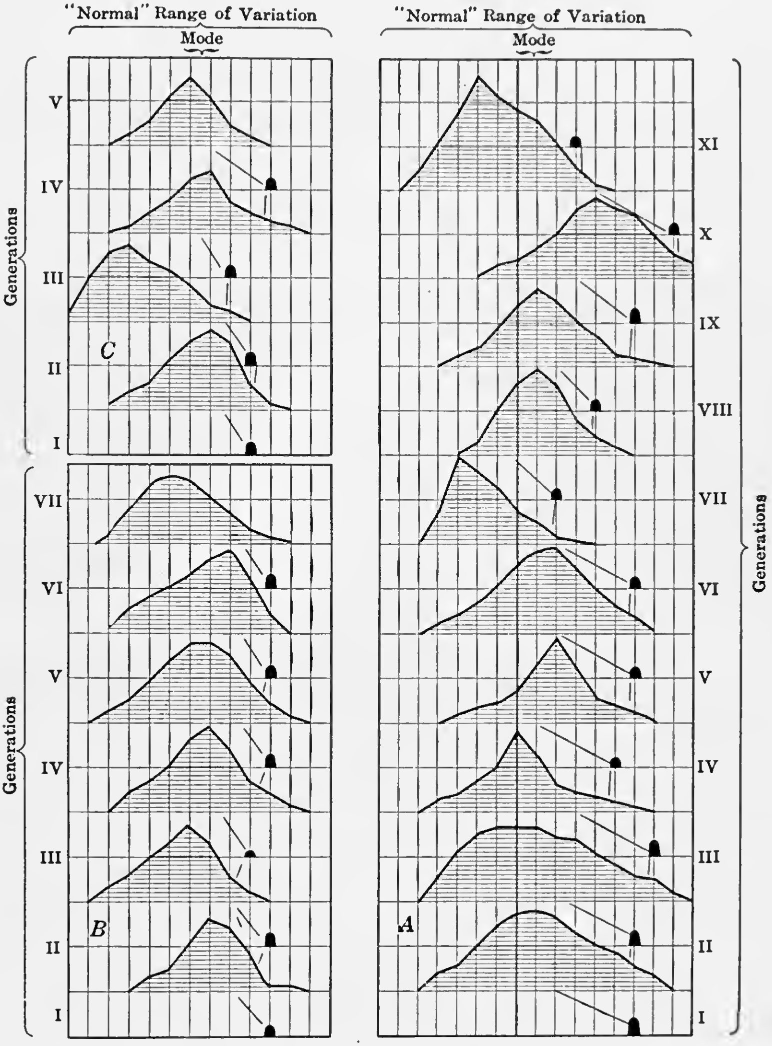


FIG. 107.—Diagrammatic representation of results of three experiments in selecting beetles in an effort to create an albinic strain from a pure strain. (*From Tower.*)

biotypes can be differentiated from one another so that they "breed true." How these distinct biotypes originate will be considered in the following chapter, the fact that they exist is the chief consideration here. The effect of "mass" selection in causing temporary changes in heterogeneous varieties of plants and races of animals is easily understood by the aid of the diagram shown in Fig. 108. The area within the large curve represents a mixed population or phenotypically similar group containing a number of distinct genotypes indicated by the small curves *A–Z*. Every genotype has its own variation curve and is distinct from each of the others, but they intergrade with each other so completely that the population appears as an entity. Now if one should select individuals from either extreme of the population, say at 90 or 70, it is clear that such individuals might belong to any one of four or five genotypes. If selection in the same direction were continued a strain would be established with a mode distinct from the mode of the original population. These strains could be maintained by continual selection and in time a single genotype might be isolated when selection would be said to have changed the type permanently. But selection changed nothing—it only isolated a certain genotype or genotypes from the original mixture. Tower's results in selecting for the purpose of creating albinic and melanic strains of beetles as illustrated in Fig. 109 may be explained in this way. The original population shown at *A* consisted of a number of distinct biotypes. By the isolation of several extreme variants Tower separated plus and minus strains which he was able to maintain for eight generations by practising intensive selection. In the eighth generation he divided each population in half, continuing intensive selection with one portion and stopping all selection in the other. By this method he was able to maintain the plus and minus strains and at the same time to observe that in the ninth generation the mode of the

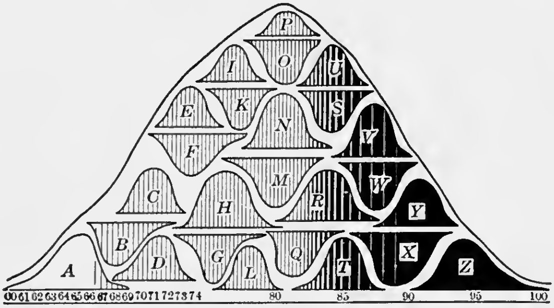


FIG. 108.—Schematic diagram showing the relation of a population to the biotypes composing it, or of a phenotype, to the genotypes or pure lines within it. (*After Lang from Goldschmidt.*)

progeny of the unselected eighth generation population lay much nearer to the mode of the original population. Within three generations the unselected strains had moved back to the mode of the species. Now it is to be remembered that Tower was dealing with an obligatory allogamous species. Moreover, what is now known concerning body pigmentation in Drosophila makes it altogether likely that quite a large

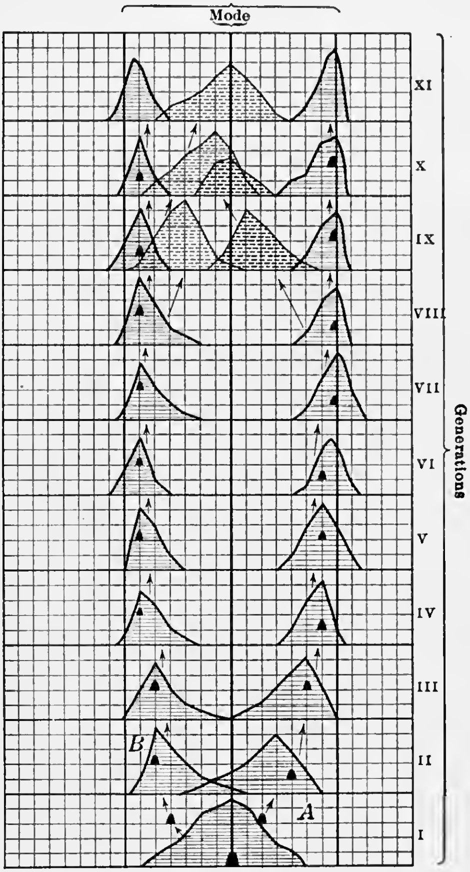


Fig. 109.—Diagrammatic representation of the results obtained by the creation of albinic and melanic strains from a mixed population of beetles. (*From Tower.*)

number of genetic factors are concerned in the degree of pigmentation of these beetles. Hence selection of phenotypes for a number of generations did not isolate genotypes, *i.e.*, the plus and minus strains were not homozygous. As this is an allogamous species undoubtedly most of the individuals in the original population were heterozygous for many factors. Furthermore, Tower did not select single pairs but always took several pairs as parents for each generation. While the selection of similarly pigmented individuals would tend gradually toward a homozygous condition,with respect to the specific factors conditioning pigmentation, yet it is altogether likely that under the conditions of the experiment a considerable degree of heterozygosity was maintained. In other words the selection practised did not isolate pure lines, the plus and minus strains did not become homozygous. Much of the work done in the past in ameliorating animals and plants has been by this method of selecting phenotypes but not genotypes, which accounts in part for the frequent necessity of continuous selection in maintaining improved strains or breeds. In reviewing the development of plant breeding we shall note certain cases of early recognition of the effects of genotypic selection, a principle which is now accepted as fundamental in all breeding operations.

CHAPTER XIV

MUTATIONS

Baur's third category of variations comprises all inheritable changes due to causes other than segregation and recombination of genetic factors. Although comparatively little is known concerning the specific causes of mutations, yet it is possible to distinguish between two general classes of such inheritable variations according to the nature of the genetic units involved. These classes are (1) alterations in genetic factors, and (2) deviations in the number of chromosomes. We designate the first group as *factor mutations* and the second as *chromosome aberrations.* Since the first group is of vastly greater importance to agriculture than the second, we shall consider the latter very briefly before engaging in discussion of the former, which we deem worthy of recognition as mutations in the strict sense.

Chromosome Aberrations.—By the aid of cytology it has been demonstrated that inheritable changes are occasionally induced, in plants at least, by irregularities in the behavior of the chromosomes during mitosis or meiosis, such that certain germ cells contain fewer or more chromosomes than the number typical of the species. Aberrant forms in several plant families are now known to differ from the parent species in chromosome number. Some have only a single chromosome more or less than the parent, while a few are known in which the original number is doubled. It is possible that aberrations occur involving all combinations of numbers between these two extremes. In various forms of Lamarck's evening primrose (*Œnothera lamarckiana*), whose typical number is 14, according to Gates the following aberrant numbers have been reported—15, 20, 21, 22, 23, 27, 28, 29, 30. Aberrations involving the doubling of the number of chromosomes typical of the species is known as tetraploidy because there are four times the haploid number typical of the parent. Occasionally aberrations or hybridization between diploid and tetraploid forms result in triploidy.

There is a limited amount of evidence which indicates that groups of species have arisen by progressive alterations in chromosome number. Thus in Drosophila, Metz has found ten species in which the chromosome numbers range from 6 to 12 and the larger numbers appear to have arisen by subdivision of the large dumbbell-shaped chromosomes found in the species having smaller numbers. Evidence that doubling of the chromosome number may occur during somatogenesis has been found by Farmer and Digby in the interesting hybrid, *Primula kewensis.* The original plant, which was sterile, "had 18 and 9 chromosomes in its premeiotic and postmeiotic nuclei respectively," but in the fertile plants which were propagated asexually from it, as well as in similar fertile hybrids which were produced in later experiments, the diploid and haploid numbers were 36 and 18 respectively. Having found by means of careful measurements of the chromosomes in the two forms that the nuclei in both forms contain the same volume of chromatin, the authors conclude that the increase in number may be attributed to transverse fission of the 18 larger chromosomes and not to the fusion of two nuclei.

From a study of chromosomal dimensions in relation to phylogeny, Meek "arrived at the conclusion that the widths of chromosomes are successively greater in higher zoological phyla, and that this dimension is constant for very large groups of animals." But Farmer and Digby have shown that such a conclusion is without foundation since "closely related forms may possess chromosomes differing widely in shape and size and character." Hence they conclude "that phylogenetic affinity is not, necessarily, correlated with chromosome width." They also point out that "unfortunately we know practically nothing about the phylogeny of the chromosomes. No convincing hypothesis has been put forward to explain how these remarkable bodies have become organized, nor how their peculiarities have either been brought into existence or are kept so true for a given species." However, we are reminded by Glaser that chromatin is present in bacteria though not in the form of a nucleus and it may not be too much to hope that cytology may yet discover the principal stages in the development of the chromosomes and establish such correlation as may exist between this development and organic evolution. Certainly extended investigations of chromosome numbers must be made before chromosome aberrations can be considered an important factor in evolution. Except that certain chromosome aberrations, such as tetraploidy causing gigantism, might be of economic value, in general this class of mutations is of minor importance in breeding.

Factor mutations, on the other hand, are of prime importance and of general occurrence. Factor mutations have appeared in controlled cultures of many animals and plants and the character differences conditioned by them are as a rule such as distinguish varieties of a single species. Moreover, varietal characters are Mendelizing characters in the narrow sense and the existence of simple Mendelian phenomena among all classes of sexually propagated organisms proves that factor mutations are of general occurrence. Although it is probable that every factor mutation has a certain effect upon every character in the organism, yet the visible effects of some factor differences are restricted to a single character. According to their visible effects, therefore, we recognize two classes of factor mutations: (1) those conditioning apparently only single characters; (2) those having a visible manifold effect on the soma. Cases involving mutations of the second class are known in several species of animals and plants. An interesting example is the oak-like walnut, *Juglans californica* var. *quercina*, which appears to differ from the parent species by a single factor difference, Fig. 110. But this variety is distinct from the species type in nearly all gross morphological characters.

Fig. 110.—A seedling of the oak-like walnut (left) and of the California black walnut, the parent species (right.)

The Nature and Causes of Factor Mutations.—Our knowledge of genetic factors is entirely of an inferential sort and it is probable that these ultimate hereditary units are no more likely to be objectively perceived than are the atoms of which all matter is generally believed to be composed. But our present understanding of biochemistry and the chromosome mechanism of heredity leaves no room for doubt concerning the theoretical nature of these factors. Living protoplasm is generally considered as composed of very complex organic compounds. The phenomena of stereochemistry, especially the substitutional or cyclic changes which occur within various compounds under proper conditions, suggest that similar compensatory relations exist between the substances composing the living cell. Yet cytological observations indicate that the chromatin is the only permanent constituent of the nucleus and that the chromosomes are unaffected by the regular physiological processes of metabolism, growth and reaction to stimuli even though they play a very definite rôle in all these activities. As was explained in Chapter IV, the chromosomes are linear series of loci whereat are located specific factors. According to the multiple allelomorph hypothesis more than one factor may exist at a given locus. Since the chromosomes appear to consist of the only permanent substance in the nucleus, it is conceivable that at each locus there exists a unique chemical system; yet it is not unreasonable to suppose that occasionally substitutional changes similar to those known to take place in less complex organic compounds may occur here.

The contributions of Reichert on the specificity of proteins and carbohydrates as a basis for the classification of animals and plants are based on the fact that such substances as serum albumin, hemoglobin, glycogen and starch exist in stereoisomeric forms. That is, "each kind of substance may exist in a number of forms, all of which forms have the same molecular formula and the same fundamental properties in common, but each in accordance with variations in intramolecular configuration has certain individualities which distinguish it from others. . . . It has been found that the number of possible forms of each substance is dependent upon the possible number of variations of the arrangements of the molecular components in the three dimensions of space, or, in other words, of variations of molecular configuration, the possible number in case of each substance being capable of mathematical determination. Thus, we find that serum albumin may exist in as many as a thousand million forms. Hemoglobin, the red coloring matter of vertebrate blood, is a far more complex carbon compound than serum albumin, and theoretically may exist in forms whose number is beyond human conception, running into millions of millions. The same is true of starch." Having in mind this complex molecular structure of protoplasmic constituents and the phenomenon of substitutional changes of atoms or radicals by which such complex compounds are transformed, we can express a conception of the nature of factor mutations.

To be specific let us suppose that some unusual condition occurs in a certain germ cell of a normal female Drosophila such that a single atom in each of the very complex molecules of the substance unique for the locus *W* in the *X*-chromosome changes place with a different atom in the surrounding nucleoplasm—the substance unique for the locus *W* is no longer capable of conditioning the laying down of red pigment in the eyes and, if the affected ovum is fertilized by a *Y*-bearing sperm, a white-eyed male appears, the result, as we say, of a factor mutation. This conception of factor mutations is useful as a basis for the multiple allelomorph hypothesis. In order to explain how two or more factors may have the same locus in a chromosome, it is only necessary to assume as possible the substitution of two or more different atoms or radicals in the molecule of the complex organic substance unique for the given locus by other atoms or radicals in the nucleoplasm.

Factors are relatively stable entities however. It has been shown already that any organism must possess thousands of factors, yet mutations are comparatively rare even in Drosophila. These facts are rather difficult to harmonize with our conception of the nature of factor mutations. If substitutions of atoms or radicals occur why do they not take place more frequently? Such questions must remain obscure until we know something about the chemical constitution of the hereditary factors. Only then can we expect to understand clearly the nature of the alterations which occasionally are made in them.

In this connection the behavior of factor mutations in inheritance is of decided interest. As a rule they are recessive to their normal allelomorphs and for some time they were thought to be due to the loss of factors, this idea being associated with the presence and absence hypothesis. But on rare occasions dominant mutations have appeared. Among 150 mutations from the normal type of *Drosophila ampelophila* several, such as bar eye, dark streak on thorax, abnormal abdomen and CIII, a factor which modifies eosin eye color, are dominant over their respective allelomorphs. A few other mutant characters have been found to be dominant, such as hornlessness in cattle and red buds in the evening primrose (*Œnothera rubricalyx*), but the great majority are recessive as is indicated by the ratio in F_2 from crosses between mutants and normal individuals. The condition in F_1 by no means always indicates complete dominance of the normal character. Hence it is clear that whatever the nature of the mutation-producing chemical change may be, as a rule it is either completely subordinate to the normal condition or else it merely modifies the effect of the normal state in heterozygous individuals, making its own distinctive manifestation in one-fourth of the progeny of such individuals.

When we enquire as to what are the particular conditions or specific antecedent events that make possible or cause the assumed substitution of atoms or radicals, we find ourselves again confronted by an almost total lack of knowledge. One thing is certain however, namely, that factor mutations are not fortuitous in occurrence, because, if they were the outcome of wholly indeterminate series of events, they would be as likely to occur in one species or race as in another at a given time and with the same relative frequency under all conditions, but such is not the case. On the contrary, certain species appear to be much more prolific in factor mutations than others and, as stated in Chapter II, it would appear that inheritable variations can be induced under controlled environmental conditions in pedigree strains that have bred true for a number of generations. Furthermore, even though our knowledge of the occurrence of factor mutations were so meager as to furnish no basis for reasoning and even though future observations of the same might seem to indicate that they are fortuitous, we should still be justified in assuming the existence of specific causes for factor mutations. It has been clearly shown by Pearl that, while natural phenomena are the result of long series of antecedent events or conditions, yet these are not all of equal determinative value; but rather that there are always specific causes which are few in number, immediate in time and large in relative quantitative effect. It does not seem necessary to present here the course of reasoning on which this conclusion rests. The important thing for agriculture is the fact that factor mutations are caused and the possibility that some of the determinative antecedent conditions are external to organisms, *i.e.*, that they exist in the environment and are controllable by man. The problem of the exact nature of factor mutations is only a phase of the general problem of the nature of living protoplasm, the solution of which is one of the ultimate aims of biology. But it is possible at least that experimental research may reveal methods by which factor mutations can be induced in both plants and animals.

Factor Mutations Both Germinal and Somatic.—Factor mutations appear to occur in undifferentiated cells, the germ plasm or embryonic tissue in animals and either the germ cells or any meristematic tissue in plants. Occasional discontinuous variations are found in animals which might seem at first to be due to factor mutations in the developing soma. But most of these abnormalities are more satisfactorily explained in other ways. Thus, gynandromorphism, or the condition of having one side of the body male and the other female, has been reported in insects more than a thousand times according to

Morgan. Without doubt it is caused by some irregularity in the process of fertilization. Homeosis, or the replacement of one organ by another, is known to have followed mutilation. Examples of the modification of characters by environmental conditions are given in Chapter II. There are many similar variations in animals, none of which are hereditary. However, we shall again refer to the possibility of somatic mutations in animals.

There is no direct evidence as to the cytological time of factor mutations, but the stage in the germ cell cycle of animals at which factor mutations are most likely to occur would seem to be shortly before or during the process of maturation. This is indicated by the sporadic appearance of mutants. The first observed mutation in *Drosophila ampelophila* was white eyes, which were found in a few males among several hundred individuals in a pedigreed red-eyed race. Similarly with other sex-linked mutant characters that have been observed in this species, they have appeared either singly or at most in a few individuals. Had these mutations occurred at an earlier stage in the germ cell cycle, more gametes would have been affected and more mutant individuals would have been found. Obviously the length of time that must elapse before a factor mutation can manifest its existence depends upon two things in addition to the stage in the germ cell cycle at which it occurred: (1) its relation to its normal allelomorph, *i.e.*, whether it is dominant or recessive; (2), its relation to sex determination, *i.e.*, whether it is sex-linked or not. A mutation from W to w in an X-chromosome of a normal male Drosophila would have produced a heterozygous red-eyed female in the next generation and no white-eyed flies whatever. One-fourth of the progeny of such a female would in turn be white-eyed if she mated with a normal male. Similarly with any non-sex-linked recessive character which upon its first appearance in pedigree culture is found in more than a single individual the probable order of events is as follows. A mutation occurred in a single germ cell of a single individual, which mated with a normal individual, thus giving rise to one heterozygote among its progeny. This heterozygous individual mated with a normal individual, producing heterozygotes among one-half of their progeny. Finally some of these heterozygotes mated together and one-fourth of their progeny bore the recessive mutant character.

It would seem, therefore, that factor mutations in animals occur in the germ cells shortly before or during maturation and the time of appearance of a mutant character depends upon the relation of the mutant factor to its normal allelomorph and whether or not it is contained in the sex chromosome.

In plants factor mutations may occur in any meristematic tissue as well as in the germ cells. Observations on the occurrence of mutant seedlings indicate that, as in animals, germinal mutations usually occur just before or during the maturation process. The strongest evidence for this conclusion is the fact that, so far as known, new dominant characters appear first in only one or two individuals. The following cases illustrate this point. The red-leaved evening primrose, *Œnothera rubricalyx* (Fig. 118) has been known to occur but once in all Œnothera cultures and then in a single plant. The red sunflower, *Helianthus lenticularis coronatus,* as reported by Cockerell, first appeared as a single plant which proved later to be a heterozygous dominant. A purple-leaved mutation in hemp, *Cannabis sativa,* is reported by Dewey to have first appeared in two pistillate plants in a closely inbred strain of normal green plants. Had these mutations occurred at some preliminary stage in germ-cell formation, the change in chemical constitution would have been transmitted to several or many gametes and a considerable number of individuals would have appeared instead of only one or two.

FIG. 111.—Bud sport from a white flowered gladiolus bearing red flowers on one side of the stalk and showing one flower half red and half white; a sectorial chimera (see Chapter XXII).

Factor mutations in meristematic cells, or vegetative mutations, as distinguished from those originating in the germ cells, give rise to simple *bud sports* or to *chimeras* according to the location of the mutating cell. A bud sport is a shoot or branch which differs genotypically in one or more characters from the remainder of the plant. Here the factor mutation must occur in one of the undifferentiated cells of the very young shoot. Just as in the case of factor mutations in germ cells, so in vegetative mutations the somatic effects range from single visible character differences to manifold effects in which many structural details are different. An example of bud sports in which the factor mutation induced a single character difference is shown in Fig. 111. The early gladiolus known as "The Bride" is a white variety of *Gladiolus colvillei,* a red-flowered form, and doubtless originated from it as a seed or bud mutation. In 1915 there appeared in a row of "The Bride" a single stalk bearing partly red and partly white flowers. That this grew from a corm which was an offshoot from a typical white-flowering corm is certain. Furthermore, that the mutation occurred very early in the development of this corm and not sometime during the growth of the flower stalk is proved by the following observation. In the autumn following the discovery of the mutant stalk it was carefully lifted and the corm from which it grew was separated from the cluster of white-flowering corms. It was observed that there were smaller corms located very close to the mutant corm. The following spring one flower stalk bore red and white and the other only red flowers. In gladiolus the young corms push out from near the base of the old one. Hence the original mutant corm must have consisted partly of cells capable of producing red pigment in the flowers. That the cells having this altered chemical constitution comprised about one-half of the corm is indicated by the position of the red and white flowers on the stalk. This illustration is hardly typical of all bud sports in that the mutation occurred too late in the development of the young shoot to change all the cells in the corm and so make all the flowers red. It was chosen first, because the mutant character is dominant,[1] which makes it certain that the sport was due to mutation rather than to segregation, and second, because it also illustrates the origin of chimeras. In many cases of discontinuous bud variation the entire shoot is affected. Cases of bud variation presumably caused by factor mutations which condition manifold character differences are occasionally found in the citrous fruits. The so-called Australian Navel orange has undoubtedly arisen a number of times from the commerical variety, the Washington Navel orange, from which it differs in its propensity to rank vegetative growth combined with low productivity. Also the fruits are rough and of poor quality. Numerous other distinct types of oranges and lemons have been discovered, usually as a single tree or merely a branch on a tree of the commonly cultivated variety (see Fig. 161).

A chimera is a mixture of genotypically diverse tissues in the same shoot. The nature, categories and artificial production of chimeras and graft hybrids are discussed in Chapter XXII. Here it is only necessary to point out that as they occur in nature they undoubtedly owe their origin to factor mutations. In the red and white flowered gladiolus an entire shoot became composite in nature through a factor mutation in a meristematic cell very early in the development of the stem. If the mutation had occurred later on at just the right point in the vegetative cone, it might have produced a single red and white flower. This is apparently the manner of origin of the odd stripes on certain fruits such as the lemon shown in Plate II. In this case it is evident that mutations occurred in two different cells. In one case the factor change resulted in the laying down of yellow pigment of a deeper shade ("deep chrome," No. 17*b* of Ridgway's Color Standards) than that normal for the variety, which is lemon chrome. In the other case the mutation

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[1] *G. colvillei* is a hybrid between *G. cardinalis*, which has bright scarlet flowers and *G. tristis*, which has white or yellowish flowers.

resulted in the production of some red pigment along with the yellow, thus causing the narrow sector of deep orange chrome (Ridgway, No. 11*h*). That each of these changes occurred in a single cell is indicated by the fact that the differently colored sectors are sharply defined throughout and that the extremities of the orange red sector are extremely narrow. J. B. S. Norton reports the origin of a color chimera in the Acme tomato in which a branch of lighter green foliage appeared and the lighter colored tissue could be traced down the stem to a point where it had apparently originated in a single cell. Expanding as the stem grew, first a portion of a leaf was involved and finally an entire bud was included, thus giving rise to the sport branch. Undoubtedly this is the usual manner of origin of natural chimeras.

We have examined several typical cases of factor mutations in animals and plants. From this evidence it is clear that factor mutations occur in undifferentiated cells—the germ cells in animals and either the germ cells or any meristematic cell in plants. There is, of course, no *a priori* reason why mutations should not occur in the somatic cells of animals. A fairly common meristic variation is the reduplication of repeated parts and it is possible that this departure from normal development is conditioned by a factor mutation. The discovery of a germinal mutation causing reduplication in animals would support this idea. Such a mutation has been discovered by Miss Hoge who reported a recessive factor for reduplication of the legs in the Drosophila. This possibility of somatic factor mutations in animals has little practical significance on account of the impossibility of propagating domestic animals asexually. It has considerable theoretical interest, however, in its possible bearing on the origin of certain diseases such as cancer.

Vegetative Mutation *Versus* **Somatic Segregation.**—Since the majority of bud sports are characterized by the replacement of a dominant with a recessive character, it is not strange that both bud sports and chimeras have been generally considered as due to "somatic segregation" in heterozygous individuals. It is not yet known whether bud sports occur more frequently in heterozygous than in homozygous individuals. But this consideration is of less importance than the fact that somatic factor mutations do occur, which seems to be well established. To mention an illustrative case, Emerson has shown that the experiments of de Vries, Correns, Hartley, East and Hayes, and himself, "all indicate that certain somatic variations are inherited in strictly Mendelian fashion. All these somatic variations consist in the appearance of self-colors on plants that are normally variegated in pattern. The fact that variegated plants occasionally throw both bud sports and seed sports with self-colors is not, in general, to be taken as an indication that the variegated plants in question are heterozygous. Such behavior seems to be insepa-

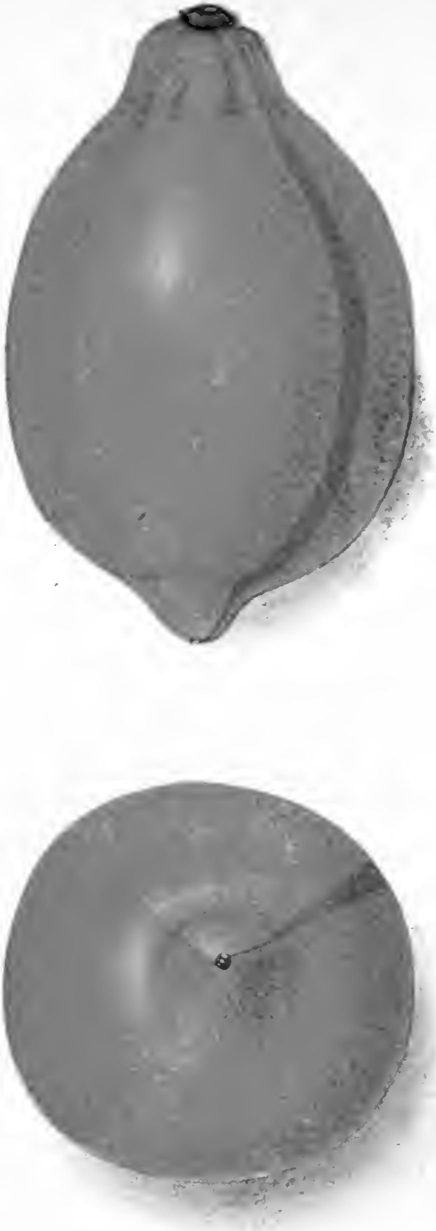

Plate II.—**Chimera in a lemon.**

The broad sector of orange and the narrow sector of orange red were caused by factor mutations which occurred presumably in single cells at a very early stage in the development of the fruit.

rably associated with variegation. Correns has pointed out that variegated Mirabilis plants cannot be considered mosaics of green and 'chlorina' types due to heterozygosis, since they do not segregate into chlorina and green, but into variegated and green. The same reasoning applies to variegation in the color of maize ears. Variegated-eared plants do not throw reds and whites, but reds and variegates. The conclusion seems irresistible that self-color occurring as a somatic variation is due to the change of a Mendelian factor for variegation into a factor for self-color. If this be granted, the behavior of these variations in later generations is a mere matter of simple Mendelian inheritance."

If bud sports are caused by mutations and if most bud sports involve a change from the dominant to the recessive condition of a certain factor, it follows that the change in chemical constitution must affect both of the duplex factors present in the somatic cell in order that the recessive character may appear. To those who think of mutations as fortuitous events, this may seem an obstacle to the conception that bud sports are the result of factor mutations. But from the point of view that factor mutations are caused, probably by some specific internal condition, it would seem most natural for the cause to have the same effect on both factors. Obviously this conception assumes that in such cases the specific cause, whatever it is, has the same potentiality in all parts of the nucleoplasm, and there is no *a priori* logical objection to such an assumption. At the same time there is good evidence that mutations do sometimes occur in only one of a duplex pair of factors. Hartley reports "a remarkable ear (Fig. 112) occurring in a field of white dent corn which had for many years been grown as a reasonably pure corn, but which occasionally, as many white corns do, produced a red ear." But this ear was only partly red since about one-fifth of its surface was occupied by variegated grains which appear to be white in the picture. Hartley tested all the grains on this ear and found that the red grains produced a crop of 84 red ears and 86 pure white ears, while the variegated grains

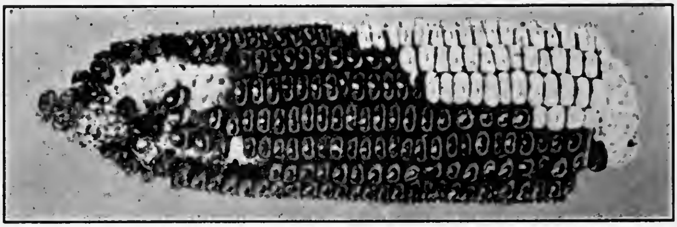

FIG. 112.—Bud sport and chimera in an ear of corn. This ear appeared in a field of white dent corn. The apparently white kernels, occupying about ⅕ of the surface, were actually variegated, being marked with "fine red lines, or streaks, radiating from the caps down the sides of the kernels." (*After Hartley.*)

produced 39 variegated ears and 36 pure white ears, which is clearly a 1:1 ratio in each case. This proves that both types of grains were heterozygous for a dominant mutant factor and that both of the factor mutations occurred in only one member of a duplex pair of factors. Presumably the mutation from white to variegated occurred first, and later the mutation from variegated to red in a cell so located that, as the shoot developed, only a portion of the ear was affected.

There appears a very important obstacle to the conception of "somatic segregation" in that the mechanism of cell division is apparently one of the most nearly perfect and regular of natural systems and that the orderliness of procedure is especially notable in undifferentiated tissue, where bud sports and chimeras commonly originate. To assume that the occurrence of self-colored flowers on variegated plants is due to chromosome aberrations in mitotic divisions is much less plausible than to explain such phenomena by assuming a simple factor difference as responsible for self-color and variegation, and that changes from one state to the other are possible under certain conditions. This is the only reasonable hypothesis by which to explain mutations from the recessive to the dominant condition of a pair of factors, as we have seen in the case of Hartley's ear of red and variegated corn. Therefore, while chromosome aberrations are known to occur during mitosis and aberrant numbers of chromosomes have been found in senile and diseased tissues, yet, in general, bud sports and chimeras are satisfactorily explained on the basis of factor mutations; whereas "somatic segregation" as the term has been used by Bateson, Gates and others implies the common occurrence of breaks in the mechanism of mitosis such as are not known to occur in normally functioning somatic cells.

It should be remembered that horticultural literature contains numerous peculiar cases of discontinuous variation, many of which have been described or "explained" as "somatic segregations" resulting from hybridization. We believe that most of these cases can be explained much more reasonably in terms of factor mutations. But certain discontinuous variations in plants are undoubtedly the result of neither factor mutations nor chromosome aberrations in vegetative tissues. For example, persistent and deciduous calyx lobes are sometimes found on fruits of the same plant especially in the rose family. Tufts has described the occurrence of this phenomenon in the Le Conte pear and the Transcendant crab-apple as "somatic segregation," assuming that some sort of segregation-mechanism exists in the division of somatic cells. Data from the pear tree gave a ratio of 3.15 deciduous to 0.85 persistent lobes. But to assume irregularities in chromosome behavior such as would cause segregation preceding the formation of nearly one-fourth of the calyx lobes on the tree is unwarranted in view of the general regularity of the process of mitosis (see p. 60). It has been shown by Babcock and Lloyd that no special significance should be attached to the occurrence of a ratio which, under the laws of simple sampling, could not occur oftener than once in 1,155,000,000,000,000 times, especially in view of the fact that these two varieties are presumably complex hybrids, and the persistency and deciduousness of the calyx lobes were variable in the parents. Hence to use the term somatic segregation in attempting to explain phenomena such as these is not only unwarranted but positively misleading.

The multifarious manifestations of dimorphism in plants are, in general, the result of alternative expression of inherited characters rather than alternative transmission of different factors. There are, to be sure, various cases of dimorphism within species, such as the different forms of flowers described by Darwin or the zygomorphic and peloric snapdragon flowers, which usually do not appear together on the same plant and which exhibit alternative inheritance when crossed. But there are many species which bear different forms of branches, leaves, flowers or other organs on the same plant. Cook has described dimorphic branches in cotton, coffee, cacao, the Central American rubber tree and the banana, also dimorphic leaves in cotton, hibiscus, okra and allied genera. The open and cleistogamous flowers of the violet make a familiar example of dimorphism in the same plant. In all these cases it appears that the individual plant contains all the factors conditioning the expres-

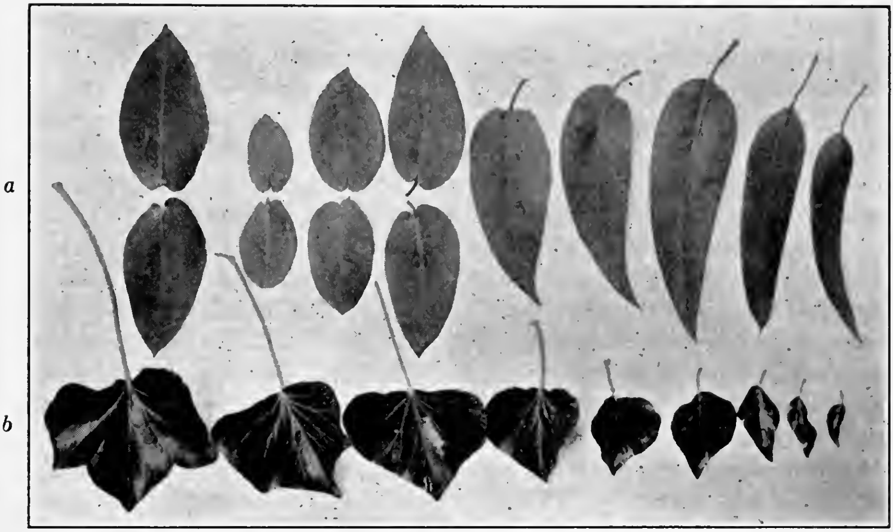

FIG. 113.—Transition from one form of leaf to another on the same branch in (*a*) *Eucalyptus globulus* (*b*) *Hedera helix*.

sion of the alternative forms. It seems reasonable then to explain the variations in somatic expression of the genetic factors present by internal changes of some sort. Frequently these variations appear as localized stages in ontogeny and it is possible that internal secretions (hormones) play a more important rôle in plant development than has been realized. The recent experiments of Loeb on *Bryophyllum calycinun* indicate not only the association and possible identity of root-forming and geotropic substances in this plant, but also that the leaves produce growth inhibiting substances which pass downward through the stem and which may accompany or may be identical with the root-forming hormones. Cook has shown that sometimes two extremely different forms of leaf occur on adjacent nodes but even such abrupt transitions might result from an internal reaction occurring in the interim between the development of the two successive leaves. Moreover, the transition from one leaf form to the other is frequently gradual as in the two series, each from a single branch, shown in Fig. 113. We conclude, therefore, that most cases of dimorphism in the same plant are not caused by factor mutations but rather that they should be classified with those cases of "fixed dimorphism" so frequently found in insects and illustrated by the earwigs in Fig. 20.

"Mutations" in the Evening Primroses.—Credit for directing attention to suddenly appearing new forms of animals and plants both as material for origin of species and for improvement of domesticated races belongs to the Dutch botanist, Hugo de Vries. Other naturalists had previously noted such aberrant or anomalous organisms but without attaching much significance to them. Thus in the works of Darwin, especially in "The Origin of Species" and "Animals and Plants under Domestication," there are frequent references to aberrant individuals or sports and to curious groups of plants and animals like the niata cattle, which Darwin admits probably originated as definitely distinct individuals among the typical species group. Yet Darwin never considered such aberrant individuals or groups as playing any significant rôle in evolution. On the other hand, de Vries became so convinced of the general occurrence and significance of suddenly appearing, heritable variations that he proposed a theory of evolution by mutation in which he applied Darwin's great principle of natural selection to these mutations as the general method of origin of species. The investigations which led him to this conviction extended over a period of nearly 20 years, during which time he brought under experimental cultivation some hundred species of plants that grow wild in Holland. They all exhibited more or less continuous variation; also he was able to isolate numerous strains which differed from the normal wild type with respect to some peculiar feature. But de Vries was searching for evidence of species "in the making" and he believed that by sufficient searching he should locate a species in which the transformation into new forms was proceeding on a scale large enough to make possible the direct observation of species formation. In none of the particular races that he collected did he observe profound discontinuous variations until in 1886 he discovered a feral group of large-flowered evening primroses (*Œnothera lamarckiana*) growing in a suburb of Amsterdam. They had escaped into an abandoned potato field from a nearby park. The source of this particular evening primrose has been traced by de Vries. About the middle of the 19th century seeds of *Œ. lamarckiana* were imported into England from Texas. De Vries' race came from an estate near Hilversum, the seed having been obtained originally from an establishment in Erfurt, which de Vries thinks must have obtained their seed from England. It has never been found as an indigenous species either in Europe or America. This beautiful plant is much prized as an ornamental and is known to have escaped from cultivation in various places.

Fig. 114.—*Œnothera lamarckiana.* (*From a painting. See de Vries, Gruppenweise Artbildung.*)

"Lamarck's evening primrose is a stately plant, with a stout stem, attaining often a height of 1.6 meters and more (see Fig. 114). When not crowded the main stem is surrounded by a large circle of smaller branches, growing upward from its base so as often to form a dense bush. These branches in their turn have numerous lateral branches. Most of them are crowned with flowers in summer, which regularly succeed each other, leaving behind them long spikes of young fruits. The flowers are large and of a bright yellow color, attracting immediate attention, even from a distance. They open toward evening, as the name indicates and are pollinated by bumblebees and moths. Contrary to their congeners they are dependent on visiting insects for pollination. *Œ. biennis* and *Œ. muricata* have their stigmas in immediate contact with the anthers within the flower buds, and as the anthers open in the morning preceding the evening of the display of the petals, fecundation is usually accomplished before the insects are let in. But in *Œ. lamarckiana* no such self-fertilization takes place. The stigmas are above the anthers in the bud, and as the style increases in length at the time of the opening of the corolla, they are elevated above the anthers and do not receive the pollen. Ordinarily the flowers remain sterile if not visited by insects or pollinated by myself, although rare instances of self-fertilization were seen . . . . Ordinarily biennial, it produces rosettes in the first, and stems in the second year" (de Vries).

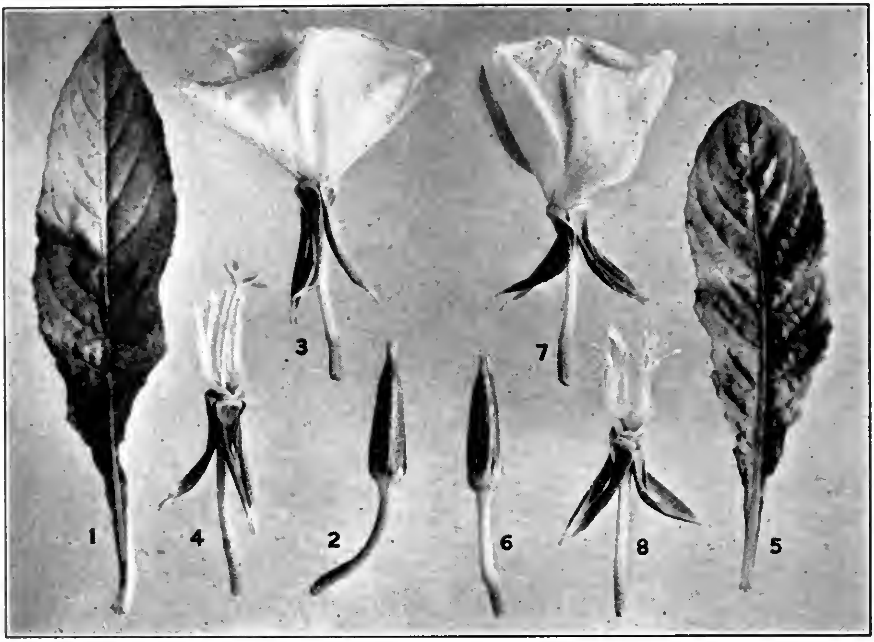

Fig. 115.—Leaf, flower bud, flower and essential organs of *Œnothera rubrinervis* (1–4) and *Œ. brevistylis* (5–8). The specimen of *brevistylis* came from a red pigmented strain grown by Dr. R. R. Gates; the original *brevistylis* had no more red pigment than *lamarckiana.*

De Vries' original discovery consisted of the location of two aberrant groups among several thousand *lamarckiana* individuals. One of these new forms had smooth leaves and was named *lævifolia,* the other had very short styles and was named *brevistylis.* Each differed somewhat with respect to other characters as well (see Fig. 115) but were named for their most striking difference from the parent species. De Vries next proceeded to hunt for more new forms. By transplanting rosettes from the original locality to his garden he carefully compared them when they flowered the second year and saved guarded seed from the "mutants" so that he might test the inheritance of the new forms. He also gathered seed from two different *lamarckiana* plants in the open and these were the source of his *lamarckiana* "families." Of one of these families he raised several thousand plants from self-fertilized seed in each generation for seven generations and in each successive population he discovered a number of "mutants." This experiment is summarized in Table XLIV.

TABLE XLIV.—PEDIGREE OF A FAMILY OF Œ. LAMARCKIANA, 1886–1899

Generation	Gigas	Albida	Oblonga	Rubrinervis	Lamarckiana	Nanella	Lata	Scintillans
I	..	..	...	...	9			
II	..	..	...	...	15,000	5	5	
III	..	..	...	1	10,000	3	3	
IV	1	15	176	8	14,000	60	73	1
V	..	25	135	20	8,000	49	142	6
VI	..	11	29	3	1,800	9	5	1
VII	..	..	9	0	3,000	11	....	
VIII	..	5	1	0	1,700	21	1	
Total.....	1	56	350	32	53,509	158	229	8

This summary shows that among a total of some 50,000 seedlings of self-fertilized *lamarckiana* plants seven different new forms appeared with varying frequency. The first two to be recognized and isolated for testing were *nanella* and *lata* (see Fig. 116). The dwarf variety, *nanella,* was also found blooming among the typical *lamarckiana* plants at the original station and these plants, like those dwarfs that appeared in the experimental garden, always bred true if self-fertilized. *Lata* on the other hand proved to be self-sterile because entirely devoid of viable pollen. When fertilized with *lamarckiana* pollen it produced 15 to 20 per cent. of *lata* and the remainder *lamarckiana.* Later on de Vries discovered a hybrid strain of *lata* that produced some viable pollen and when self-fertilized these plants produced the same proportion of *lata* and *lamarckiana* progeny. For this reason de Vries considers it an inconstant species. In the third generation another new form appeared, which unlike *nanella* and *lata* was more robust than *lamarckiana.* It also had considerable more red pigment in the epidermis. This was especially marked in the marginal region of the sepals (see Fig. 118) and on the developing fruits. This form was named *rubrinervis* and since it bred true when self-fertilized it was considered a well-defined "progressive" species, *i.e.*, a species capable of maintaining itself in the wild state. In the fourth generation four additional forms were found. One of these, *gigas*, appeared only once in de Vries' cultures but the one plant found in 1895 produced nearly 300 plants of *gigas* type from self-fertilized seed and the strain bred true thereafter. In recent years it has appeared a number of times in other strains of *lamarckiana*. This form is decidedly more robust than *lamarckiana* and the leaves are

FIG. 116—*Œ. lamarckiana, lata* and *nanella*. (*From colored plate in de Vries' Mutationstheorie, vol.* 2.)

broader and of a deeper green, as is shown by Fig. 117. De Vries classified this form also as a progressive species. *Albida* and *oblonga* were classified as distinct but weak species, incapable of perpetuating themselves in a state of nature and hence were called "degressive." The seventh form, *scintillans*, proved to be inconstant from the beginning, self-fertilized seed always producing some *lamarckiana* seedlings, as well as *scintillans*, *oblonga*, *lata* and sometimes *nanella*. The two new forms found growing wild in 1886, *lævifolia* and *brevistylis*, never appeared among the experimental cultures but because they, like *nanella*, appeared to have lost something that characterized *lamarckiana* and to be distinguished from it by one definite character, de Vries classified these together with *nanella* as "regressive" species or "retrograde" varieties at the same time pointing out that they possessed the qualifications of

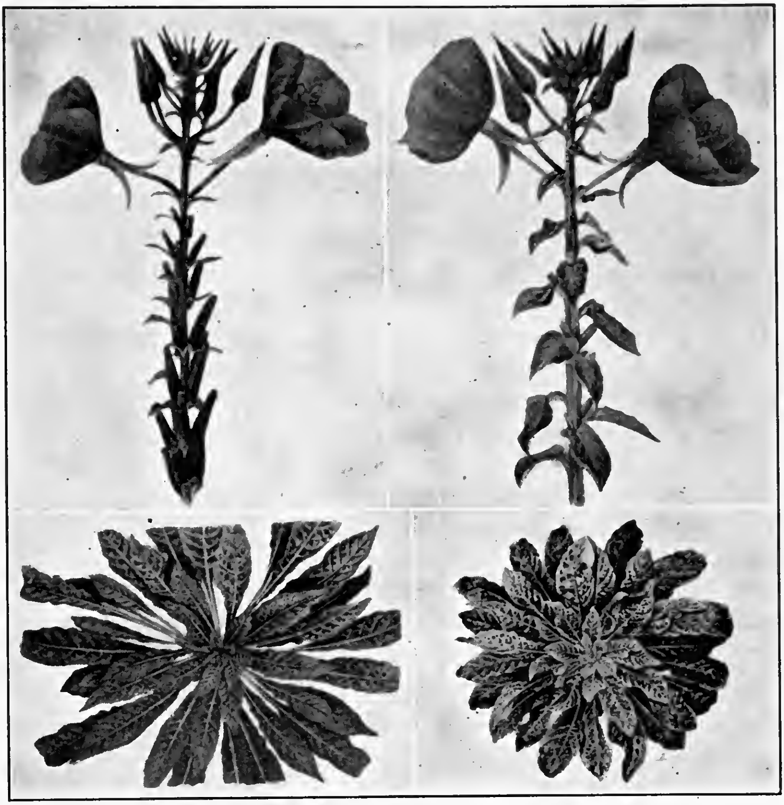

FIG. 117.—*Œ. lamarckiana* (*left*) and *gigas* (right), flower stalks and rosettes. (*From de Vries.*)

elementary species. De Vries, therefore, classified the "mutants" as follows:

I. Progressive species—*gigas, rubrinervis.*
II. Degressive species—*albida, oblonga.*
III. Regressive species or retrograde varieties—*nanella, lævifolia, brevistylis.*
IV. Inconstant species—*lata, scintillans.*

These were considered the important mutations although several others were recognized and given names but because of sterility or lack of space and time for growing them they were not preserved.

The Mutation Theory of Evolution.—Based on the observations and experiments above reviewed, de Vries formulated a set of "laws of mutability" for the evening primroses which serve as an epitome of his theory of evolution. Omitting further discussion of the evidence for the present, the laws themselves are stated as follows:

I. New elementary species appear suddenly without intermediate steps.

II. New forms spring laterally from the main stem.

III. New elementary species attain their full constancy at once.

IV. Some of the new strains are evidently elementary species, while others are to be considered as varieties.

V. The same new species may be produced in a large number of individuals.

VI. Mutability is entirely independent of fluctuating variability.

VII. The mutations take place in nearly all directions. To these an eighth must be added in order to complete the theory:

VIII. Natural selection eliminates all unfit mutants originating in the wild.

De Vries found many examples of the sudden origin of new forms in the history of domesticated animals and plants and pointed out various practical applications of his discovery, to some of which we shall have occasion to refer later. For the present it is necessary to give further consideration to the evidence in the case of the Œnothera "mutants" and to the interpretation thereof in order to arrive at a definite conception of the true nature of these aberrant forms. For this purpose it will be necessary to summarize in a general way the researches which have been made since de Vries' original work.

The publication of "Die Mutationstheorie" aroused widespread interest and brought forth certain criticisms concerning the biological basis for de Vries' conclusions. The opponents of the theory assumed *Œnothera lamarckiana* to be of hybrid origin and pointed out that upon such a basis the so-called mutations are merely recombinations of ancestral characters. The controversy which arose over these questions stimulated investigation to such an extent that the Œnothera literature of the past decade would fill many volumes. These investigations have proceeded along three definite lines: (1) crossbreeding experiments, (2) cytological studies, (3) observations and collections in the field together with pedigree cultures. The last of these can only be mentioned. See the recent reviews of Davis and Bartlett where further references are given. The results of the other two bear directly upon the problem of classifying de Vries' original "mutations."

Concerning the first method of investigating the genetics of Œnothera, there have been many crossbreeding experiments in both Europe and America. Until recently most of the data derived therefrom have been viewed as impossible of interpretation on a Mendelian basis. But since 1914 certain investigators have come to believe that breeding experiments with Œnotheras have very little value as a means for exact genetical analysis unless complete germination of all viable seeds is assured. In that year Renner pointed out that seed sterility in the evening primroses may cause apparent nonconformity with Mendelian principles. Following up this suggestion with seed germination tests and breeding experiments in which all viable seeds were germinated, Davis came to the conclusion "that large proportions of Œnothera seeds sprout in the earth only after many weeks or even months and that this habit of delayed germination must have given in many of the cultures described in the Œnothera literature hardly more than glimpses of the genetical possibilities. We cannot feel certain that the records of any cultures of Œnothera so far reported are complete for their possible progeny, and consequently the ratios of classes described in breeding experiments and the percentages of 'mutants' calculated cannot be accepted as final in exact genetical work. We are not in a position even to guess what may be the change of front when exact data become available. . . . Consequently we have at present in the Œnotheras no standard material of genetic purity with which forms under suspicion may be confidently mated to determine by crossbreeding the uniformity of their viable gametes. Until such material is discovered we shall be working largely in the dark in our attempts to analyze the genotypic constitution of Œnotheras." The same author, is inclined to interpret data from his most recent Œnothera breeding experiment (*biennis* and *franciscana*) as giving "positive evidence of a segregation of factors in the F_2 generation of a character to be expected in Medelian inheritance." This inference is the more noteworthy inasmuch as in the past this author has not committed himself positively to a Mendelian interpretation of any particular data on the Œnotheras. That certain characters in this group are conditioned by specific genetic factors, seems to be generally accepted. For example, it is highly probable that the deeply pigmented character of *Œ. rubicalyx* is conditioned by one or two specific factors. This new form (see Fig. 118) was discovered by Gates in 1907, among a population of over 100 *rubrinervis* plants grown from self-fertilized seed of *rubrinervis*. The original *rubricalyx* plant when self-fertilized produced 12 plants, 11 *rubricalyx* and 1 *rubrinervis*, which would indicate that the original *rubricalyx* plant was heterozygous for one or more factors for excessive production of anthocyanin and that *rubricalyx* is dominant to *rubrinervis*. Gates has raised ten generations of *rubrinervis* (more than one pedigreed strain) and found it to breed true and he has one strain of *rubricalyx* that has bred true for five years, but as yet there are no data on the results of a cross between them where the F_2 progeny were grown on a large scale and with controlled seed germination. However, in F_1 *rubricalyx* is dominant. Another Œnothera character which is inherited in simple Mendelian fashion is the typical feature of *brevistylis* (Fig. 115). *Brevistylis* is known to breed true when self-fertilized and the results of various crosses indicate that the short style is conditioned by a single factor, although it is not always completely recessive in F_1. Thus we find that, while most of the experimental breeding data on œnotheras cannot be interpreted in terms of ordinary Mendelian concepts, neverthe-

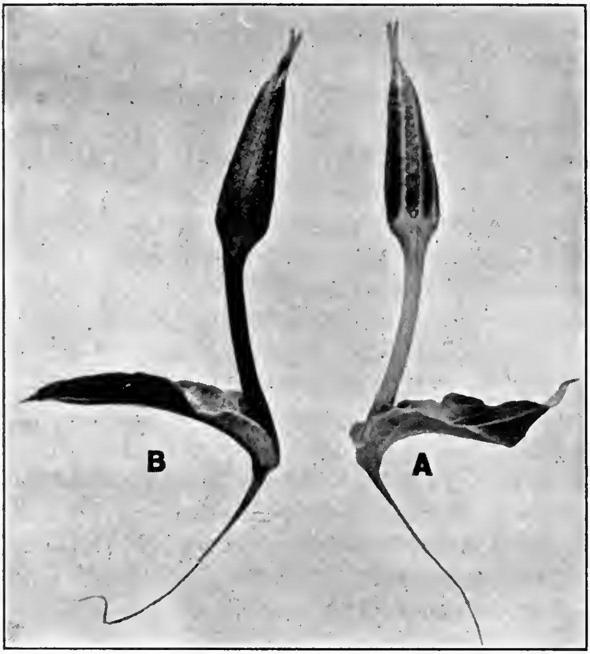

FIG. 118.—Flower bud and leaf of *A*, *Œnothera rubrinervis*; *B*, *Œ. rubricalyx*. The deeper pigmentation of *rubricalyx* is not confined to the bud and lower side of the leaves, but is also present in the stems. The rosette leaves also show more or less color on the midrib in *rubricalyx*.

less characters have been discovered that appear to be inherited according to simple Mendelian rules. We conclude, therefore, that some of the *lamarckiana* derivatives are the result of factor mutations.

The cytological studies on Œnothera have yielded important information concerning the chromosome numbers of various species and "mutants." With reference to *Œ. lamarckiana* and its derivatives especially the chromosome counts of Miss Lutz, Gates, Davis and others are of great interest. *Lamarckiana* has 14 chromosomes as have also most of the "mutants" which have been derived from it, but the sexually deficient and inconstant form, *lata* (see Fig. 116) has been found always to have 15 chromosomes. Furthermore, actual cases of a distribution of 6 + 8 chromosomes in the heterotypic division of pollen mother cells have been observed in *lamarckiana* and *rubrinervis*. It is safe to assume, therefore, that *lata*-like "mutants" result from the union of a gamete containing 8 chromosomes and one containing the normal number, 7. There is also good evidence that *Œ. gigas* is the result of tetraploidy. Several different plants of this type have been found to contain 28 chromosomes or thereabouts. However, there is a giant race of the Chinese primrose which has only 24 chromosomes, the number typical of the species, while another has 48 chromosomes. It seems then that gigantism is associated with tetraploidy but that it is not necessarily caused by an aberration in chromosome number. Thus we find that at least one, and perhaps another of the original *lamarckiana* derivatives are due to chromosome aberrations during meiosis.

Of the nine original mutants we have now definitely classified two—*brevistylis* as a factor mutation and *lata*, the result of a departure from normal chromosome number, and we have found that a third, *gigas*, exhibits an extreme chromosome aberration. What about the remaining six—*lævifolia, albida, oblonga, rubrinervis, nanella* and *scintillans?* There is no evidence of a simple factorial relation between them and the parent species. One of them, *scintillans*, must remain in the doubtful class until its chromosome numbers have been determined, but the inconstancy of this form suggests that it should be classed with *lata* and *gigas* under chromosome aberrations. The remaining five, *lævifolia, rubrinervis, nanella, oblonga* and *albida*, are known to have 14 chromosomes. Based on the evidence set forth in Chapter XII, it seems to us that one and only one category is open to these five forms and that probably *albida, oblonga* and most of the new forms that have appeared not only in cultures of *lamarckiana* and its derivatives but also in other species of Œnothera, are the result of chance recombinations of factors due to a condition of substrate hybridity. This expression, as has already been explained, is meant to imply that "mutating" species such as *Œ. lamarckiana* are merely species hybrids which happen to result from combinations of different *reaction systems* such that the majority of their germ cells are similar. Hence they breed true in the main but occasionally throw the new combinations of diverse elements which have come to be known as "mutants."

In conclusion, it may be well to state our reasons for restricting the term, mutation, to those changes in specific factors, which result in the appearance of new Mendelizing characters. This term was used by de Vries to designate a more or less comprehensive change which appeared suddenly, without warning, giving the impression that a full-fledged new species had sprung from a *pure*, *constant*, old species much as Athena sprang from the head of Zeus. We cannot conceive of new species originating in this way except in certain exceedingly rare cases, which fall under the two categories already described and illustrated, viz., (1) single factor mutations having such a profound manifold effect that the new form would be generally recognized as a distinct species, and (2) chromosome aberrations during mitosis or meiosis. We have found that the majority of the new forms derived from *Œnothera lamarckiana* do not fall into either of these categories and that the most reasonable explanation of their origin is based on the assumption that *Œ. lamarckiana* is of hybrid origin. Therefore, if the term, mutation, is to retain the meaning originally given it by de Vries, we cannot continue to classify the majority of new Œnotheras or other organisms resulting from hybridization as mutations.

On the other hand, the fact that most discontinuous, inheritable variations are caused by alterations in genetic factors and that these factor mutations play an important rôle as one means for organic evolution, seems to justify their recognition as mutations in the strict sense. By limiting the meaning of mutation as we propose all the objectionable implications previously connoted by the term are removed. The desirability of accomplishing this has been indicated by Agar, who states:

> "The greatest opposition to modern views of genetics has come from those who consider that they have taken away the philosophical basis of the theory of evolution and especially of the evolution of adaptation. For, while mutation could quickly bring about specific diversity, the evolution of complex adaptive structures is undoubtedly most easily grasped when the inheritable variations presented to natural selection are minute and abundant. This difficulty, though real, would undoubtedly have assumed smaller proportions had it not been for the natural fact that the earliest mutations studied were large morphological ones, and consequently that these have become fixed in many minds as types of mutational change."

There is now abundant evidence that genetic diversity is expressed in minute morphological and physiological differences, and hence that mutations produce those small inheritable differences logically required for the explanation of adaptation through natural selection.

PART II.—PLANT BREEDING

CHAPTER XV

HISTORICAL INTRODUCTION

Plant improvement is nearly as old as agriculture. Our earliest agriculturists must have protected the trees or plants that yielded food or shelter. Under protection the desirable forms among the chosen species were preserved. The finest example of this earliest plant improvement is found in rice, which has been cultivated for 5000 years or more in India and China and has long been grown in Egypt, East Africa, Japan, the Philippines, Java, Turkey and Italy. The remarkable plasticity of this species has enabled it to produce literally thousands of locally adapted forms. The oldest records of intentional preservation of superior plants are found, according to Darwin, in ancient Chinese encyclopedias that were translated by the Jesuits during the 18th century. The best plants and fruit trees were used for propagation; an imperial edict recommended the choice of large seed; and even the Emperor Khang-hi is said to have originated the imperial rice by preserving and propagating a form which he noticed in a field. The original progenitors of our most important crop plants are mostly lost in antiquity, their descendants having been preserved by man's conscious or unconscious selection of desirable mutants or natural hybrids.

The Beginning of Plant Breeding.—Long before any one thought of making a philosophical study of plant improvement the hybridization of flowers and the preservation of choice strains or favorite varieties was a common practice among gardeners and husbandmen. According to Fruwirth hybridization was practised in ancient times in China with various flowers, in Italy during the Roman Empire with roses, and in the 17th century in Holland with tulips and primulas; and the artificial pollination of the female date palm was mentioned by Theophrastus as the beginning of the study of plant culture. The earliest systematic work in the production of new varieties, of which we have authentic records, was done by the Dutch flower fanciers. The hyacinth, according to Darwin, was introduced into England in 1596 and in 1629 eight varieties were known. During the next hundred years or more the selection of varieties was carried on by the Dutch growers until, in

1768 nearly 2000 sorts were known in Holland. But in 1864 only 700 varieties were found in the largest garden in Haarlem, which fact indicates a gradual process of elimination of the less desirable selections of earlier years.

Pioneers in Plant Breeding.—The systematic breeding of crop plants was begun in Europe during the latter part of the 18th century. Jean Baptiste Van Mons, a Belgian physician and professor of physics and chemistry in the University of Louvain, pursued plant breeding work as an avocation. But so great was his zeal in an effort to demonstrate certain theoretical ideas which he held concerning the improvement of fruits that the results of his labor were extensive. His experiments were begun in 1785. Thirty-eight years later he had 80,000 seedling trees in his "Nursery of Fidelity," as he called it, at Louvain. He distributed cions without charge to many countries including America. He specialized on pears and his first catalogue, issued in 1823, lists 1050 varieties. Altogether he originated nearly half that number. Van Mons' service to agriculture, especially to pomology, has been widely recognized.[1]

Three other pioneer breeders who began their work during Van Mons' life are Thaer, Knight, and Cooper, representing Germany, England, and the United States respectively. During the latter portion of the 18th and the earlier years of the 19th centuries each of these men carried on experiments in plant breeding and made contributions of tremendous importance to agriculture. Thomas Andrew Knight was the first to show the value of hybridization in plant improvement. According to Bailey, in the variety, accuracy, significance, and candor of his experiments, Knight stands to the present day without a rival among horticulturists. He was also a successful breeder of livestock and author of papers on plant physiology and breeding. Albrecht Daniel Thaer also made hybridizing experiments but emphasized the value of selection. Plant breeding was only one of his many agricultural interests and he is credited with having laid the foundation of scientific agriculture of today. Joseph Cooper disproved the current fallacy as to the entire necessity for changing seed and showed the American farmer the importance "of selecting seeds and roots for planting or sowing, from such vegetables as come to the greatest perfection, in the soil which he cultivates." Like Van Mons, each of these men had his theories, but only experience revealed the truth in those theories. Based on their experience they formulated certain rules which they knew would yield results, but frequently the conclusions reached by them were only partially true.

At least five other men deserve to be mentioned among the earlier

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[1] For a discussion of Van Mons' theories and contributions (also of the work of Knight and Cooper) see Bailey, L. H.: "Survival of the Unlike," 1906, pp. 141–159.

breeders of agricultural crop plants. Three of these worked with grains and two with fruits. John Le Couteur, during the early part of the last century, was raising what he supposed were pure and uniform varieties of wheat, when Professor La Gasca of the University of Madrid, after examining one of his fields, pointed out 23 distinct forms. This was the beginning of Le Couteur's collection of 150 varieties of wheat, some of which were introduced to the trade. One of them, "Bellevue de Talavera," is still known as a pure and uniform variety. De Vries points out that Le Couteur simply assumed that the progeny of his selected plants would be like the parents and experience justified the assumption. Thus be became the first to discover the importance of selecting individual plants in the improvement of cereals.

Patrick Shirreff was also celebrated about the middle of the century as a breeder of cereals. His method differed from that of Le Couteur only in that he searched for very exceptional plants as the starting points of new varieties. During his lifetime he discovered seven new varieties, which according to Darwin, were grown extensively in Great Britain, but only four of them had permanent value. He also proceeded on the assumption that his single selected plants would breed true and each did so. According to de Vries, he considered the occasional appearance of a distinctly superior plant as merely accidental.

Frederic F. Hallet, like Le Couteur and Shirreff, practised the rigid selection of individual plants in breeding wheat. Although he proceeded on the theory that by choosing the best spike on a certain plant and the best grain in the spike he would obtain corresponding improvement in the variety, yet he did not rely on mere apparent superiority, but tested each grain on each spike. He then selected the finest plant of all. He began his work in 1857 and made important introductions during the 60's. While Le Couteur and Shirreff assumed that the selection of a single plant was sufficient and thenceforth gave their attention to multiplying the new variety, Hallet practised continuous selection within his selected strains. He obtained considerable increase in yield as a result of his early selections but little or no increase due to continuous selection within pure strains. The success of these three pioneer wheat breeders was unquestionably due to the fact that they practised the isolation of pure lines some of which were superior to ordinary varieties.

Charles Mason Hovey was the "father of the American strawberry." As early as 1830 Hovey "had a list of 30 strawberries of his own origination, all springing from the "Hovey," which, together with "Boston Pine," had been introduced a few years earlier. Hovey crossed a native American species with the imported "Pine" variety, which is supposed to have sprung from the beach or sand strawberry of the Pacific Coast some years after its introduction into Europe. Some of Hovey's new varieties stood the test of years and his work served to stimulate further efforts to improve the most important horticultural crop of America.

Ephraim Wales Bull produced the Concord grape as a result of eleven years of patient work in crossing the native species, *Vitis labrusca*, with European varieties, raising the seedlings and testing selections. "From over 22,000 seedlings there are 21 which I consider valuable," he writes. Although the hybrid nature of the Concord and other derivatives of *Vitis labrusca* has been questioned, the evidence from extensive tests of selfed seedlings of this and several other standard American varieties as reported by Hedrick and Anthony seem to indicate that they are really hybrids between American species if not between *V. labrusca* and *V. vinifera*. Whatever the origin of the Concord may have been, its sterling value is evidenced by its history. Introduced in 1853, "ten years later the Concord grape was spread over the entire northern part of the United States and is now widely used in the temperate regions of most parts of the earth." Ephraim Bull's service to his fellow men seems to have been all but forgotten while he was still living, since "he died neglected, in poverty, broken in spirit." Vast as would be the value of his contribution if it could be computed, even more valuable was the inspiration he gave, "which has helped to make plant breeding one of the great forces in cheaply feeding the world.[1]"

The demands and possibilities of developing agriculture aroused the ambitions of two far-sighted agriculturists—Martin Hope Sutton and Pierre Louis François Lévèque de Vilmorin. A student of botany from his boyhood, Sutton had already made improvements in a number of plants when the Irish potato famine of 1847 drew public attention to his work through the substitutes which he suggested for the devastated potato crop. Later on the introduction of the Golden Tankard mangel, the Magnum Bonum potato, and the Marrowfat pea helped to establish the high reputation which the firm of Sutton and Sons came to hold throughout the world. They greatly improved many flowers as well as crop plants. Sutton's "Permanent Pastures" is still a standard work on grasses.

In 1843 Vilmorin took charge of the seed establishment which had already passed through the hands of two generations of this remarkable family. His father, André Lévèque de Vilmorin, had conducted a selection experiment with carrots about ten years earlier. Besides the main-

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[1] The earliest hybridizers of grapes in America, according to Waugh, were Dr. Wm. Valk of Long Island (1845) and John Fisk Allen of Massachusetts (1846 or '47). Waugh also states that the two foremost American grape hybridists are E. S. Rogers of Massachusetts, who began in 1848 and distributed many numbered seedlings for trial in 1858, and T. V. Munson of Texas, who has probably added more to the practical American fruit list in his hybrid grapes than has any other plant breeder.

tenance of work already under way, Vilmorin undertook two projects which yielded results of the greatest importance to the entire world. One was the collection of wheats and other grains from many countries in order to compare them and to select those of greatest value. In connection with this work on grains he invented the pure-line method of selection and progeny test which came to be known as the "Vilmorin Method" and which has been used so successfully with wheat and other self-fertilized plants. From our present knowledge of pure lines we can understand why this method was effective. Vilmorin's other important project was the improvement of the sugar beet. Previous to 1850 the beets had been selected according to form only. This method of selection began as early as 1787 on the seed farm of H. Mette in Quedlinburg, Germany, according to Legier. Selection on the basis of specific gravity was practised from 1850 to 1862, when the method of determining sugar content by means of polarized light was introduced. His success made beet-sugar production a commercial possibility and gave his name an enduring place in history.

More Recent Progress in Plant Breeding.—The great world movements of the 19th century following the improvement of transportation facilities, the migration of peoples, industrial development and the growth of international trade, together with the improvement of farm machinery, resulted in the extension of agricultural industries and gave a greater impetus to plant breeding. This activity was manifested first in Europe and later, particularly in the United States Department of Agriculture and the state experiment stations, in America. Naturally the efforts at improvement were concentrated in the main on the crop plants producing the raw materials of importance in the world's markets, such as wheat and other small grains, sugar beets, corn, cotton, forage plants, the apple and other fruits. The methods employed were those which had been used in the past for the most part, but they were systematized and combined for more effective utilization. These methods may be classified under the following heads:

1. Mass selection.
2. Line selection and progeny test.
3. Hybridization followed by direct utilization or selection and fixation of new varieties.
4. Clonal selection.

Mass Selection.—The method of mass selection consists simply in picking out choice plants from the main crop and sowing the seed from them *en masse*. It has long been used, especially in improving small grains, but it has also been used with many other crops. With this method it has usually been found necessary continually to repeat the selection of best plants in order to maintain the improvement already gained. One of the earliest breeders to use this method was André Lévèque de Vilmorin, who began selecting carrots about 1830. Soon thereafter selection of sugar beets for seed production was begun in France and Germany, first according to form of the root alone, but later according to specific gravity and actual analyses of sugar content. Mass selection later became the principal method of improving small grains in Germany, and it has been known as the German method of "broad breeding." The earliest prominent breeder of small grains was W. Rimpau, who began his work with rye in 1867 and developed the famous Schlanstedt variety. Later he worked with wheat extensively, first by mass selection and, more recently, by hybridization of varieties and subspecies. Although there have been scores of successful breeders of each of the important small grains in Germany, Rimpau was the first to engage in this work on a large scale.

Mass selection in maize was begun as early as 1825, when J. L. Leaming, of Ohio, began the selection of best ears from his field for seed corn. By repeating this process he soon developed a superior strain that came to be known as the Leaming variety. The same simple method was employed in originating Ried Yellow Dent (1847), Morley Prolific (1876), and Boone County White (1885). The famous Illinois corn-breeding experiments, which will be described in later chapters, were begun in 1896 by Cyril G. Hopkins, then Professor of Agronomy in the University of Illinois. Among the other investigators who have participated in this undertaking are East, Shamel and L. H. Smith. The general result of the project has been the most convincing proof of the efficacy and practicability of mass selection in corn, not only for the chemical and physical characters of the grains but for other characters of the corn plant as well.

The improvement of cotton by mass selection has doubtless been practised for centuries. Authentic records of the earlier methods used in foreign countries are scarce, but the characteristic variability in length of fiber, combined with the very practical value of increasing the average length, must have appealed to growers, at least in the more progressive cotton growing regions of the world. In the South Carolina islands according to Webber the sea island types of cotton have been developed by consistent mass selection for early maturity, increased length of lint, and greater productiveness from a West Indian perennial type which was originally unsuited to conditions under which its derivatives are now grown so successfully. Mass selection in cotton has been resorted to also in the campaign against various plant diseases, particularly cotton wilt, and for early maturity to avoid the ravages of the boll weevil.

Line Selection and Progeny Test.—Turning now to the second of the four general methods, we find that the *progeny test* of individual plants was first used by Le Couteur and Shirreff. But it was Louis de Vilmorin who first gave special attention to the value of the progeny test (1856) and, contemporaneously with Hallet, practised the selection of single plants, *i.e.*, of pure lines in wheat, oats and barley, followed by separate tests of their progeny. This method was first used in America by Willet M. Hays who began the improvement of small grains at the Minnesota Experiment Station in 1888. Convinced by the results of extensive variety tests that systematic breeding would be required in order to secure a marked increase in yield of first class wheat, Hays devised the centgener method of grain breeding, which, briefly, consists of planting about 100 seeds from each selected plant in trial plots; the more promising centgeners being selected for testing on a larger scale. Hays' work resulted in the isolation in 1892 of two plants whose progeny within a decade were grown on thousands of acres. Although many new strains were secured, the rigid tests of several consecutive years in which the most promising strains were compared with each other and with the best commercial varieties, resulted in securing but few really superior varieties. However, these made possible an increased production of wheat throughout the northern states and in Canada.

The Swedish Seed Association was organized in 1886 and established an experiment station at Svalöf. During the first 5 or 6 years only mass selection was practised, but soon after Hjalmar Nilsson became director in 1891 the "Vilmorin Method" was introduced. At Svalöf it came to be known as the "System of Pedigree" or "Separate Culture." Nilsson was led to adopt this system as the method for originating new varieties by the accidental discovery that the only wheat plots that were entirely uniform were grown from single plant selections. The new varieties produced at Svalöf are now grown throughout the agricultural portion of Sweden. This station is also engaged in the systematic improvement of peas, clovers, grasses and potatoes. All this work is based on mass and line selection followed by field tests and distribution.

The first application of the pure-line conception to a naturally cross-fertilized plant was made by Shull and by East working independently with corn. By guarding and self-pollinating individual plants for successive generations, a number of morphologically distinct strains were isolated, thus proving that the original population was a mixture of biotypes. These same methods, however, had been employed for a number of years by Webber, Hartley, and probably others in working with corn, cotton, and other naturally cross-fertilized plants. In recent years the plant-row test has been used for the improvement of old strains or production of new ones. In Germany, von Lochow in 1894 adopted a modified form of line selection in the improvement of rye, which is also naturally cross-fertilized.

Timothy breeding was undertaken by the New York (Cornell) Experiment Station, under the direction of Hunt, Gilmore and others in 1903. To begin with, samples of seed were secured from 22 states and 11 foreign countries. Although it had been long cultivated in certain parts of Europe, there were no distinct varieties of this species of grass (*Phleum pratense*) because it is normally cross-fertilized. Many interesting variations were found among the plants grown from the various samples, some of them being of great commercial value. After several years of experimental work 17 new sorts were selected as most promising. These had been increased vegetatively by division and subjected to progeny tests with both cross-pollinated and self-pollinated seed. In two years tests the 17 selections gave an average increased yield of 36⅗ per cent. above ordinary timothy. If such an increase in production of timothy could be extended throughout the country, it would, according to Webber, add over $90,000,000 to the value of the annual hay crop.

Hybridization.—The third general method of plant breeding in the light of genetical science holds great promise of future possibilities. In spite of Knight's early demonstration of the value of varietal crosses in breeding, this method did not come into general use until the latter part of the nineteenth century. According to Darbishire, another English horticulturist, John Goss, made some of the identical crosses used by Mendel, and noted the phenomena of dominance in F_1 and recombination in F_2, but failed to grasp the significance of the facts he observed. According to Munson, it was the horticulturist, A. J. Downing, who in 1836 first called the attention of American breeders to the possibilities in hybridization. After his success with strawberries, Hovey, in 1844, definitely championed the cause. The achievements of Hovey, Downing and others soon led to the general adoption of cross-fertilization as a method of breeding. In their efforts to secure varieties having certain combinations of desirable characters, the crossing of varieties of small grains was employed to advantage by Rimpan, Blount, Pringle, Hays, Nilsson and others in later years. The remarkable Marquis wheat which has proved so valuable in the northern wheat regions is a hybrid according to Carleton which was probably made by A. P. Saunders at the Agassiz (British Columbia) Experiment Farm in 1892. The application of this method in the production of disease resistant commercial strains has been attempted. R. H. Biffin began his study of wheat breeding in 1909 in the service of the National Association of British and Irish Millers. The demand was for a beardless, rust-resistant variety of high yielding power and good milling quality. Not being able to discover any single variety which combined all these characters, Biffin attacked the problem from the Mendelian standpoint and has attempted to secure the desired combinations through the hybridization of a low quality, rust-resistant form with a variety very susceptible to rust but whose characters are otherwise superior. Biffin found that susceptibility to yellow rust (*Puccinia glumarum*) is dominant to rust resistance, in the cross between Rivet and Red King, but that resistant forms appeared in the F_2 generation which bred true for resistance. This discovery marks a definite forward step in the breeding of disease resistant plants. However, the problems of disease resistance are complicated by the variability of the parasitic organisms involved.

Hybridization of maize was begun as early as 1878 at the Michigan experiment station and was taken up from time to time at certain other stations. In 1900 the U. S. Department of Agriculture began a large series of experiments in crossing corn, using "all types obtainable." This work has resulted in the distribution for trial of many promising selections. Following the striking experiments of East and Shull in crossing strains of corn that had been inbred for several generations, many experiment stations began the crossing of varieties and strains for increased production as well as for new combinations of characters.

With cotton, the recent work of Balls in Egypt has furnished a basis for the pedigree and hybridization method of breeding. Although cotton is self-fertilized to a large degree, yet it is visited by insects during the early morning hours so that there is always a certain amount of natural crossing. It is very susceptible to environmental effects and its chromosome number is large (haploid number 20). These conditions make improvement by crossing a difficult matter. Cook noted the fact that parent characters are sometimes intensified in the F_1 in cotton and recommended the use of F_1 hybrid seed of proved crosses as a means of enhancing the quality of the lint. He also suggested a practicable and economical method of producing and utilizing such hybrid seed.

Apple breeding by crossing varieties was begun by Knight but this method has not been used extensively in Europe. In America the crossbreeding of apple varieties probably was begun by Charles Arnold of Ontario, Canada, about the middle of the last century. Other early hybridizers who worked with varieties of the common apple, *Pyrus malus*, were F. P. Sharp of New Brunswick, who began crossbreeding in 1869 and C. G. Patten of Iowa, who commenced somewhat later, but who has worked continuously with apples and pears since 1879. In this connection recognition is due Peter M. Gideon and the host he represents, who have produced new varieties of apples by raising seedlings and selecting the best. Most of the new sorts obtained in this way are of hybrid parentage. More recently important work on variety crossing of apples has been done by Macoun in Canada, Hedrick in New York, and Evans in Missouri.

The composite crossing of three or more varieties in an attempt to effect a desired combination has been used successfully in small grains, as well as in many flowers. Referring to grains alone, William Farrer of Australia, A. N. Jones of the United States, and John Garton of England have used this method successfully. In the opinion of Carleton, Farrer leads all breeders in the production of hybrids that have come into practical use. He continually practised composite crossing, as many as six different varieties or subspecies entering into the ancestry of many of his new sorts, some of which are of superior production or milling quality as well as being disease resistant.

Interspecific hybrids have frequently been produced by breeders seeking some definite goal, occasionally with striking success, especially among fruits. Even intergeneric hybrids have been reported, but the known cases, with the exception of orchids, are of slight importance to agriculture. For example, van der Stok secured a fertile hybrid between corn and teosinte in the hope that some of the hybrids would bear good sized ears and be resistant to chlorosis, a hope which was not, however, realized. A few similar cases are known, particularly among cereals, but very little use has been found for them. In fact, utilization of wide crosses is rather definitely restricted to direct employment of the F_1 in cases where conditions of seed production are particularly favorable for producing large quantities of hybrid seed or where the hybrid may be propagated by clonal multiplication.

Alfalfa culture appears to be capable of still further extension through crossing of species. According to Fruwirth hybrids between common alfalfa, *Medicago sativa*, and *M. falcata* are easily produced and occur abundantly wherever plants of the two species grow near each other, the crossing being effected by insects, especially bees. This was reported in 1877 by Urban. These hybrid forms are known as *M. media* Pers. (*M. varia* Martyn., *M. versicolor* Ser.). Seeds of these hybrids produce forms that can be considered *M. media*, and, while flower color and pod form are inconstant, the plants bear more seed and grow more luxuriantly than *M. falcata* and adapt themselves to varied soil conditions. Westgate has found good evidence that the well known hardy Grimm alfalfa originated as a natural hybrid between these species, and that it was not a product of acclimatization. Piper in 1908 called attention to the desirability of securing hybrids between *M. sativa* and the yellow-flowered Siberian species, and Hansen has recently determined the practicability of producing such hybrids on a large scale by mixed field plantings. Experts of the Bureau of Plant Industry of the U. S. Department of Agriculture have made an enormous number of attempts to cross different species of Medicago but utterly without success except in the case of *falcata* and *sativa*. Selfed *sativa* and especially *media* (*falcata* x *sativa*) give many aberrant forms. A very common one under greenhouse conditions is a form with very short internodes and very small leaves. This is presumed to be the form which Southworth mistakenly reported as a hybrid between *M. sativa* and *M. lupulina.*

In various fruits and in many flowers the crossing of species has yielded many valuable varieties. Some cases among flowers will be discussed in the following chapter. Among tree fruits the next hybridizers of species after Bull were the men who undertook to combine the hardy character of the Russian apples, which had been introduced during the 80's. Dr. William Saunders, then Director of the Dominion Experimental Farms, began this work in 1894. Similar work, with apples, cherries, plums, etc., has been carried on very extensively, and already with important results, by N. E. Hansen of the South Dakota Experiment Station. The production of a list of peach varieties adapted to the Gulf Coast States was the work of H. H. Hume, then of the Florida Experiment Station, and of P. J. Berckmans in Georgia. This was accomplished largely through the hybridization of the Chinese Saucer or Peen-to peach, *Amygdalus platycarpa,* with commercial varieties of the common peach, *Amygdalus persica.* The work of Webber and Swingle with crosses between various species of Citrus has received international recognition, not only because of the results secured but on account of the possibilities in the improvement of citrous fruits which it revealed. The production of aphis-resistant plums among hybrids of distinct species, as reported by Beach and Maney, exemplifies an important line of attack in breeding disease-resistant plants.

No small part of Luther Burbank's fame is due to his success in crossing species. Among the many interspecific hybrids which he produced should be mentioned plumcots (hybrids between plums and apricots), the Royal walnut (*Juglans Californica* × *J. nigra*), the Primus and Phenomenal berries (hybrids between species of Rubus), many valuable plums and a host of flowering plants. In his work with plums, as well as in the production of certain flower novelties, Burbank practised composite hybridization. An illustration taken from de Vries' account of Burbank's work, is the pedigree of the Alhambra plum, shown in Fig. 119.

An equally if not more important phase of Burbank's work is his discovery of novelties and his perfection of the same by means of selection. His method is hardly to be classified as mass selection, nor is it line selection in the strict sense. An important feature has been the use of very large numbers of seedlings either of introduced species, commercial varieties, or his own hybrids. It is by the use of his unusual power of observation, which Wickson thinks amounts to a gift of intuition, in choosing say a dozen seedlings from as many thousand, that this one man has accomplished so much. His methods of hybridization, also, have been such as to economize time rather than insure certainty as to ancestry.

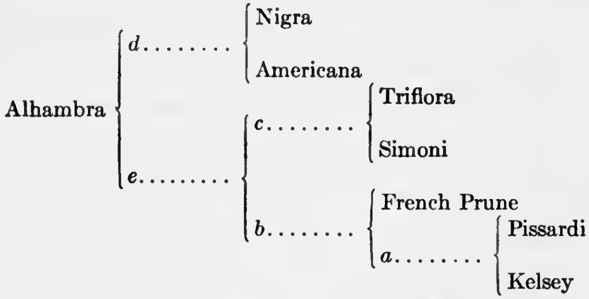

FIG. 119.—Ancestry of the Alhambra plum.

His aim has always been the tangible result rather than advancement of scientific knowledge.

Clonal Selection.—Under the term clonal selection is included all methods of plant improvement based upon the utilization of asexual means of multiplication, whether by selecting the most favorable clones from a mixed population, or by selecting and propagating favorable variations within clones. In potatoes many commercial varieties are definitely known to be mixtures of different clones, and improvement may be effected by simply selecting those which are most productive and most desirable from a market standpoint. A unique instance of clonal selection is that followed in Oklahoma and other regions along the northern limits of the range of Bermuda grass. There the cold winters kill off the less hardy strains; those that remain are propagated by distributing sod. In alfalfa many improved strains have been produced by the selection and multiplication of superior individuals. This work has been carried on by the Bureau of Plant Industry of the U. S. Department of Agriculture and various stations, especially those in South Dakota, Kansas and Arizona. The propagation of improved strains by means of cuttings is of great practical value, and Hansen recommends the use of tobacco planting machines for the setting of rooted alfalfa cuttings.

A phase of clonal selection which has recently come into prominence is *bud selection*, although the occurrence of bud variations, particularly of bud sports, has long been a matter of common knowledge. Munson (1906) seems to have been the first to call attention definitely to the possibilities in fruit improvement by selection of buds from superior individuals or vegetative parts, although Bailey had on several occasions previously pointed out that varieties sometimes originated from buds. During the past ten years many practical experiments in bud selection have been conducted, but with diverse results.

The aim of the foregoing review has been to present the more prominent historical examples of the four general methods of plant breeding. Further details can be obtained from the authors cited and from Fruwirth's *Die Züchtung der landwirtschaftlichen Kulturpflanzen* (The Breeding of Agricultural Crop Plants). This useful work, consisting of five volumes, is partly in its second and third revised editions and is the most complete and thorough treatise on plant-breeding methods.

Organization of Plant-breeding Work.—Growing appreciation of the importance of plant improvement to agriculture has led to organized effort along certain lines, some of which are discussed briefly below.

Seed and Plant Introduction.—The first teacher of plant breeding in America was also her first agricultural explorer. In 1882 Budd went to Europe and Asiatic Russia for the purpose of studying horticultural problems. He was accompanied by Thero Gibbs of Canada, and the expedition was financed by the Iowa State Legislature and the Canadian Government. As a result of this exploration many hardy shrubs and trees were introduced into America. The Russian cherries and apples were of especial importance as they have been used, notably by Saunders and Hansen, in the production of new varieties, which are sufficiently hardy to resist the cold winters of the northwest portion of the great interior plain. Bailey, in 1894, called attention to the similarity in climates and floras of eastern America and eastern Asia and emphasized the "abundant reason for looking toward oriental Asia for further acquisitions, either in other species or in novel varieties." His wise foresight in this matter has received repeated verification in the numerous valuable introductions of Wilson and of Meyer. About this time the U.S. Department of Agriculture began to give serious attention to the introduction of seeds and plants from foreign countries under the supervision of Galloway. A few years later this important work was put in charge of Fairchild who has organized the present efficient system of agricultural exploration, seed and plant introduction, trial gardens and distribution of promising material.

Collections of Plant-breeding Material.—The importance of bringing together a working collection of all available species and varieties within a group in which improvement is desired has been increasingly appreciated since the work of Vilmorin. The importance of local variety trials has long been realized and the collections of cultivated varieties at various experiment stations have proven very useful for purposes of selection of better adapted sorts as well as for some work in hybridization. Well-known examples are the sweet pea, peony, and chrysanthemum collections at Cornell University and the collections of apples, plums, and grapes at the Geneva, N. Y., Experiment Station. But, on account of the time and expense involved in the work of hybridization, it is highly important that the most promising forms which exist be secured, if possible, at the beginning of such projects. Some of the older collections of living plants, such as Arnold Arboretum and the New York, Brooklyn, and Missouri botanical gardens, as well as the Government Office of Seed and Plant Introduction, have given valuable assistance in supplying new and rare material to breeders. The transportation of pollen has also been resorted to, especially by the U. S. Department of Agriculture in its breeding of Citrus and it is known that, with proper precautions, some kinds of pollen can be sent by mail half-way around the world and still be viable. However, certain much desired crosses can be secured only after repeated efforts and the trial of various methods. Moreover, the response of introduced forms to local conditions is a most important consideration. All too often a supposedly promising new plant has proven entirely unfit for certain localities. These considerations are leading to the establishment of large working collections of our more important semi-permanent crop plants, especially the tree fruits. For example, the University of California Citrus Experiment Station is accumulating a collection which will include all the known species and varieties of Citrus and allied genera which will endure local conditions.

Research on Plant Groups.—A breeding program such as that contemplated by the institution just mentioned involves the necessity of extensive botanical investigations. In this particular instance it is fortunate that extensive work has already been accomplished by the U. S. Department of Agriculture since already a large amount of data on the botanical relationships and geographical distribution of the members of the Citrus group has been collected. As a result of these studies and explorations several new and very promising forms have been introduced and have already been utilized in breeding experiments by the Bureau of Plant Industry. Similar investigations of the genus Prunus are also under way by the Department. The recent explorations of date growing countries and studies on the varieties of dates is another illustration of the sort of work that is needed, not only among fruits in general but in the field crops as well.

Organization of Plant Breeders.—In December, 1903, the American Breeders Association was organized under the auspices of the American Association of Agricultural Colleges and Experiment Stations. During the first seven years of its existence the publications of this organization were restricted to the annual reports of its meetings. These reports contain the papers which were presented at the meetings either in full or by title. In 1910 the Association undertook the publication of a quarterly journal, the *American Breeders Magazine,* and discontinued the publication of annual reports. This magazine in January, 1914, became the *Journal of Heredity,* which is published monthly. At the same time the American Breeders Association changed its name to the American Genetic Association. With its policy of unrestricted membership from the beginning this organization has done great service in fostering the common interests of geneticists and practical breeders. There are state associations of plant breeders in New York, Wisconsin, Minnesota, Illinois, Pennsylvania, Ohio, Nebraska, and Georgia. In certain other states the agricultural and horticultural societies have fostered plant-breeding work to a greater or less extent. The meetings held with their addresses and discussions, the exhibits of new introductions and occasional demonstrations in plant improvement by the experiment station or other agencies, have aided in bringing to the seed growers and farmers of the United States the knowledge of superior plants and their practical value. The Canadian Seed Growers' Association has fulfilled a similar mission.

Summary.—Starting with the sporadic efforts of a century or more ago to find some better varieties of fruits and grains, there has been a gradual broadening of the great movement to increase agricultural output and raise the quality of raw materials by means of plant improvement. Throughout the later stages of this development scientific knowledge has become increasingly important until now the specialist on a particular crop plant may invoke the aid of every branch of agricultural science in selecting his material for breeding operations, making the desired crosses and selecting the progeny. All this has been done without much, if any, *definite* knowledge concerning the *heredity* of the plant in question. Within a decade the science of genetics has developed to a stage where it is capable not only of furnishing a rational explanation for the phenomena of variation and heredity which in the past seemed obscure and contradictory, but also of guiding the breeder who will familiarize himself with the established principles of the science, so that he may reach his goal with greater speed and economy. It is the purpose of the following chapters to set forth these principles in as clear and practical a manner as possible. It will be assumed, of course, that the reader is familiar with the fundamental treatment of the preceding chapters.

CHAPTER XVI

ON VARIETIES IN PLANTS

The multiplicity and diversity of the varieties of cultivated plants never fail to impress the thoughtful observer. The cereals, fiber plants, legumes, root crops, and tree fruits which comprise most of the important agricultural crop plants include some 30 species. It is safe to assume that within this small group of species over 5000 distinct varieties are known at present. Of rice alone there are thousands of varieties in cultivation. Among flowering plants we find the same diversity. The rose, lily, chrysanthemum, violet, carnation, sweet pea, dahlia, gladiolus, tulip, and hyacinth of our gardens and greenhouses represent not more than 200 species, while of roses alone as many as 1000 named varieties are now listed in European catalogues. In general the longer and more widely cultivated species contain the larger groups of varieties, partly because of the greater opportunity for their discovery and partly because these species have been subjected to conditions most favorable for the production of varieties. Before attempting to discuss the conditions or operations that lead to the production of new varieties it is necessary to enquire into the natural processes by which varieties have been produced.

The Origin of Domestic Varieties of Plants.—Agriculturists have made use of three general methods in creating new varieties of cultivated plants, viz.: (1) the utilization of mutations or sports; (2) the employment of hybridization and selection methods; and (3) the utilization of clonal diversity. The utilization of mutations should be interpreted to include not only the discovery and multiplication of mutant forms, but also the recombination of mutant characters in new varieties by hybridization. We include selection in the same category with hybridization, because according to the hypothesis which we have championed throughout this text, its effectiveness usually depends upon the existence of germinal diversity such as follows hybridization. In certain cases, of course, selection methods have depended for success upon the utilization of mutations having minor character effects. The origin of varieties by these three different methods may be illustrated by considering in some detail the horticultural history of certain plants. Since the ancestors of most of our crop plants are now extinct, we may turn for this purpose to some of the more recently domesticated species, the histories of which are known more precisely.

Origin of Sweet Pea Varieties.—The sweet pea, *Lathyrus odoratus*, provides an excellent illustration of the origin of varieties by the utilization of mutations. Its history as a horticultural plant is known from the beginning and has been thoroughly reviewed in publications of the Cornell Station. The sweet pea was introduced into Holland and England from Sicily via Italy in 1699, and was first illustrated in a description published in 1700. The drawing is reproduced in Fig. 120. It will be noted that in habit it was similar to the cultivated sweet peas of the present day and the height to which it would climb was "6 or 7 feet," but the flower stems were short and bore only two flowers, while the flowers themselves were relatively small, with erect or reflexed standard and conspicuous, depressed wings. In color the standard was reddish purple and the wings light bluish purple. From this modest beginning there have been developed several distinct types of plant and flower forms and a list of named varieties, even within the most highly developed type of flower (the Spencer or waved form), which includes over 500 entirely distinct colors, tints, shades, and combinations. By far the greatest amount of this work has been accomplished during the past 50 years, during which period hybridization has been used

FIG. 120.—Commelin's drawing of the sweet pea in Hort-Medici Amstelodamensis, 1700. (*After Beal.*)

extensively in creating improved varieties. But before hybridization was resorted to there were a dozen distinct color varieties which had arisen by mutation. Besides color mutations there have occurred spontaneous changes in flower form, flower size, and number of flowers on the stem, in stature and habit of the plant and in season of bloom, some of which are described below.

Flower Color in Sweet Peas.—The chronology and probable ancestry of the color varieties of the sweet pea which appeared during the first 180 years of its horticultural history are shown in condensed form in Table XLV. This summary is based upon Beal's excellent historical review, from which citations to original sources have been obtained.

Apparently the course of events was about as follows. From the original type form there appeared first white mutations (Plate III, 3.) If we call the simple flower-color factor complex *CRB*, in which *C* and *R* are complementary factors producing red, and *B* an epistatic factor which modifies that color to purple, then these mutations apparently depended upon a change in either *C* or *R* to the recessive, white condition. The Painted Lady variety, red instead of purple, shown in Plate III, 2, appeared very soon after this, apparently as an independent mutation in the factor *B* from purple. By the close of the eighteenth century two other color types, black and scarlet, had been added to the list. The wild form and Painted Lady are bicolors, that is, the wings are lighter in color than the standard. The new color type scarlet (Plate III, 5,) apparently resulted from a recessive factor mutation conditioning the development of full color in the wings along with a certain intensification of color in the standard. Black (Plate III, 6,) was probably also merely a factor mutation for more intense pigmentation from the wild color type. Early in the eighteenth century a "blue" form, var. *caeruleus*, was described in the trade, but its genetic relationships have not been clearly defined. Plate III, 8, which is taken to represent it has not been copied from a particular variety as was done in the case of the other types. Further additions shortly followed in the form of a "striped" variety, and of a "yellow" variety. The latter (Plate III, 4) unquestionably originated as a factor mutation from white, the former may have arisen as a factor mutation in purple. Plants with primrose yellow flowers have since been observed a number of times in white cultures, but never in red ones. This practically closes the account of the origin of color mutations up to the year 1880, after which time hybridization was resorted to extensively in the creation of new varieties.

Form and Size in Sweet Peas.—The changes in form and size of flower in the sweet pea have been no less striking than those in color, and they have been responsible for a large portion of the popularity which it enjoys. Today one can scarcely recognize in the favorite varieties of

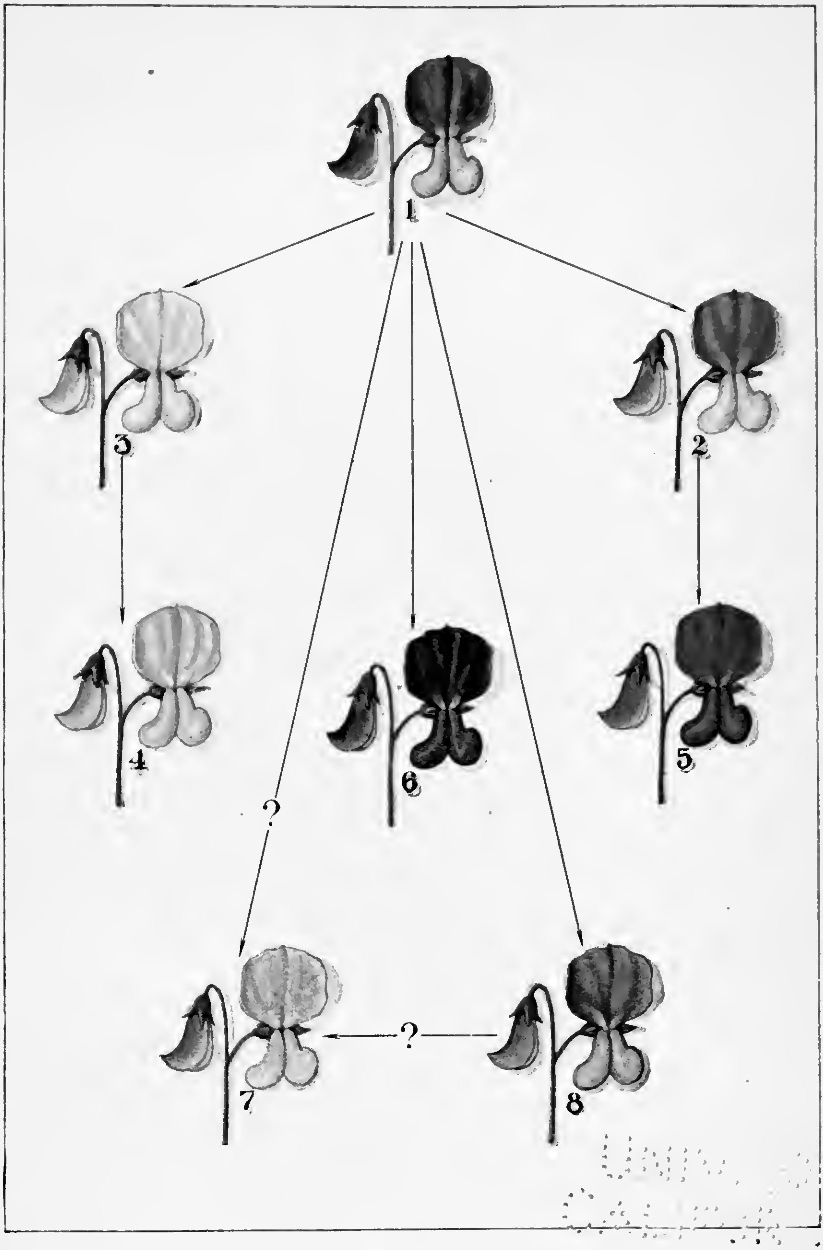

Plate III.—**Oldest Varieties of the Sweet Pea.**

1. The original wild form. 2. Old Painted Lady. 3. White. 4. Yellow. 5. New Painted Lady or "Scarlet." 6. "Black." 7. "Blue Edged" (=purple picotee?). 8. "Blue."

Numbers 4–8 are reconstructions based on modern varieties because the original varieties listed under these names cannot be identified with absolute certainty. But it is highly probable that they were very similar to the types shown above and that they originated by mutation in the order indicated.

TABLE XLV.—ORIGIN OF THE EARLIER COLOR VARIETIES OF THE SWEET PEA[1]

1700			purple and blue—*CRBE*			
1718	white (*cRBE* or *CrBE*)					
1731	white	Painted Lady (= pink and white) *CRbE*				
1793	white	Painted Lady	scarlet—*CRbe* (= deep rose)	black (= dark violet)		
1806	white	Old Painted Lady	New Painted Lady or Scarlet	dark purple	?	blue
1817				?	striped (= purple with brown, lavender or white?)	
1824	yellow (= primrose?) white					
1840	white	Old Painted Lady	New Painted Lady	dark purple and deep violet	?	dark bluish purple and pale blue
1845–49				New Large Purple	New Striped	
1850				New Large Dark Purple		?
1860	yellow (= primrose?)					Blue Edged
1865			Scarlet Invincible			
1870 List	yellow, white	Painted Lady, Crown Princess of Prussia (pink and rose pink).	Scarlet Invincible, scarlet, scarlet striped with white.	black, Imperial Purple, black with light blue.	purple striped with white.	Blue Edged
1880 List	yellow, white	Painted Lady, Crown Princess of Prussia, Fairy Queen (= pink on white), Queen (= light pink and pink purple).	New Painted Lady, scarlet, Scarlet Invincible, scarlet striped with white.	Black, Black Invincible, black with light blue, Large dark purple, Imperial purple, Purple Invincible.	purple striped with white, Invincible Striped Violet Queen.	Blue Edged[2] Butterfly[3] Captain Clarke[4] Heterosperma[5]

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[1] In each case the color of the standard or banner is given first and of the wings second; the descriptive terms and variety names are identical with those in the original descriptions.

[2] Described by Bailey and Wyman as purple-lilac in color (= purple picotee).

[3] Quite similar to Blue Edged according to Beal (= purple picotee).

[4] = "white merging into pink and purple, wings white with purplish cast, wings edged with blue" (= purple picotee).

[5] No description available; mottled seeds?

the garden traces of the early peculiar form of the flower portrayed in Plate III. In the original form the standard was erect, narrow at the base, notched at the top, and reflexed or slightly rolled at the sides. From it have been derived three distinct flower types; the grandiflora, the hooded, and the popular waved Spencer forms. The origin of the first two named is in some doubt. The hooded character was found in some of the earlier varieties. It was sometimes associated with notches in the sides as in the Butterfly (Fig. 121), and this character is found also in some of the present day favorites. Bateson reports that hooded is recessive to grandiflora or erect type of standard. Some of the earliest varieties of improved grandiflora form were Queen of England (1888), Blanche Ferry (1889) and Alba Magnifica (1891). The waved or Spencer form is of more recent origin, and authorities are agreed that it arose as a "sport" from a beautiful, pink, hooded variety, Prima Donna. The pronounced waviness of standard and wings which characterizes this type had not appeared before in sweet peas.

Fig. 121.—Forms of sweet pea flowers—the standard or banner. Open or grandiflora form (upper row left to right)—Alba Magnifica, Shasta, Golden Rose. Hooded form (middle row)—Butterfly, Admiration, Dorothy Eckford. Waved form (lower row)—Elsie Herbert, Apple Blossom Spencer, White Spencer. (From Beal.)

The two upper series in Fig. 121 indicate the more recent progress in enlarging flower size. Alba Magnifica and Butterfly were great acquisitions in their day and were doubtless considerably larger than the oldest varieties. The first definite reference to size is found in New Large Purple, listed in 1845. As this occurs in the darkest color group and 15 years before the hybrid origin of a new variety, Blue Edged, was even suggested; it probably represents a factor mutation. That such mutations actually occurred in the sweet pea is proved by the fact that Countess Spencer and Gladys Unwin were both decidedly larger than Prima Donna from the very first. The same is true as regards number of flowers in the cluster. Prima Donna, according to Beal's description, bore two or three, usually three, flowers on a stalk, while Countess Spencer has three to four flowers in a cluster. Many of the recent Spencer varieties bear almost uniformly four-flowered clusters. The original form and earliest varieties had two flowers in the cluster. The oldest varieties definitely known to bear more than two flowers on a stalk are Invincible Scarlet (1865) and Crown Princess of Prussia (1868). As these antedate the era of hybridization it is probable that the increased number arose by mutation.

Fig. 122.—On the left, Snapdragon sweet peas. On the right, double sweet pea, White Wonder. (*From Beal.*)

Novelty forms have also arisen from time to time. In double sweet peas there are two standards instead of one. In some varieties this character has been fixed by selection so that most of the flowers come double. It gives the effect of increased size (Fig. 122). In the snapdragon type of flower (Fig. 122) the standard is folded around the wings. It is recessive to erect standard and gives a simple Mendelian ratio of 3 erect to 1 snapdragon in F_2.

Habit in Sweet Peas.—There are several distinct types of plant in the sweet pea the origin of which may be definitely ascribed to mutation. The first Cupid plant (Fig. 123*a*) appeared among plants of the tall, white-flowered variety, Emily Henderson, in 1893. The growers, C. C. Morse & Co. of San Francisco, raised seven acres of the new variety in 1895 and every plant was true to type. This mutation has since occurred in a number of widely separated localities. The bush type also originated as a mutation from the tall form. The investigations of the factor relations of bush and Cupid sweet peas have been described in

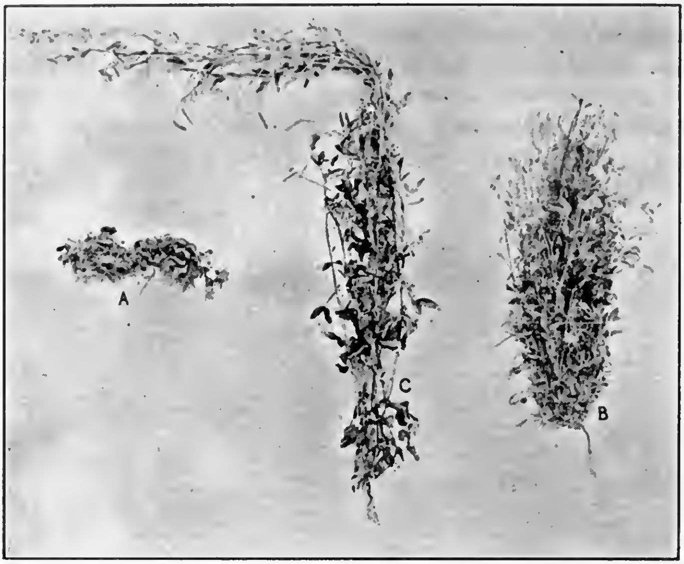


FIG. 123.—*a*, Cupid or prostrate, dwarf sweet pea; *b*, bush or erect, tall form; *c*, Cupid × bush F_1, the ordinary tall form (folded over in order to photograph). (*From Bateson.*)

FIG. 124.—Dwarf or Cupid sweet peas. *I*, ordinary or prostrate Cupid; *II*, erect Cupid, the F_2 double recessive from bush × Cupid. (*From Bateson.*)

a previous chapter. Semi-dwarf, early-flowering sports have appeared even more frequently than those of the Cupid type. They have been made the basis of the winter-flowering types of sweet peas. Ordinary sweet peas pass into a semi-dormant condition for a time after germination, growing very slowly until sideshoots have been developed. The winter-flowering sorts, however, promptly send up a central axis which begins blossoming as soon as it has attained a height of from two to four feet. The Blanche Ferry group of varieties apparently had their inception in a mutation of this sort which a woman in northern New York noticed among some plants of the Old Painted Lady. She selected them for about twenty-five years after which they passed into the hands of a seedsman. From this stock a series of early flowering mutations have arisen in the order shown below. Black-seeded varieties are indicated by (*b*) and white-seeded ones by (*w*).

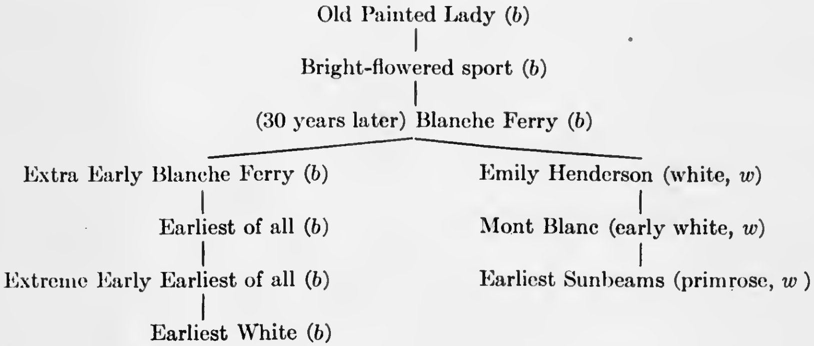


FIG. 125.—New varieties of sweet peas which originated by mutation among the progeny of Old Painted Lady.

Hybridization and Selection in Sweet Peas.—The era of extensive hybridization in sweet peas dates from about the year 1880, consequently we can say but little of definiteness after that time with respect to the origin of new factors in the sweet pea save in a few particularly favorable cases. Laxton's Invincible Carmine was the earliest recorded new variety which was produced by crossing, and its parents are reputed to have been Invincible Scarlet and Invincible Black. We can easily understand, therefore, how it originated, for it is apparently merely an improved form of Invincible Scarlet resulting from the inclusion of the factor for intense pigmentation of Invincible Black in the factor complex of Invincible Scarlet. Similarly by hybridization it has been found possible to establish families of varieties such as the Spencer, the hooded, the grandiflora, and the winter-flowering sorts. Hybridization has throughout been merely a means of fully utilizing germinal differences which have arisen by mutation. It is true that in most cases we cannot say just when the particular features of form, color, and habit have arisen but we know that there was only one original form, and fragments of the history (Beal and Hurst) are sufficiently clear to give us assurance in advancing this explanation of the rôle of hybridization in the creation of varieties of sweet peas. There is no authentic instance of a variety having originated from hybridization of the sweet pea proper, *Lathyrus odoratus*, with any other species of Lathyrus, consequently the possibility of such germinal diversity is precluded. Similarly in the case of selection for more obscure characters such as number of blossoms in the cluster, size of flower, and vigor of growth, apparently the things that have been utilized in cases of improvement are mutations and new combinations of mutant factors.

FIG. 126.—Four types of rose: *a*, typical modern Hybrid Tea rose, *b*, typical Hybrid Perpetual rose; *c*, the Damask rose, which was popular in old gardens; *d*, the old single *Rosa gallica*. (*Reproduced from The Garden Magazine by permission.*)

Creation of Varieties of the Rose.—No finer examples of the origin of horticultural varieties by means of hybridization could be found than the garden roses of today. The genus Rosa is widely distributed in the Northern Hemisphere and contains several hundred species of which, according to Wilson, twenty-six have been utilized in the production of our garden roses. But these twenty-six species fall into fifteen distinct groups, and in habitat they represent Asia, Europe, and North America.

The most important group of modern roses are the Hybrid Teas for they include garden and forcing varieties which combine marvellous beauty of form and color with vigor and hardiness (Fig. 126*a*). Four or possibly five distinct species enter into the ancestry of the group, as shown by the following pedigree. The Hybrid Perpetuals (Fig. 126*b*) are of mixed ancestry, all being hybrids of the Damask Rose (Fig. 126*c*) crossed either with Hybrid Bourbon or Hybrid Chinese varieties.

The hardy, disease-resistant Japanese species, *Rosa rugosa* and *R. wichuriana* have entered into the ancestry of some of the best modern roses. Thus, the American Pillar variety is a hybrid between a red Hybrid Perpetual crossed with a hybrid between *R. wichuriana* and *R. setigera*, the Prairie Rose of America. Again, the Silver Moon variety is a result of crossing *R. lævigata*, the Cherokee Rose, with a hybrid between the Tea Rose, Devoniensis, and *R. wichuriana*. These examples will serve to illustrate the composite ancestry of our best roses. The practicability of this method of procuring new varieties has of course been enhanced by the possibility of vegetative propagation. Occasionally valuable varieties have arisen as bud mutations but these usually differ from the parent variety only in some definite character, like flower color or habit of growth.

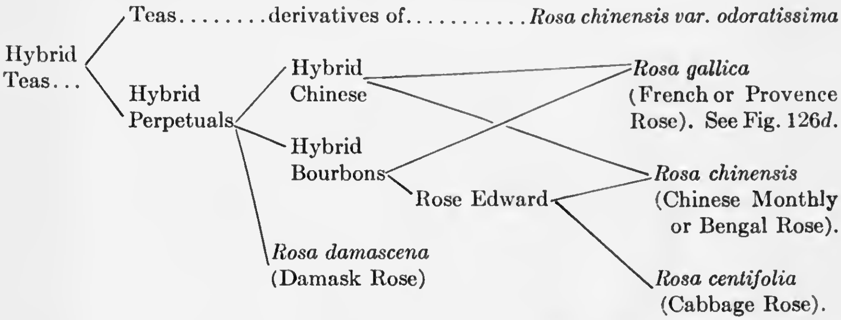


FIG.—127. Pedigree of the hybrid tea roses.

In passing it is of interest to note how extensively this method of variety creation has been used by horticulturists, particularly in species which are normally propagated by clonal multiplication. The hybrid varieties of the rhododendron rival in diversity and floral magnificence even those of the rose, and like them they have been derived from the mingling of a number of different species. But it is among the Rosaceæ particularly that horticulturists have found the most favorable subjects for hybridization. It is necessary in this connection merely to mention such familiar examples as varieties of plums, apples, strawberries, and other rosaceous fruits in the production of many of which extensive hybridization has been employed. In seed plants, also, there are many examples of like improvement. Unquestionably the amateur plant breeder can find no more fascinating or productive line of activity than that of selecting and working with some particular group of species from this standpoint.

Origin of Varieties in the Boston Fern.—In 1915 Benedict reported that he had accumulated about 40 different forms of the Boston Fern, all of which had originated so far as is known from bud sports. The following statements regarding the source of these new varieties are based on Benedict's account. The original Boston Fern arose as a bud mutation from the tropical species, *Nephrolepis exaltata.* It was first recognized as different from *exaltata* by F. C. Becker of Boston, and in 1896 it was named *N. exaltata* var. *bostoniensis.* The typical form of the species and the first sport, *bostoniensis,* are large growing ferns with uni-pinnate leaves (Fig. 128, 1). In the remarkable series of bud mutations that have been derived from *bostoniensis* within two decades, the principal characters undergoing transformation are, first, form of pinna and hence form of frond; second, size of frond; third, form of frond considered independently of pinna-form; fourth, color of foliage.

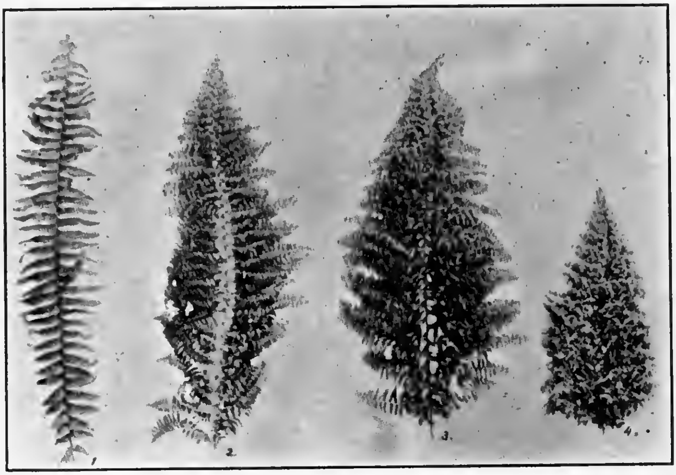


Fig. 128.—1. The original Boston fern, *Nephrolepsis exaltata bostoniensis*; 2, the first bud sport from the Boston, *N. exaltata bostoniensis Piersoni*; 3, the Pierson fern next produced *elegantissima*; 4, *N. compacta*, a sport from *elegantissima*. (*Courtesy Brooklyn Botanic Garden.*)

The original sport from the Boston fern was bi-pinnate; *i.e.*, each pinna was subdivided into little pinnæ or pinnules (Fig. 128, 2). This form appeared about 1900 in the establishment of F. R. Pierson of Tarrytown on the Hudson, and was named *Piersoni* or Tarrytown fern. It did not produce satisfactory plants because only part of the fronds were bi-pinnate; the remainder resembled the original Boston variety.

But *Piersoni* soon produced a tri-pinnate sport which was more regularly divided. Its fronds were somewhat shorter and much broader at the base, thus making the plant more compact. It was named *elegantissima* (Fig. 128, 3). Although it was unstable like *Piersoni,* its uniformity was considerably improved by selection. Soon it produced a sport of quite similar characters except that it was more dwarf which was named *compacta* (Fig. 128, 4). In both *elegantissima* and *compacta* there was variation from the tri-pinnate to the quadri-pinnate condition.

The Pierson fern also gave rise to another interesting series of new forms which exhibited variation in two more characters. In the *elegantissima* series the color of the foliage is similar to that of the original Boston form, but in the new sport, which was named *superbissima* (Fig. 129*f*), the fronds are not only shorter and the pinnæ three- or four-divided, but the foliage is of a deeper green color. Moreover, the fronds and separate pinnæ are twisted so as to give the individual frond an irregular appearance although an entire plant appears fairly symmetrical. Although *superbissima* was unstable, producing uni-pinnate fronds occasionally, it soon produced a sport that is more compact in form and which proved to be more stable. This was named *muscosa* (Fig. 129,*c*).

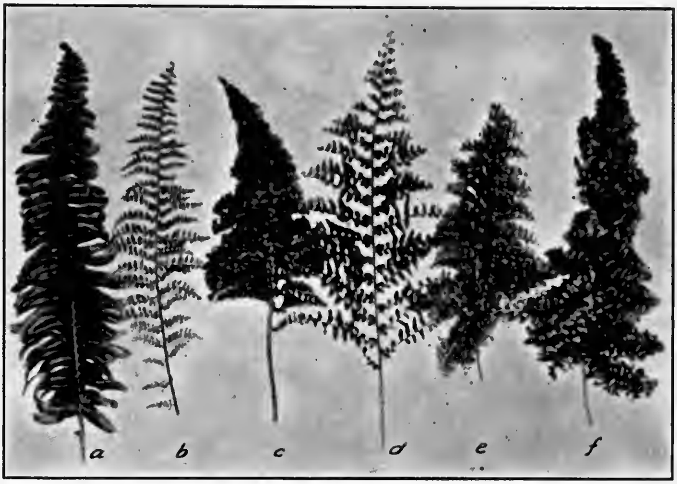


Fig. 129.—The fronds of modern commercial varieties differ greatly from those of the original Boston fern. The varieties shown here are relatively stable, although they are all likely in turn to produce new sports some of which may prove valuable. *a, viridissima*; *b, Millsii*; *c, muscosa*; *d, verona*; *e, magnifica*; *f, superbissima.* (*After Boshnakian.*)

Other distinct uni-pinnate forms that have sprung as bud mutations either directly or indirectly from the Boston fern are the dwarfs, such as *Scotti*, Dwarf Boston, and Teddy Jr., and the vigorous, broad fronded variety, *Roosevelti*. There is no regularity in the production of larger and smaller forms. That is, a dwarf form may spring from a large form or from another dwarf form as shown in Fig. 130. Another distinct group contains the more delicate, open, lace-like forms, such as *Millsii* and *verona* (Fig. 129*b*, *d*). The latter has an advantage over several earlier

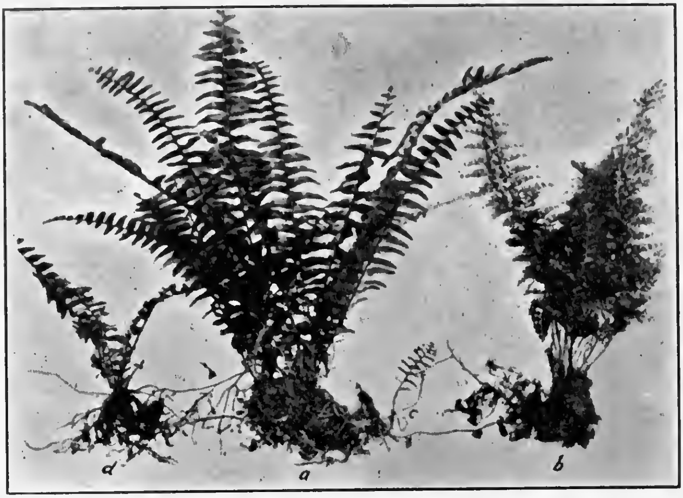


Fig. 130.—Bud mutations in sports of the Boston fern. At the right (*b*) is the form, *magnifica*, a dwarf, asexual descendant of the variety, *bostoniensis*. The fern in the center (*a*) is a sport from this dwarf. It has a tendency to produce further sports and so could not be depended upon to breed true. At *c* is shown a small plant whose single frond resembles *magnifica*. At *d* is another sport that already displays instability in having two sorts of fronds. (*After Boshnakian.*)

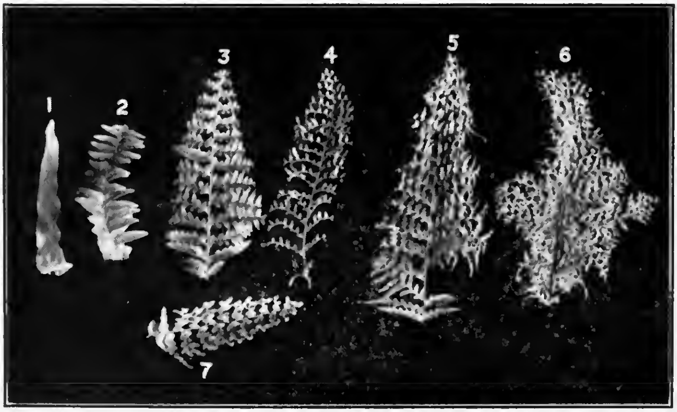


Fig. 131.—A series of pinnæ illustrating progressive variation in division. 1, Var. *bostoniensis*; 2, *Piersoni*; 3, *Whitmani*; 4, *Goodi* (or *gracillima*); 5, *Magnifica*; 6, *Craigi*; 7, *Amerpohli*. (*Courtesy Brooklyn Botanic Garden.*)

varieties of this group in that its rachis is strong enough to support the fully developed frond.

As Benedict has shown the bud mutations occurring in these ferns are more commonly regressive (showing more resemblance to *bostoniensis* than to their parent forms), but progressive mutations are found from time to time. These progressive changes take place along three main lines, viz., increase in leaf division (see Fig. 131), increase in ruffling or crisping, and dwarfing (see Fig. 132); and any form which has not reached the limits of possibility in variation along the first and last mentioned lines, may be expected to give rise to new forms showing further progressive variation in one or both of them.

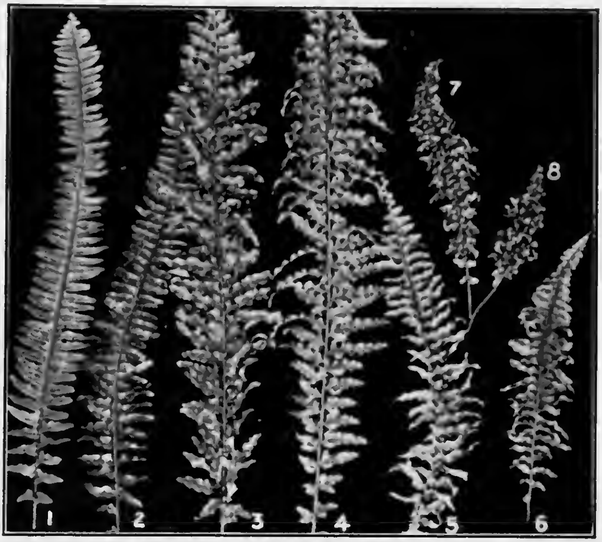


FIG. 132.—A series of fronds illustrating progressive variation in ruffling and dwarfing. 1, *N. exaltata*; 2, *var. bostoniensis*; 3, *Harrisi* (or *Roosevelti*); 4, *Wm. K. Harris* (or new sport of *Roosevelti*); 5, *Teddy Jr.*; 6–8, dwarf sports of *Teddy Jr.*; 7, *Randolphi*. (*Courtesy Brooklyn Botanic Garden.*)

That these new varieties are produced by mutations in specific factors is indicated by the independence of character changes in series of successively produced forms that differ in several characters; for example, the appearance of dwarf uni-pinnate forms as sports of dwarf multipinnate forms. Various series derived from *bostoniensis* show progressive degrees of reduction in size of frond. When a dwarf tri- or quadripinnate plant throws a uni-pinnate sport the latter retains the dwarf size of its parent. Again the difference between *Piersoni* and *superbissima*, its sport, consists of the deeper color and twisted, irregular shape of the latter. When it in turn produced *viridissima* the new uni-pinnate form retained the other distinctive characters of its parent. Finally, as Boshnakian points out, similar sports have been secured among sexually produced progeny in other species of Nephrolepis. Thus it appears that these interesting and valuable ornamentals owe their origin to alterations in specific genetic factors, *i.e.*, to factor mutations in vegetative reproduction.

We have found that new varieties of cultivated plants may be artificially produced in either of two ways, viz., by the discovery and preservation of mutations or by hybridization. Factor mutations occur in both sexually and asexually reproduced plants and frequently produce new forms of immediate economic value. Sometimes, however, the original mutation may be merely a starting point indicating the line along which selection must work. There is always the possibility that subsequent mutations in the same direction, even though they be minute, will be taken advantage of by the breeder. In the creation of new varieties for special purposes hybridization must usually be employed. The success of breeders in combining the desirable qualities of several species in the best modern varieties of the rose suggests untold possibilities in this field of plant breeding.

CHAPTER XVII

THE COMPOSITION OF PLANT POPULATIONS

Before taking up in detail the various methods of plant breeding and considering their effectiveness it is well to enquire as to the nature of the populations with which we are required to deal. By a population in this connection we ordinarily mean a variety as that word is used in the trade, although populations as found in cultivation may be made up of mixtures of varieties. Usually, however, within an established variety, that is, a strain or race bred to a given type until it reproduces that type with a fair degree of accuracy, the variations are of minor consequence and not always readily detectable. But they may be due not only to modifications consequent upon slight differences surrounding the development of individuals in a population; they may also be germinal, that is, they may arise either from Mendelian recombination of germinal differences or by actual new germinal changes. We desire to know, therefore, what sorts of populations exhibit germinal diversity, what kinds of germinal diversity they exhibit, and how the germinal diversity may be related to other characteristics of the populations.

Reproduction in Plants.—In seed plants the important factor which determines the character of the population is the kind of pollination which normally takes place. In the following classification most of our important agricultural crop plants are listed roughly with respect to this factor.

A. Plants normally self-fertilized.

(*a*) Flowers hermaphrodite, but the floral mechanism such as practically to preclude cross-pollination. Examples: wheat, oats, barley, rice, beans, peas, and most of the other legumes.

(*b*) Flowers hermaphrodite, but the floral mechanism favorable to a low percentage of cross-fertilization. Examples: cotton, tobacco, tomato, flax, and other plants having a similar floral structure.

B. Plants normally cross-fertilized.

(*a*) Flowers hermaphrodite, self-fertile, but with floral devices favorable to cross-fertilization. Examples: rye, sugar beet.

(*b*) Flowers hermaphrodite, but self-fertilization precluded on account of self-sterility of the plants. Example: sunflower, red clover.

(*c*) Monœcious plants, self-fertile, but the floral mechanism such as to favor cross-fertilization. Examples: maize, watermelon, squash, pumpkin, cucumber, and cantaloupe.

(*d*) Diœcious plants. Flowers of different sexes on different plants, thus insuring cross-fertilization. Examples: hemp, hops, asparagus and date palm.

Another class having hermaphrodite and uni-sexual flowers on the same plant is termed polygamous. The sunflower might be classified here, because its marginal ray flowers are pistillate only. Certain species of Compositæ have the marginal flowers pistillate, through complete suppression of the anthers as in the sunflower itself, and the disk flowers are hermaphrodite, but the pistil always aborts, so that in effect they are really monœcious plants. In some cases, however, they are known to be completely self-sterile, so that cross-fertilization must always take place in seed formation.

The above classification requires numerous qualifications. For example, it has been our purpose to list under Class *Aa* those plants which are so generally self-fertilized that it is not necessary to protect them to insure self-fertilization, but there are some species and varieties among them which sometimes exhibit a significant amount of cross-fertilization. The cultivated varieties of wheat are very rarely cross-fertilized, but the wild wheat of Palestine has a floral mechanism especially designed for cross-fertilization. Some varieties of rice, also, are cross-fertilized often enough in mixed plantings to make it impossible to assume self-fertilization in a given selection. In peas and beans, perhaps, the proportion of crossing is greater than in the cereals mentioned above, and in some cases it is absolutely necessary to protect them from insect activities. Thus Pearl and Surface in breeding investigations with Yellow Eye beans found it necessary to enclose selected plants in large muslin cages in order to exclude bumble bees, which were found to be effective enough agents of cross-pollination in open fields to disturb results greatly. On the other hand, however, Pearl and Surface in extensive investigations in oat breeding report not a single case of natural crossing. Also Rimpau, who carried on extensive investigations with nineteen varieties of oats over a period of six years, observed only five cases of spontaneous hybridization. Furthermore in most of the commonly cultivated varieties of wheat, barley, and rice natural crossing is so rare a phenomenon as to be worthy of special note in any observed case. We recall also Johannsen's pure line investigations with Princess beans which would have been impossible had natural crossing occurred among them in any significant amount.

Among plants having hermaphrodite flowers which are usually self-fertilized there is also vast difference in the relative proportions of self- and cross-fertilization. In cotton, Balls has found it necessary to allow for about 5 per cent. of natural crossing. In tobacco self-fertilization is the rule, but it is not sufficiently assured to obviate the necessity for protection in gathering pure seed. Especially is this true in sub-tropical regions where humming birds are prevalent for they find tobacco flowers a splendid source of sustenance and unquestionably often effect cross-fertilization between plants. Moreover these remarks concerning tobacco, although they apply to the commercial varieties, do not indicate the true state of affairs in all species of Nicotiana, for a few species are completely self-sterile. Thus in *N. alata grandiflora* some individuals are actually completely self-sterile and others exhibit no bar whatever to self-fertilization. It is especially important, therefore, in dealing with plants in this class to determine these data for the particular species and varieties and the special conditions attending the experiments.

Under *Ba* we have included rye in spite of general statements as to its self-fertility. This classification appears to be justifiable in view of reports of von Rümker and Leidner on results of inbreeding rye. The difficulties in the self-fertilization of rye appear to be technical ones, rather than physiological, consequently reports as to its self-sterility must be in error. This is of interest in connection with the next following class which includes plants which are self-sterile. We have already mentioned the case of *Nicotiana alata grandiflora* in a given population of which both self-fertile and self-sterile individuals may be found. Other complications arise from contradictory reports as to self-sterility in some species belonging in these two groups. Thus there are reports that flowers on a given plant are sterile with their own pollen, but exhibit a certain degree of fertility when pollinated from some other flowers on the same plant. In effect such relations give results which are equivalent to self-fertility, but in some breeding operations it is important to know the exact relations, because it may be necessary to take advantage of them in special cases. It is probable that in general any difference which may be found in the fertilizing power of pollen derived from different flowers on a given plant are non-essential, and dependent upon some such factor as relative maturity of pollen with respect to the receptive period of the stigma.

Among plants which are self-sterile are included a large number of the horticultural varieties which are normally propagated by means of clonal multiplication, but in which suitable pollination is necessary for fruit-setting or for the fullest abundance of fruit-setting. Orchard planting methods provide for this by mixing varieties which are known to act as efficient interpollinating agents. It is important to note that something more than a mere mixing of varieties is necessary; for the best results accurate knowledge should have been gained beforehand of the particular varieties which are most effective when planted together. Self-sterility in improved tree and bush fruits is a not unimportant consideration in practical horticultural operations. It is, also, of interest to note in passing that there is a possibility in particular cases of discovering and overcoming the bars to self-fertility which are normally operative in such cases.

Populations of Plants Normally Self-fertilized.—Continued self-fertilization in a population normally results in the automatic elimination from it of all heterozygous individuals. The operation of this principle can be seen very clearly by considering the simplest case, a heterozygote for one pair of factors self-fertilized through a number of generations. Thus we see from Table XLVI that the general expression in this case for the percentage of heterozygotes after n generations of inbreeding is $\frac{1}{2^n}$. If we set this value equal to 1 per cent., we get

$$2^n = 100, \qquad n = 6.64+.$$

Accordingly beginning with a population made up entirely of individuals heterozygous for one pair of factors, it would take only seven generations of inbreeding to reduce the proportion of heterozygotes within the population below 1 per cent. As a limiting value such a population would of course consist of 50 per cent. AA and 50 per cent. aa.

Table XLVI.—Proportions of Different Genotypes and Percentages of Heterozygotes in a Population of Self-fertilized Plants

Generation	AA	Aa	aa	Percentage of heterozygotes
0	....	2	....	100.0
1	1	2	1	50.0
2	3	2	3	25.0
3	7	2	7	12.5
4	15	2	15	6.25
5	31	2	31	3.125
n	$2^n - 1$	2	$2^n - 1$	$\frac{1}{2^n}$

Jennings and others have given generalized formulæ for determining the percentage of heterozygotes where any number, m, of pairs of heterozygous factors is involved in the original population. Thus starting out with a single plant having m pairs of heterozygous factors, or a population consisting wholly of such plants, the value for h, the proportion of heterozygous individuals, is given by the expression:

$$h = 1 - \left(\frac{2^n - 1}{2^n}\right)^m.$$

This expression is very useful for determining the degree of homogeneity which a hybrid population may be expected to exhibit after a given number of generations of self-fertilization. Thus assuming that there are 10 pairs of factors in a given cross, what proportion of heterozygotes will there be after five generations of sowing? The formula is

$$h = 1 - \left(\frac{2^5 - 1}{2^5}\right)^{10}.$$

Solving we obtain $h = 0.27$; in other words, the chances are only about one in four that a plant selected from a population of this kind will be heterozygous. If there are 100 pairs of factors and ten generations of self-fertilization only 9 per cent. of the population will be heterozygous. Thus we see how powerful is the tendency of self-fertilization to reduce the population to a homozygous condition.

The number of homozygous genotypes to which the population will be reduced, it should be remembered, is given by the expression, 2^m, in which m again is the number of pairs of heterozygous factors. If there are 10 pairs of heterozygous factors in the original individual, then the population will ultimately be reduced to 1024 different homozygous genotypes; if there are 100 pairs of such factors, the number of different kinds of genotypes is approximately $1{,}267{,}666 \times 10^{24}$.

We should always remember in working with formulæ such as these that they are only valid for conditions postulated in the premises. For the above formulæ the following conditions are assumed: roughly equal viability of all genotypes, absence of any natural selection, and independent segregation of factors. Obviously none of these conditions is fulfilled in any even moderately complex population. We have already considered many examples of different viability in diverse genotypes, of which the many different Drosophila mutants provide the most conspicuous examples. Similarly natural selection of necessity enters in whenever any differences whatever exist in the ability of different genotypes to survive and reproduce themselves under a given set of conditions. In addition to these two obvious difficulties the universal occurrence of linkage also profoundly disturbs the mathematical relations whenever any considerable number of factors is concerned in a given cross. It would be a very rare occurrence for even ten different pairs of factors to exhibit independent assortment in any plant species, impossible in a species like wheat which has but eight pairs of chromosomes.

The biological significance of this mathematical discussion is merely this: that it demonstrates that populations in which self-fertilization is an invariable condition in seed formation must consist entirely of pure lines, if left undisturbed for a very few generations. Mathematically the limiting condition is one in which all possible pure lines exist in constant proportions in the population, but biologically the limiting condition is one in which the population is composed only of the most vigorous and productive pure lines.

Populations as Affected by Crossing.—When a certain amount of natural crossing occurs the relations above described are somewhat disturbed. The population, of course, tends to reach an equilibrium, and for all practical purposes does reach one very soon, but the mathematical relations are much more complex than those given above. We may consider a simple case, however, and show the relations in that case. If we start out with a population consisting of equal numbers AA and aa forms, and assume that a given percentage of crossing occurs, then an equilibrium will be reached when the number of homozygotes produced by the heterozygotes in the population is equal to the number of heterozygotes produced by spontaneous crossing. Thus, if we assume 10 per cent. of spontaneous crossing in such a population, in the first generation of the 10 per cent. of AA which cross with other plants, half will be fertilized by other AA plants and half by aa. The latter will give heterozygotes, consequently the proportions of different genotypes produced by the AA plants will be $0.95AA : 0.05Aa$. Similarly aa plants produce $0.05Aa : 0.95aa$, so that in the first generation the ratio is $0.95AA : 0.10Aa : 0.95aa$. Now in the next following generation if we assume that random mating occurs among the 10 per cent. of plants which cross with other plants, then one-third of the plants in each genotype will mate with the same genotype, one-third with one of the other two genotypes, and one-third with the remaining genotype. That is, of the $0.95AA$ one-tenth or 0.095 cross, as follows: $\frac{1}{3}AA \times AA = 0.32AA$, $\frac{1}{3}AA \times aa = 0.032Aa$ and $\frac{1}{3}AA \times Aa = 0.016AA : 0.016Aa$. Similarly, of the $0.95aa$, 0.095 cross: $\frac{1}{3}aa \times aa = 0.032aa$, $\frac{1}{3}aa \times AA = 0.032Aa$ and $\frac{1}{3}aa \times Aa = 0.016Aa : 0.016aa$. Also of the $0.10Aa$, one-tenth or 0.01 cross: $\frac{1}{3}Aa \times AA = 0.0016AA : 0.0016Aa$, $\frac{1}{3}Aa \times aa = 0.0016Aa : 0.0016aa$ and $\frac{1}{3}Aa \times Aa = 0.0008AA : 0.0016Aa : 0.0008aa$. Summating like genotypes we have $0.05AA : 0.10Aa : 0.05aa$. The 90 per cent. of AA and aa plants which are self-fertilized produce $0.855AA$ and $0.855aa$ respectively, while the $0.09Aa$ plants which are self-fertilized produce $0.0225AA : 0.045Aa : 0.0225aa$. Combining these with the results of cross-fertilization we have the ratio for the second generation, $0.928AA : 0.146Aa : 0.928aa$. Now the ratio of the proportion of homozygotes to the population in the first generation is of course 0.95 and in the second generation it becomes,

$$\frac{0.928 + 0.928}{0.928 + 0.146 + 0.928} = 0.927.$$

The composition of the third, fourth and fifth generations and the ratio of the proportion of homozygotes to total population for each are shown in Table XLVII. It is evident that, under the conditions assumed in this case, the rate of change in the ratio of homozygotes to the total population becomes very gradual after the first three generations, so that for practical purposes the population has reached a state of equilibrium in the fourth generation. In this generation the ratio of heterozygous dominants to the sum of the heterozygous and homozygous dominants is 0.16 +. In this or later generations, therefore, the chances of selecting at random a heterozygous dominant, assuming dominance to be complete, are about one in six.

Table XLVII, shows the composition of the population with reference to a single pair of factors, *A* and *a*, in the first five generations when there is 10 per cent. of spontaneous crossing, assuming (1) that before crossing began there were equal numbers of *AA* and *aa* plants; (2) that among the 10 per cent. of plants which cross random mating occurs: (3) equal fertility and viability in all individuals.

Starting again with a population of *AA* and *aa* forms we find that, assuming 20 per cent. of crossing in this instance, other conditions being the same, the ratio of homozygotes to the whole population in the first four generations is as follows: 0.90, 0.86, 0.845 and 0.837; while the ratio of heterozygous dominants to the total dominants in the fourth generation is 0.27. Hence, in this and later generations the chance of selecting a heterozygous dominant is about one in four. Again, with 50 per cent. of crossing the ratio of homozygotes to the whole population in the first four generations is 0.50, 0.625, 0.649, 0.662; and the ratio of heterozygous dominants to the total dominants in the fourth generation is 0.50+, so that the chance of selecting a heterozygous dominant is one in two. In the same way the theoretical expectation for any particular amount of crossing may be calculated. It must be borne in mind, of course, that we have made no allowance for greater relative vigor and productivity in the heterozygous plants. However, the method illustrated may be utilized in working out similar problems in which the genetic relations are disturbed by such conditions as difference in viability or fecundity as well as for various amounts of crossing.

Table XLVII.—Composition of Population

Generation	*AA*	*Aa*	*aa*	Ratio x/y*
1	0.95	0.10	0.95	0.95
2	0.928	0.146	0.928	0.927
3	0.919	0.167	0.919	0.917
4	0.915	0.175	0.915	0.913
5	0.914	0.179	0.914	0.911

* x = proportion of homozygotes in the population; y = value of total population.

This brief consideration merely suggests the possibilities of mathematical analysis of the composition of populations under assumed conditions. It must be clear, however, that such analysis as applied to a given set of conditions would be of very great value in conducting breeding investigations. But it should be remembered that reliable conclusions regarding any particular case cannot be derived from such analysis unless the more important controlling agencies at least have been so carefully investigated that their combined influence can be duly estimated. On the other hand, the general principles derived from the mathematical study of the composition of populations are of universal application. These principles may be summarized as follows:

1. (*a*) Continued self-fertilization tends to eliminate all heterozygotes from the population.

(*b*) The number of homozygous genotypes to which a self-fertilized population will be reduced depends upon the number of pairs of factors involved.

(*c*) Such a population after a few generations will consist entirely of pure lines.

2. (*a*) With a given amount of natural crossing in the absence of any disturbing effects there will be an approximation toward a definite proportion of heterozygotes in the population.

(*b*) Such a population approaches very nearly a condition of equilibrium within a few generations.

(*c*) Under the influence of disturbing elements the proportion of heterozygotes may be increased or decreased, but the condition of equilibrium will be rapidly approached if the disturbing elements remain fairly constant.

CHAPTER XVIII

SELECTION

The oldest and most generally used means of plant improvement must continue to be the basic method in systematic plant breeding. Although selection is universally recognized as an effective method of breeding, yet all too long the prevailing ideas among empirical breeders regarding the way in which selection effects improvement and the reasons why selection sometimes fails in securing the end desired have been exceedingly vague. The confusion of thought concerning this matter which still exists among both scientists and laymen is largely due to a lack of clear understanding concerning the nature of variation. The variations upon which selection can be used effectively owe their origin either to mutations or to recombinations of genetic factors. On account of the differences in the composition of populations in various species of plants the effects of selection differ greatly in different crops. In order to employ selection most economically the plant breeder should understand the nature of the population with which he is working and the genetic principles underlying effective selection. It is our purpose in this chapter to set forth the principles of selection in both allogamous and autogamous species.

Selection Methods in Maize Breeding.—The maize plant is highly variable and many different varieties and strains have been produced by selection. In most of the states where corn is grown extensively the experiment stations have published bulletins on corn improvement and the subject is discussed in more or less detail in various works on plant breeding. We shall merely consider here certain methods of maize selection in order to illustrate the principles involved and to compare them with methods used in other crop plants.

Inbreeding in Maize.—Self-fertilization in maize results in marked reduction in vigor and hence in size of plant and production of seed. This was first discovered by Shull, who applied the pure line method in corn breeding, and from his results inferred that a field of maize consists of a collection of genetically distinct biotypes which may be isolated by inbreeding. East soon corroborated Shull's discovery and later East and Hayes summarized the results of inbreeding a naturally cross-fertilized plant substantially as follows:

1. There is partial loss of power of development, causing reduction in

the rapidity and amount of cell division. This phenomenon continues only to a certain point and is in no sense an actual degeneration.

2. There is an isolation of biotypes differing in morphological characters accompanying the loss of vigor.

3. The hereditary differences between these biotypes is often indicated by regression away from instead of toward the mean of the general population.

4. As these biotypes become more constant in their characters the loss of vigor ceases to be noticeable.

5. Normal biotypes with such hereditary characters that they may be called degenerate strains are sometimes, though rarely, isolated.

6. It is possible that pure strains may be isolated that are so lacking in vigor that the mechanism of cell division does not properly perform its function, and abnormalities are thereby produced.

Thus we know that any commercial variety of corn is a mixture of different genotypes and that inbreeding tends to isolate pure genotypes, *i.e.*, inbred strains tend to become homozygous. Thus it is evident that the cross-bred progeny of two different inbred strains will be heterozygous for many factors. That cross-bred maize frequently displays greater vigor than either parent was first demonstrated by Beal of Michigan in 1878. But it was not until Shull and East demonstrated the existence of genotypes in maize that the genetic significance of this phenomenon became evident. The actual cause of the increased vigor has been explained in various ways. Both Shull and East held that decrease in vigor in inbred strains is due to reduction in the number of heterozygous factor combinations and that increase in vigor in F_1 hybrids is the result of increase in the number of such combinations. The general occurrence of decrease in vigor upon inbreeding naturally cross-bred species and of increase in vigor upon crossing closely related forms led them to conclude that heterozygosis is the cause of increased physiological vigor in F_1 hybrids. Other explanations of this phenomenon have been offered, one of which was that of Keeble and Pellew, to the effect that it "may be due to the meeting in the zygote of dominant growth factors of more than one allelomorphic pair, one (or more) provided by the gametes of one parent, the other (or others) by the gametes of the other parent." East and Hayes reject this hypothesis on the grounds that this increase in vigor "is too universal a phenomenon among crosses to have any such explanation. Furthermore, such interpretation would not fitly explain the fact that all maize varieties lose vigor when inbred." But there is good evidence that all maize varieties do not lose vigor to the same extent when inbred and that certain genotypes produce much more vigorous F_1 hybrids when crossed than other genotypes. As was stated in Chapter XII, D. F. Jones has explained this increased vigor in F, hybrids in terms of dominance and linkage (p. 231, 2). The fact that different genotypes give diverse results when crossed is of immense practical significance.

The Ear-to-row Method.—This has been the method of commercial corn improvement for many years and it is well illustrated by the Illinois corn breeding experiments, which have been going on continuously for over 20 years. The original purpose of the experiments was to produce new strains which would be more valuable as a source of feed for livestock. It was found that there was considerable variation in the relative amounts of protein and carbohydrates in the grains of different ears. Accordingly selection was begun with the object of increasing the protein and reducing the starch content of the grains; also of decreasing protein and increasing starch. As oil was worth three times as much as starch per unit of weight, selection for higher oil content was also begun. A low oil strain was started for comparison and such corn was soon found to be desirable for the production of pork and beef of high quality.

The work was begun by Hopkins who picked out 163 ears of a local strain known as Burr's White, made a chemical analysis of a few grains from each ear, and on that basis sorted them into four classes, viz., high and low protein and high and low oil. The strains were grown in isolated plots from the beginning. After 9 years of selection it was found to be necessary to prevent inbreeding. Accordingly in the tenth and succeeding years about 24 ears were selected for each plot and one row was planted from each ear, then the even numbered rows were detasseled. Subsequent selections were made from the detasseled rows, the first consideration always being high yield. Usually 20 ears were taken from each of the six higher yielding rows, or 120 ears for each plot. These were tested by chemical analyses and the most extreme variants in the desired directions were selected for the next planting.

The results in general have been more regular in the high and low oil series than in the high and low protein strains. In the latter there seems to have been no very decided effect of selection after the first 10 years. Similarly there has been no continuous advance in the low oil strain since the seventeenth year of selection, but in the high strain the per cent. of oil has continued to increase slightly. The progressive effects of selection in the four series are graphically illustrated in Figs. 133 and 134. That the striking results depicted in these graphs were not caused by environmental conditions was proved by planting mixed plots with two grains of "high" and two of "low" corn in each hill so arranged that the resulting plants could be identified. This test, according to L. H. Smith, was made for three successive years, and subsequent analyses showed that under these conditions the different strains maintained their distinguishing chemical characters.

The Illinois Station experiments have included selection for many other characters of the corn plant in more recent years. One of the most striking results was obtained by selecting for height of ear on the plant. Data on which to base selection were secured by measuring several hundred stalks in the oil and protein plots, noting height of ear above the ground, total height of stalk, apparent number of internodes below the ear and number of internodes above the ear. Fig. 135 shows the result of selecting for high and low ears during five generations. Similar results were obtained from selection in the case of position of ear at maturity and total yield.

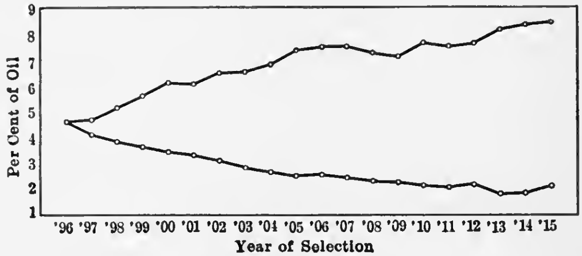


FIG. 133.—Two graphs representing the effects of selection for high and low oil content in the Illinois Station corn experiments. (*Data from Castle.*)

The striking results of these carefully conducted experiments have been cited by various authors as evidence *par excellence* for the most diverse conceptions of the *rôle which selection plays* in evolution and breeding. Thus the earlier allusions of Hopkins and Smith, the discussion in E. Davenport's text on breeding, and the recent treatment by Castle all seem to attribute a peculiar creative power to selection which meets with a certain "response" on the part of the plant. This is in line with the Darwinian idea that all fluctuating variations are heritable and that the continuous selection of minor fluctuations in a certain direction is always effective in shifting the type.

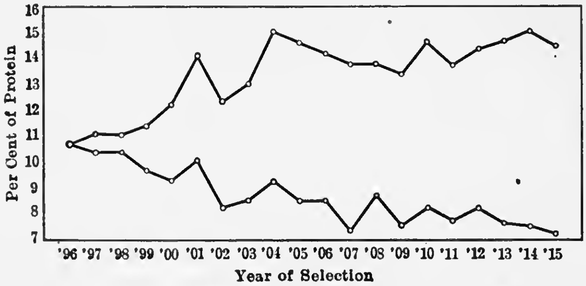


FIG. 134.—Two graphs representing the effects of selection for high and low protein content in the Illinois Station corn experiments. (*Data from Castle.*)

The futility of attempting to generalize regarding the effects of selections in plants must be obvious from what we now know about the composition of plant populations. With the application of Johannsen's genotype conception in analyzing the composition of a field of maize the problem of explaining the rôle of selection in the Illinois corn breeding experiments was immediately simplified. This was perceived by Shull who pointed out that the results of these experiments might be readily explained on the ground that some hybrid combinations of genotypes have greater capacity for the production of the desired qualities than other combinations, and that the selection has gradually brought about the segregation of those genotype combinations which had the highest capacity for the production of the desired quality.

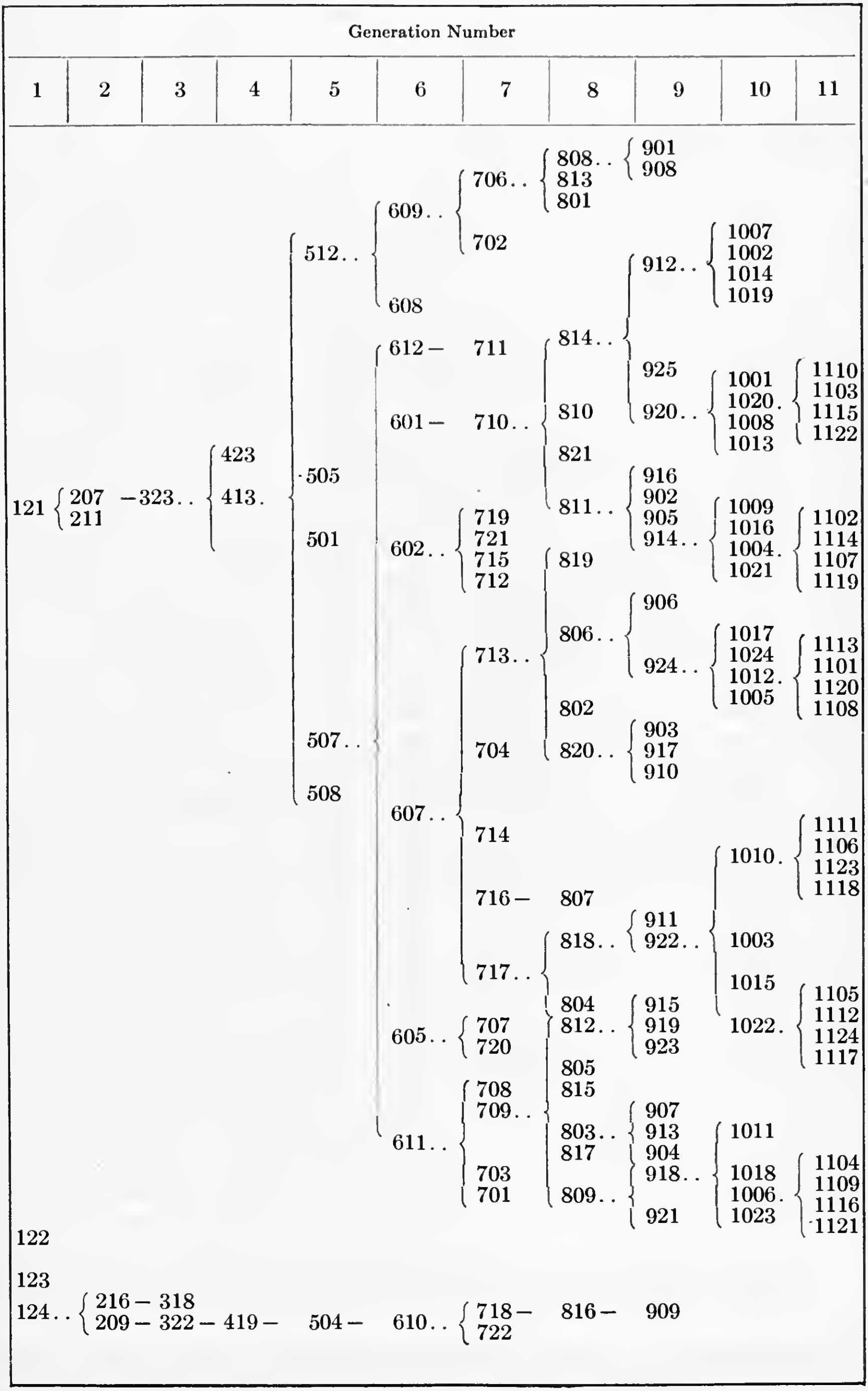
FIG. 135.—Result of selecting corn for high and low ears during 5 generations. The white tape marks the position of the ears on the front row of plants in both plots.

Meanwhile Surface had made an illuminating analysis of the data from the first 10 years of selection as reported by Smith. This treatment is so valuable as to warrant its examination in some detail. At the time the selections were made a careful record of the pedigree of each ear was kept. These pedigrees are of course for the maternal side only since self-pollination was not practised. From these data Surface prepared a pedigree chart for each of the four strains. The chart for the high-protein strain is reproduced in Tables XLVIII and XLIX. As stated above 24 ears containing the highest per cent. of protein were selected for the 163 ears analyzed in 1896. These were given registry numbers from 101 to 124 inclusive as shown in column one of the two tables. For convenience we may refer to these ears as the first generation of high-

TABLE XLVIII.—PEDIGREE CHART OF HIGH-PROTEIN CORN—PART I. (*After Surface.*)

Generation Number										
1	2	3	4	5	6	7	8	9	10	11
101										
102–	215–	320–	410–	502						
103–	208–	314..	424							
			409							
104–	214..	316–	421							
		310								
105										
			401–	514						
		306..								
106..	222		405							
	213..	315–	418							
			417							
		319..	414							
			416							
107..	219–	301								
	223									
108..	206–	321..	415							
	217		406							
109										
			407 –	510						
110			420							
		311..								
			411..	506 –	604					
111				513						
		312								
	212..									
		313								
			404							
					614					
112..		309..	402 –	515..	606					
					603					
			408							
			422							
	205–	317..		503						
			412..	509 –	613 –	705 –	822			
113..	210									
	220–	324								
114–	204–	303								
115–	224–	304								
116–	202									
117										
118–	218–	302								
119..	221–	307 –	403 –	511						
	201–	305								
120–	203–	308								

TABLE XLIX.—PEDIGREE CHART OF HIGH-PROTEIN CORN—PART II. (*After Surface.*)



protein corn. The next season 4 sound ears were analyzed from each of the twenty-four rows. From these 96 ears the 24 again having the highest per cent. of protein were selected for planting. The distribution of these selected ears among the 24 original ears is shown in column two of the tables. For example, it is seen that ear No. 124 produced 2 ears, Nos. 216 and 209, which were among the first 24 as regards protein content. Ear No. 123 on the other hand failed to produce any ear (so far as the ears analyzed showed) sufficiently rich in protein to be included among the first twenty-four. Thus 8 of the original ears fail to be represented in the second generation, while 8 other ears contributed 2 ears each for planting the following year. Exactly the same selection was practised in the second year and the resulting selected ears are shown in the third column of the tables. Of the 16 original ears represented in the second generation only one, No. 116, was dropped out in the third generation but in the next generation there is a significant dropping out of some of the original lines, so that in the fourth generation only 9 of the original 24 ears are represented by progeny. Five of the original lines contribute 80 per cent. of this generation, while two lines, 106 and 112, contribute nearly 60 per cent. Hence at the end of the fourth generation it is clear that certain of the original lines have a much greater tendency to produce ears with a high per cent. of protein. By simply selecting on the basis of the protein content of the individual ear for 4 years 70 per cent. of the original lines have been dropped.

Thus the elimination of the original lines gradually proceeds until, in the tenth and eleventh generations all of the high-protein corn is the offspring of a single ear, viz., No. 121. It will be remembered that in the tenth year the method of detasseling alternate rows and saving seed from these only was put into effect. But this change in method could not have induced the results we have noted because line No. 121 had demonstrated its superiority over all the others as early as the seventh generation. This isolation of a single line was brought about therefore simply by selecting each year those individual ears that showed the highest per cent. of protein. Starting with a protein content of 10.92 per cent., at the end of the third year (fourth generation, 1899) the protein content was only 11.46 per cent. or a gain of 0.54 per cent. But the next year (fifth generation) the protein content jumped to 12.32 or a gain of 0.86 per cent. in 1 year. Referring now to Table XLIX it is seen that it is in 1899 that a great reduction was made in the number of lines represented, for in the fifth generation only six of the original twenty-four lines remain. Furthermore it is just here that line No. 121 begins to show its superiority since 5 of the 15 ears selected in 1900 or 33⅓ per cent. come from this line.

The course of events in the other three strains was similar but not quite so striking. In the low-protein strain only two of the twelve original lines are represented in the eleventh generation; in the high-oil strain three lines out of twenty-four are maintained throughout the 10-year period; and in the low-oil strain only two lines out of twelve are represented in the eleventh generation.

These results are exactly what would necessarily accrue in any allogamous species under continuous selection for a given character, provided the degree of expression of that character is dependent upon a number of genetic factors. That several chemical characters of the corn grain, including protein and oil (fat), are inherited in accordance with Mendelian principles was determined by Pearl and Bartlett in 1911. In a cross between a white sweet corn and a yellow starchy corn determinations were made by direct analysis of the percentage content of the grains of the pure parent races and the F_1 and F_2 progeny in respect to nine chemical constituents. These are listed in Table L, which also indicates the dominant and recessive conditions of these characters in the cross studied.

TABLE L.—GENETIC RELATIONS BETWEEN CERTAIN PHYSIOLOGICAL CHARACTERS OF THE CORN GRAIN.

Character	Dominant	Recessive
Moisture	High	Low
Nitrogen and protein	Low	High
Crude fat	Low (incomplete dominance)	High
Ash	Low	High
Crude fiber	Low	High
Pentosans	Low (incomplete dominance)	High
Sucrose	Low (incomplete dominance)	High
Dextrose	Low	High
Starch	High	Low

This evidence, although worked out quite independently, supplements Surface's analysis of the Illinois data in a remarkable way. Although there are technical obstacles to a clear cut determination of the factor relations involved, yet there is no question whatever that these characters of high and low protein and oil are conditioned by unit factors. *A priori* there is no objection to assuming the existence of several factors which affect the percentage of protein, for example, and that the original ear, 121, of the superior line in the high protein strain represented a genotype rich in high protein factors. Similarly in the other strains, continual ear-to-row selection has gradually eliminated all genotypes except the one, two or three as the case may be of highest or lowest factor combinations.

Thus we see that selection has *created* nothing in the course of these justly famous experiments; it has served merely as a means of isolating particular combinations of factors which condition oil and protein production in the corn plant. Moreover, this sorting process has not been entirely regular or continuous. The saltations or jumps revealed by Surface's analysis were directly consequent upon lump elimination of a number of mediocre lines. These results, therefore, are in entire harmony with the known nature of allogamous populations. This conclusion is further corroborated by the recent report of Reitz and Smith on the statistical study of indirect effects of selection for high and low protein and oil. These authors state:

> "It is found that four distinct types of corn as regards length, circumference, weight of ears, and number of rows of kernels on ears are so well established that we may assign orders of values to the means of these characters that persist with but a few exceptions in such changes of environment as have been experienced in 11 years of planting, from 1905 to 1915.
>
> "While a few slight but progressive changes have been noted, the selections for chemical composition from 1905 to 1915 have not changed decidedly the differences in mean values of these characters. In fact, we are unable to assert with any high degree of probability that the strains differ more or less with respect to these characters *during the second half of the period* 1905 to 1915 than during the first half."

The italics are ours. It is of especial significance that careful biometrical study has failed to reveal any progressive change as a result of continued selection in these strains of corn. For the results of these experiments have been cited as evidence *par excellence* by Castle in support of his hypothesis of factor variability.

The ear-to-row method has been modified in various ways but it still forms the basis of most systems of commercial corn breeding. A popular feature of systematic corn improvement is the use of score cards in judging. A special development of the score card method of selection is the use of selection index numbers as advocated by Pearl and Surface. In this plan arbitrary values are assigned to various characters of the corn ear, for example, such as absolute size of the ear, average percentage depth of the grains, etc. The idea is to combine in a single numerical expression the values of a series of variable characters with regard to all of which the breeder wishes to practice selection at the same time. The index numbers of different varieties are not directly comparable but for a given variety they may be useful as an adjunct of the score card method. However, their use requires more attention to details and hence greater expense than most breeders can afford to give. Their use in plant breeding will probably be limited to experiment stations (see Chapter XXXI).

The danger of continued ear-to-row selection or "narrow breeding" within a variety was pointed out in 1909 by Collins, who emphasized the importance of "broad breeding" in such crops as exhibit loss of vigor when closely inbred. About the same time Williams inaugurated the *remnant system* of corn breeding at the Ohio Experiment Station and the plan was adopted by the Ohio Corn Improvement Association. The plan calls for an ear-to-row test plot each year in which ears are carefully tested for productiveness. Only half of the grains on each ear are planted in the test plot, the remainder being retained until the following year under the term "remnant." The ear-to-row test plot need not be isolated as no seed is saved from it. The next year the remnants of a few, usually four, of the highest yielding ears are planted in an isolated breeding plot, and the stalks from all of the ears planted in this patch, except those of the highest yielding ear, are detasseled. Seed ears are selected from the detasseled rows and grown the next year in a multiplying plot to supply seed for general planting. After this method is under way on any farm, there is maintained on the farm each year a small isolated breeding plot, a multiplying plot, and an ear-to-row test plot. This method successfully excludes from the breeding plot all individuals except those whose producing power has been found to be very high. At the same time it provides for the intercrossing of these most productive strains, and by continuing the tests from year to year the work will "tend toward the selection of the best producing ears for all or average seasons." According to Hartley, "The choice of a high yielding variety is important; the choice of high yielding ears is even more important." The remnant system combines this result with the advantages attendant upon intercrossing of distinct strains. Rye, clover, beets, timothy and other grasses are suited to this method of breeding. It was with rye that Rimpau first employed the system that later came to be known as the German method of broad breeding.

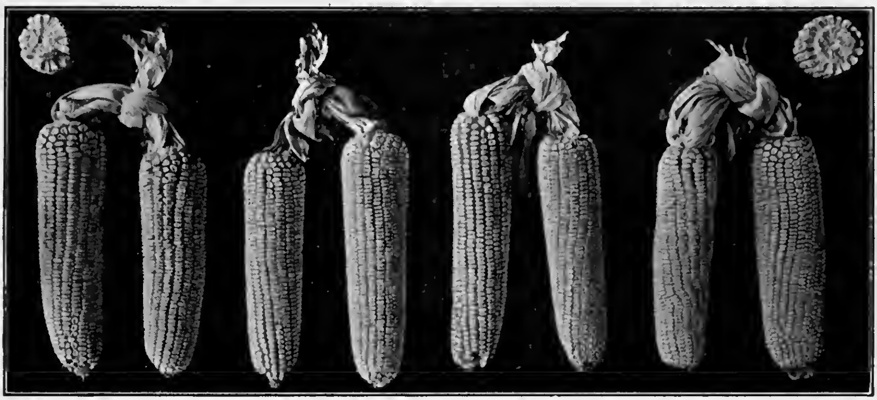


Fig. 136.—Delta Farm White Dent, a superior strain of maize adapted to the bottom lands of the interior valleys of California. It is the result of 30 years of continuous selection of seed in the field before harvesting. The original material consisted of a mixture of all the types of corn commonly grown at that time. A convincing demonstration of the practical value of seed selection as a general agricultural practice.

An interesting illustration of what can be accomplished in maize merely by mass selection, when a definite ideal is maintained and seed is selected in the field before harvesting, is found in the Delta Farm White Corn shown in Fig. 136.

Selection Methods in Breeding Close-pollinated Plants.—The successful methods of breeding wheat have been reviewed in preceding chapters. Compared with the methods required for corn the work of isolating genotypes in wheat is relatively simple. Most commercial varieties of wheat are a mixture of pure lines which can be isolated by single plant selections. In Fig. 137 is shown a typical head from each of 7 different pure lines isolated by selecting single plants from a plot of Defiance wheat. Nos. 1 and 2 did not have an average of one grain per spikelet while Nos. 6 and 7 bore from 4 to 7 grains per spikelet. If Nos. 6 and 7 prove to be superior in other characters also, they need only to be multiplied in order to yield greatly improved strains of the Defiance variety. It was by this method that Roberts in 1906 isolated a pure line of Turkey wheat that appears very promising for the Great Plains Region. It is worthy of note that this superior pure line was the 135th

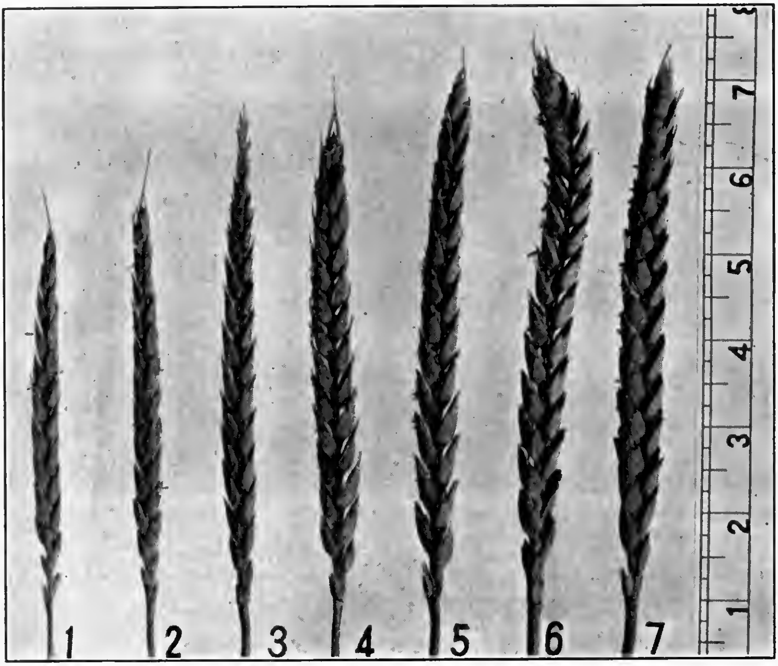


Fig. 137.—Typical heads from seven pure lines of Defiance wheat. Nos. 1 and 2 do not yield one grain per spikelet on the average; Nos. 6 and 7 yield from 4 to 7 grains per spikelet. Note tendency to club type in No. 6.

single head selection made by Roberts in 1906. Altogether he made 557 selections from nearly 200 different varieties; but nearly 415 of these were discarded within 2 years.

The Plant-to-row Method.—Single plant selections are usually grown in garden rows, each row from a different plant. Final selection of the individual plants should be preceded by field observations, noting habit, vigor, disease resistance, season of bloom, time of maturity, productivity, etc. Each of these plants must be harvested separately and careful records should be made concerning yield and other important characters. It is on the basis of the field observations and the data from the harvested plants that a further selection must be made. From each of the plants finally selected sufficient seed is taken for a row of about 25 plants. The rows should be evenly placed and plants should be equidistant in the row. By subjecting these rows to severe selection the future work may be considerably reduced. Hence careful notes should be taken throughout the season and at harvesting time. Of several hundred rows only a few may be found good enough to be continued. The third year the

Fig. 138.—Spreading and erect pure lines of Gypsy wheat, 1907. (*After Williams, Ohio A.E.S.*)

FIG. 139.—The erect pure line of Gypsy wheat in 1909. (*After Williams, Ohio A. E. S.*)

FIG. 140.—The same pure line (on the right) now known as the Gladden variety, as grown in 1915. (*After Williams, Ohio A. E. S.*)

seed from the selected rows is sown in small multiplying plots. At the Maine Station these plots are 1–2000 acre in area and usually in duplicate (see Fig. 141). These plots are subjected to still further selection and only the best retained. The next step is to sow each selected pure line in one or more field plots. At Maine 1–40 acre plots are used and each line is tested in duplicate or quadruplicate plots for several years and only those that are superior in some respects at least to commercial varieties are retained. At the Ohio Experiment Station according to Williams, "In following the pure line method of selection, decided differences in winter resistance, stiffness of straw, yield of grain and breadmaking qualities have been found in the progeny of individual heads selected from ordinary varieties of wheat." In Fig. 138 are shown two very distinct pure lines of Gypsy wheat as they appeared in 1907. In Figs. 139 and 140 the same pure line appears as grown in 1909 and 1915 respectively. This selection, has been introduced under the name of Gladden.

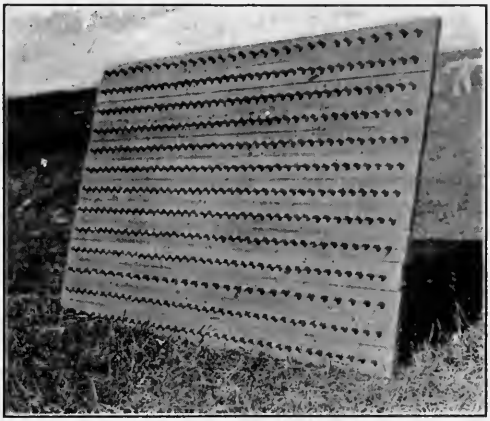


Fig. 141.—Planting board used in pure line work with small grains at the Maine Experiment Station. It provides a plot 1/2000 acre in area with the plants nearly as close together as when sown in the field. *(After Surface and Zinn, Maine A. E. S.)*

Ineffectiveness of Continued Selection Within Pure Lines.—Convinced of their failure to make any progress as a result of continued selection within pure lines, some experiment stations have abandoned this line of work. Hutcheson has reported on the results of 13 years of continuous selection in six pure lines that were isolated by Hays in 1901. These pure lines represent five of the sub-species of common wheat, *Triticum vulgare.* In brief the method consisted of selecting each year the best 100 grains from each of five or more best plants in each line. This seed was planted at regular distances in centgener plots the following year, each centgener representing a single plant selection. Hutcheson says, "the indications are that from a practical breeder's standpoint permanent improvement in pure lines in small grains, if possible, is certainly not rapid or apt to be very marked." He also suggests that much more rapid progress could be made by isolating pure lines from mixed populations and combining the desirable characters of these lines by hybridization.

Other crops in which the method of selecting pure lines is applicable are oats, barley, peas and beans. Notable improvement has been made in oats by this method at the Svalöf, Cornell University and Maine Experiment Stations. The general method of procedure at the Maine Station is indicated by Surface and Zinn in their bulletin on pure line varieties of oats (see p. 371). The pure lines finally retained came from only three varieties, viz., Banner, Irish Victor and Imported Scotch. It is noteworthy and consistent with Mendelian principles that the physiological characters which result in higher yield are not necessarily associated with morphological characters in the plant or grain. Similar results with winter-resistant barleys have been reported by Spragg of the Michigan Station. The practical importance of the selection of pure lines as one phase of a complete system of breeding as practised with autogamous species is given further attention in Chapter XXI.

Selection which is to result in the isolation of the most superior genotypes must begin with individual plants. In diœcious and self-sterile plants this method is inapplicable. Here the breeder must begin with phenotypically similar individuals and continue inbreeding of similar plants for several generations in order to isolate approximately uniform strains. The earlier improvement of the sugar beet was accomplished by mass selection. But in recent years the producers of commercial seed have introduced a system of line selection. According to Briem, reliable seeds cannot be obtained by selection in the lump, nor from a single generation of mother beets followed by the cultivation of seed roots. An individual selection must be made the characteristics of which are assured by testing for three generations. That is to say, since the beet is a biennial 6 years are required to obtain seed of guaranteed quality for the seed roots and another 2 years must pass before the market product is ready. Briem's opinion is in harmony with Pritchard's conclusion that continuous selection is not an efficient method of sugar beet improvement and that the improvement of the past is the result of isolating mutations (see p. 369).

In emphasizing the importance of finding the best genotypes within a chosen species or variety the usefulness of mass selection should not be overlooked. It is frequently the first or only practicable step to take in purifying a commercial variety. The so-called "running-out" of varieties can be prevented by reasonable care to avoid mixing seed and by occasional mass selection from the field. Seed selection of this sort is of the greatest practical value to agriculture and it is applicable to most sorts of field and garden crops.

The Practical Importance of Keeping Varieties Pure.—Many farmers do not regard purity of varieties as a matter of great concern, but continue to use impure seed from year to year. Since the main object of breeding work is to produce new and better varieties, and since a true variety differs definitely from all other varieties, it is of great importance that its purity and hence its identity be maintained. The need for care in this regard is of course much greater in naturally cross-fertilized species than in self-fertilized forms, yet even in the latter the mixing of varieties may detract greatly from the market value of the crop. It is not impossible for an impure variety or a mixture of varieties to give good returns for a year or two or even longer. When one considers, however, the rapidity with which the number of distinct strains may be increased by occasional crossing the danger of such practice will be realized. For this reason all agencies supervising the collection of stock seed of commercial varieties of corn, sorghum, cotton, etc., should exercise every possible precaution against mixing varieties or collecting seed that may have been crossed with other varieties. As Newman points out, however, there are certain circumstances under which the planting of mixed sorts may have their advantages. Thus a variety may contain strains which differ from each other for example chiefly in their response to different soil conditions. Were a variety of such composition sown in a field in which the soil is exceedingly variable it is possible that a better average would be maintained than from an absolutely pure sort which demands more exact conditions. Yet even here the practice marked of careful mass selection in the field would doubtless result in marked improvement. In general, however, the difficulty of knowing the real nature of the strains which compose a mixed variety makes it unsafe to depend upon the possible virtues of maintaining the most advantageous mixture. Proved sorts of general adaptability offer much greater promise.

CHAPTER XIX

HYBRIDIZATION

The usual purpose of the plant breeder who resorts to hybridization is to secure new and better combinations of characters among the progenies resulting from his crosses. Improvement of a given species may consist merely in the elimination of undesirable characters or of the production of entirely new combinations of characters already existing within the species. In this work the application of the Mendelian principle of segregation and recombination is of the greatest practical value. By concentrating his attention on only a few important characters at a time the breeder can sometimes secure the desired combinations in F_2. But at the same time one who is informed in regard to modern genetical principles will be prepared for possible disappointment in meeting an early realization of his aim. Moreover, he will understand how to select in F_2 and later generations for further testing. He will realize that a specific character difference in his parental forms may be conditioned by more than one factor difference; also that some specific factors display considerable variability in expression; and that linkage, crossing-over, multiple factors and multiple allelomorphs may play a rôle in conditioning or preventing the particular character combination for which he is striving. Furthermore, the ideal sometimes demanded of the breeder involves character complexes which include all the functions of the plant. As has been shown already the comparative difficulty between different cases of this sort depends directly upon the number of chromosomes possessed by the species in question. Finally, demands are sometimes made for the "creation" of characters which are unknown in available phenotypes and for which there is no genotypic representation within the species. In such cases recourse may be had perhaps to species hybridization. But those who are familiar with the results of species hybridization will be prepared for complete disappointment from the first. It is not the motive of these remarks to discourage intending hybridizers, but merely to warn against the anticipation of success in all cases simply because of the generality of Mendelian principles. Hybridization, even of varieties, in order to be generally successful must be intelligently performed and in the long run the experimentalist who is the most thoroughly informed concerning his plants will stand the best chance of securing the improved forms he desires. Each species has its own morphological and physiological peculiarities and general methods will need to be modified to some extent in almost every case.

General Method.—Some results of value have come from promiscuous crossing of varieties and species that appeared to give promise of desirable combinations. Considerable hybridization has been done in this way especially in establishments where large collections are maintained and by seedmen and nurserymen who have undertaken such work as a side issue. Some of the most important results of such work have been the accidental discovery of unforeseen possibilities or limitations in crossing. But many important results have come from carefully planned and executed experiments and the demands of modern agriculture necessitate systematic procedure in the employment of hybridization in plant improvement. Such procedure includes six steps.

1. *Choice of Parents.*—This involves two important matters: first, decision regarding the object to be attained which implies thorough familiarity with existing conditions affecting crop production; second, comparative study of existing varieties or of species that may yield the desired result.

2. *Culture of Parent Plants.*—Hybridization is painstaking work and when carried on extensively it is time-consuming and, therefore, expensive. While it is sometimes necessary to use certain plants, especially shrubs and trees, wherever they happen to be growing, yet it is always advisable to concentrate materials so far as possible and to grow them under protection in the breeding garden or greenhouse. Arrangement of the details of culture should include consideration of the optimum conditions for normal fruitfulness of the intended mother plants. These plants in some cases must be kept under observation and prepared for crossing by reducing vegetative growth and restricting blooming and the setting of fruit.

3. *Protection of Pollen.*—Flowers on intended male parents should be guarded in order to prevent contamination with pollen of other plants.

4. *Castration of Hermaphrodite Flowers.*—This must be accomplished before anthesis and is usually done shortly before the flower opens in order to avoid needless mutilation. But in some close-pollinated species it is necessary to emasculate very young buds. The operation consists of removal of the stamens and can usually be accomplished easily by using a pair of fine pointed forceps or scissors. The castrated flower is then protected with some sort of covering until ready for pollination. In monœcious plants it is necessary to guard the young pistillate flowers which are to be pollinated.

5. *Pollination.*—The transfer of pollen from guarded flowers of the male parent to the prepared flowers of the mother plant should be accomplished before or just at the time the stigma becomes receptive.

In many species this receptive condition of the stigma is evidenced by the secretion of a viscid fluid on the stigmatic surface. It has been thought that premature pollination wrought disastrous effects on the resulting progeny, but evidence is conflicting on this point. Certain it is that in some species, for example, wheat, no untoward results appear from pollination at the time of castration. Plants with small, entomophilous flowers such as clover and alfalfa may be hybridized by enclosing the insects in a cage surrounding the intended mother plant or plants.

6. *Protection of Pollinated Flowers and Developing Seed.*—The most commonly used device is the paper bag tied with a string or lead wire or fastened securely with a copper wire label on which the necessary data are written. In many cases ordinary manila bags of suitable size are entirely satisfactory. Where wasps give trouble by cutting holes the use of bags made of ramie fiber will be found more satisfactory since these bags are made with a glossy surface, but even these will give way under the attack of wasps in course of time. Bags made of thin paper which has been treated with oil or paraffine are best for withstanding insect attacks and for use on delicate plants. Many special devices, such as glass or celluloid cylinders plugged with cotton and firmly supported, are used upon occasion.

Method of Hybridizing Maize.—The technique with this plant is simple, but when working among plants growing in close proximity to each other considerable care is necessary in order to prevent accidental crossing. For protection of the pollen manilla or ramie bags, size No. 8, are tied over the top of the plant just as the staminate inflorescence (tassel) is beginning to appear. The female flowers to be crossed must be covered before any of the stigmas (silks) have protruded through the tip of the ear and become exposed. The most satisfactory covering for this purpose is a strong paper bag about the size of the bags used for the tassels. It has been found economical of time to use bags which are folded so that the center line of the bottom is exposed (*not* "square bottom" bags) and to slit the bottom, fold over once and fasten with a wire clip before covering the ear, with minimum danger of introducing foreign pollen. This device makes it possible to examine the development of the stigmas. After stripping off the leaf subtending the young ear to be covered the bag is pulled down over the ear as far as possible and tied securely to the stem of the plant. When the stigmas are well developed and while they are still fresh the bag containing the tassel is removed from the intended male parent and carried to the plant which is to be pollinated. A hole is torn in one corner of the bag, the top of the bag covering the ear to be pollinated is then opened, the pollen is dusted over the stigmas and the bag enclosing the ear is closed immediately thereafter and securely fastened. Full data concerning the cross are recorded on a wooden label with copper wires which is attached to the ear. If it is desired to make a second pollination the bag containing pollen may be tied to the plant alongside the ear and the same process repeated one or two days later. By close observation of the developing stigmas and pollinating at the most propitious time well developed ears can be secured from a single pollination. Fig. 142 illustrates the principal features above described.

Fig. 142.—Hybridization of maize. Right, plant just previous to anthesis with leaves subtending ears stripped off; left, the same plant with bag enclosing tassel and cylinders covering ears.

Method of Hybridizing Wheat.—This plant has numerous hermaphrodite flowers arranged in a branched spike (Fig. 143, upper left). Each spikelet bears two rows of bracts or glumes (Fig. 143, 2). The lowest two bracts are sterile but each of the next four usually subtends a flower while at the top of the spikelet are two or three rudimentary flowers. Each flower consists of an ovary with two much branched stigmas (Fig. 143, 12, 13) and three stamens which are shown in cross-section in Fig.

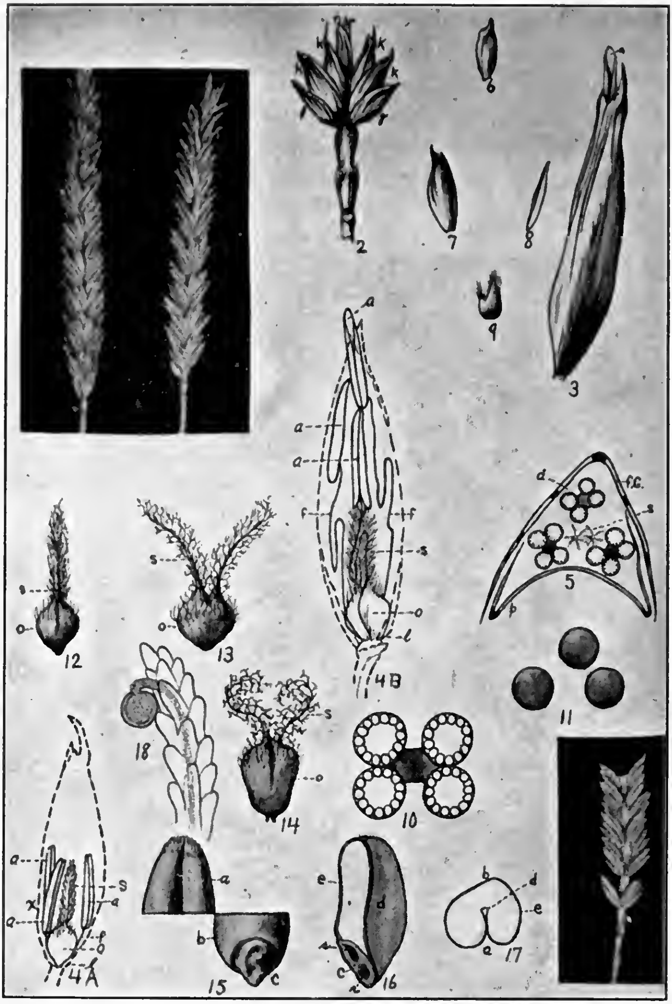


Fig. 143.—Details of wheat inflorescence.

The smaller spike is Fife and at its left is shown a Blue Stem spike. In the lower right-hand corner is a spike from which small late flowers have been removed preparatory to crossing.

At 2, spikelet, natural size, with a few joints of the rachis; *f* and *g* are flowerless glumes; *k*, florets bearing seeds; *r*, rudimentary florets.

3, a single flower closed just after flowering, ×3.

4*A*, longitudinal diagram before flowering, ×2.5; anthers marked *a*; ovary, *o*; stigma, *s*; filament, *f*.

4*B*, diagram of floret just after flowering, ×3, showing how anthers are held within the envelope.

5, transverse diagrammatic section, or floral plan, as is made by cutting across 4*A* at *x*, ×6; *fg*, flowering glume or lemma; *p*, palea; *a*, anthers; *s*, stigma.

6, flowerless glume; 7, flowering glume or lemma; 8, palea; all slightly reduced.

9, lodicule, ×4, shown also at *L* in 4*B*.

10, cross-section of anther, ×26; showing the pollen sacs and the central mass of tissue to which they are attached.

143, 5. The essential organs are completely enclosed by two bracts, the floral glume or lemma, which bears an awn in bearded varieties, and the smaller palea. The lemma and the palea open for a short time during anthesis, but as a rule some pollen is shed upon the stigma before the flower opens. The flowers remain open only a short time in cool climates

Fig. 144.—Hybridizing wheat. Note position of operator and his equipment, consisting of a box containing strips of paper and pins for covering the wheat heads and tags for labeling, a flask of alcohol for sterilizing the hands and instruments, a pair of forceps and a scalpel. Pollinated heads which have been wrapped and labeled are shown at the left.

11, pollen grains, round and smooth, 55 micro-millimeters in diameter.

12, ovary and stigma just prior to flowering; 13, at the time of flowering; and 14, shortly after flowering.

15, 16 and 17, the mature seed; *a*, the ventral side; *b*, the dorsal side; *c*, the germ or chit; *s*, the stem end of the germs; *r*, the root end; *e*, outer layers or bran; *d*, the incurved surface of bran on the ventral side of the seed. The white portions of 16 and 17 are the floury interior consisting of cells containing the gluten and starch from which white flour is made. (*After Hays and Boss, Minn. A. E. S.*)

but a number of natural hybrids in wheat have been reported, especially in sub-tropical countries. In the immature flower the anthers are short and closely packed around the pistil. Just before anthesis the filaments lengthen sufficiently to allow the anthers to protrude when the flower opens. Castration can be accomplished without difficulty by choosing flowers nearly ready to open and removing the later flowers on the upper portion of the spike as shown in Fig. 143, lower right. With a pair of fine forceps the lemma and palea are forced apart and the anthers carefully removed. From a head of the desired male parent anthers just ready to burst are then removed and an anther is placed in each of the castrated flowers (Fig. 144). Two pairs of forceps should be used, one for castrating and the other for pollinating; or, if the same instrument is used, it should be sterilized by dipping in alcohol between each operation. After pollination the spike is bagged or wrapped with several thicknesses of cheesecloth and labeled with a paper string tag. The use of the cloth and light weight tag is to be preferred because most grain plants will support this extra weight without staking (see Fig. 144).

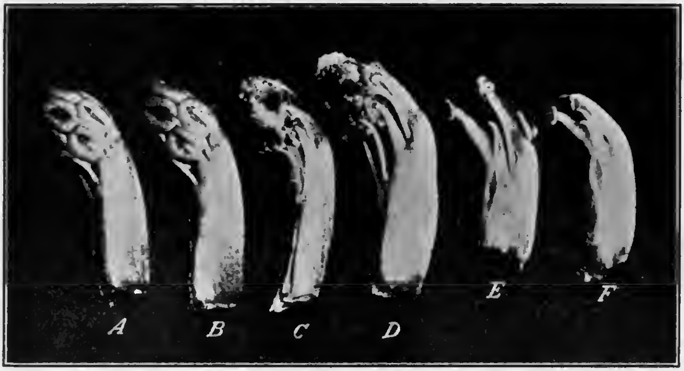


Fig. 145.—Sexual columns of alfalfa flowers (enlarged 7 diameters), showing different stages of development: *A* and *B*, anthers just before dehiscence: *C* and *D*, anthers dehisced; *E* and *F*, after treatment with water jet previous to artificial pollination. (*After Oliver.*)

A Method of Hybridizing Alfalfa.—An ingenious method of crossing this and similar small flowered species has been worked out by Oliver. The essential points are as follows: First, have pollen from male parent at hand ready to be applied to the prepared stigmas. This is accomplished by taking a flower from a raceme of the male parent, securing the banner between the thumb and forefinger and pressing a pin against the suture of the keel, beginning at the base and gradually drawing it upward. When this is done carefully the stamens and pistil come out gently without disturbing the masses of slightly adhesive pollen (see Fig. 145, *C*, *D*). Now with the aid of self-closing forceps sever the sexual organs from the flower and lay aside ready for application to the stigmas of the flowers which are to be depollinated. Second, select a raceme in which the terminal buds are about to expand and cut away all the buds and flowers except three or four near the center of the raceme. The flowers should not be mutilated in any way and should be handled as little as possible. In these flowers the stamens will have dehisced perhaps a day or two previously but the pollen cannot reach the stigma until the flower is tripped. When the tripping is uncontrolled the sexual column (pistil and stamens) flies upward and strikes the banner with considerable force and pollen grains are imbedded on the receptive stigmatic surface. It is necessary therefore to trip the flower gently and to prevent the stigma from touching the banner which is accomplished by inserting a short pin between the sexual column and the banner (see Fig. 146, *C*). Third, depollination is accomplished by the use of a fine jet of water from a dental chip blower; "the jet may be of sufficient force to remove even the empty anthers without injury to the stigma." Then remove the water adhering to the flower with a piece of clean, soft blotting paper. Fourth, apply the waiting pollen to the depollinated stigma and gently remove the pin allowing the stigma to press against the banner (Fig. 146, *F*). "The operation is performed in much less time than it takes to describe it and the operator is rewarded by a fairly high percentage of success-

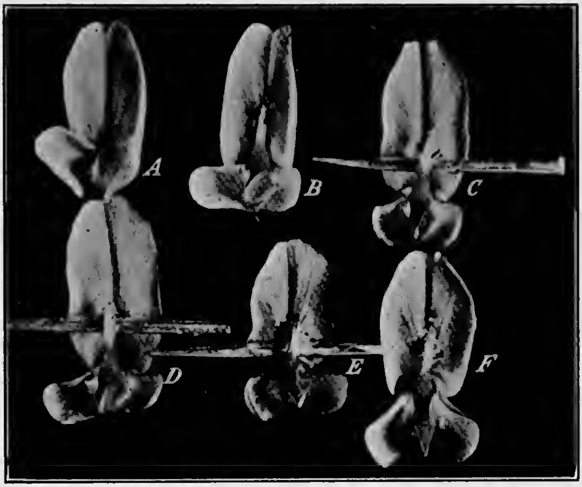


Fig. 146.—Flowers of alfalfa (enlarged 4 diameters) showing method of depollinating and crossing: *A*, untripped and unpollinated; *B*, tripped and self-pollinated; *C*, tripped against a pin to prevent self-pollination and permit depollination; *D*, after depollination with water jet; *E*, after artificial pollination; *F*, after withdrawal of pin the stigma presses against the surface of the banner. (*After Oliver.*)

ful crosses." The various implements mentioned above are shown in Fig. 147.

Some of the Difficulties Attending Hybridization.—(*a*) *Different Seasons of Maturity.*—This is a common obstacle to the crossing of different forms. When it involves merely growing periods of unequal length the difficulty can be overcome easily by planting at such times that the various forms will flower simultaneously. When this is not feasible it becomes necessary to resort to some method of preserving the pollen. It has been found that pollen of certain species will retain vitality for weeks or even months if it is kept very dry. Miss Kellerman reports that the most effective method tried by the Bureau of Plant Industry was as follows: anthers were placed in dried vacuum glass tubes, *e.g.*, tube filled with anthers 1–2 inches, cotton ½ inch, exhausted to about 0.5 mm. pressure in the presence of sulfuric acid, the tube then sealed. As far as practicable the pollen was kept at a temperature of 10°C. A simpler and very useful method is to make a double container by fitting a small vial inside a larger one and partially filling the space between the two with anhydrous calcium chloride or sulfuric acid, filling in the upper portion with absorbent cotton and tightly corking the larger vial. The anthers or pollen grains are placed in the inner vial after it has been thoroughly sterilized and allowed to dry.

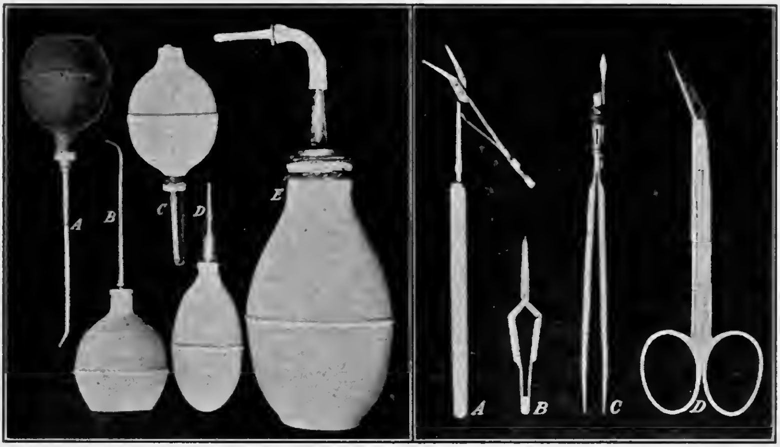


Fig. 147.—Implements used in castrating and depollinating hermaphrodite flowers. Right, self-closing forceps, ordinary forceps, scissors and scalpel. Left, chip blowers and syringes. (*Courtesy U. S. Department of Agriculture.*)

(*b*) *Failure of Fertilization.*—This may be due to many causes ranging from simple morphological maladjustments to complex physiological relations amounting to antagonism. Probably a very frequent cause of unsuccessful crosses is failure of the pollen to germinate. When repeated failures indicate that this may be the difficulty it will be worth while to try the application of a film of water or weak sugar solution to the surface of the stigma before pollination. By the aid of this simple device crosses have been secured between certain species of beans which had been repeatedly attempted without success. In this connection it may be well to give a word of warning. While it is always advisable to ascertain what one's predecessors have accomplished or failed to accomplish, the hybridizer should remember that both plants and local conditions are variable, and what may have been impossible at one place may be possible at another. Or the adoption of simple devices such as the water film on the stigma may be the determining factor. Much perseverance is sometimes necessary.

(*c*) *Susceptibility to Mutilation.*—Some plants are much more sensitive to mutilation than alfalfa. It appears that some are suceptible to merely removing the anthers from the ends of the filaments. In such cases it is necessary to resort to special methods for protecting the stigma from self-pollination. The details will depend upon the structure of the flower and whether it is protandrous or protogynous.

Conditions favorable for hybridization may be summarized as follows: ideal conditions for flowering and fruiting; receptive stigmas; viable pollen; morphological and physiological compatibility between pollen and pistil; resistance of flowers to manipulations.

Species hybridization is generally more apt to be attended by difficulties than is the crossing of varieties, although certain varieties of the same species have been found mutually incompatible in crossing. In general crosses are most successful when made between closely related species. The reason for this is clear when the genotypic differences between distinct species are considered as differences between homologous factors, *i.e.*, factors which condition similar characters as was explained in Chapter XII. It is possible that in very closely related species the factors conditioning similar morphological and physiological characters are themselves similar, if not in a specific sense at least in terms of the whole reaction system. The new combinations of these similar systems of factors which would be formed in F_1 hybrids, would be compatible with the vital functioning of the zygote including the production of viable gametes. In widely separated forms, on the other hand, the reaction systems must be very different, thus causing corresponding reduction in the chances of favorable combinations among the hybrid zygotes. While it is impossible to judge with certainty of the possibilities of species crosses by somatic resemblances and differences, yet the taxonomic relationships of forms it is proposed to hybridize serve as a general guide in forming such estimates. No hybrids between different plant families are known and few authentic cases of intergeneric crosses have been reported. While many first generation crosses between different species are more vigorous than either parent, others are known to be exceedingly weak. Unless repeating crosses which have already been made, the hybridizer of species is exploring the unknown and there is always the possibility that his results may be of interest to science as well as of practical value.

The Svalöf Method of Creating Populations.—Progress in plant improvement by means of hybridization experiments will always be limited by the available supply of experts as well as by facilities and time. Any method, therefore, that enables the breeder to secure desirable new combinations of parental characters without the enormous amount of detail involved in a system of pedigree culture, is worthy of serious consideration. Such a method was devised by Nilsson-Ehle and has been used at Svalöf with success. According to Newman, "two known sorts are crossed and the whole progeny from all second and succeeding generations is sown together *en masse*. The object of this plan is to allow the severe conditions of winter and early spring to either destroy or expose the weaknesses of as many of the more delicate combinations as possible. In the latter case the breeder is given an opportunity to assist nature in her work of elimination by practising a form of mass-selection. While there is thus effected in a very simple manner a gradual weeding out of a great mass of unfit combinations, the progeny of a crossing at the same time gradually assumes the character of an ordinary mixed population, the different combinations becoming automatically constant as time passes. The advantages of working with constant forms will be appreciated by all breeders as will also the fact that through the above arrangement the number of combinations which may arise through the repeated segregation of inconstant forms in each succeeding generation will have increased immensely. . . . While the above system requires a considerable length of time before any definite results can be reached, yet it requires very little work until the time comes to make selections. Numerous crossings of this kind may therefore be carried forward with the regular work and thus provide a constant source of new material."

CHAPTER XX

UTILIZATION OF HYBRIDS IN PLANT BREEDING

Although the special uses to which plant hybrids may be put are very numerous, they fall into two categories, viz., first, the production of new desirable combinations and, second, the production of increased vigor in the first hybrid generation. The first category includes all phases of the usual purpose of crossing plants, which was briefly discussed in the preceding chapter. The new character combinations desired may be exclusively morphological or physiological or, as is more often the case, they may represent combinations of both kinds of characters involving many factors. In the simpler cases involving only a few pairs of independent factors the breeder who is familiar with the Mendelian principles of heredity can easily compute the number of F_2 individuals that he must grow in order to secure the desired combination. Even in the most complex cases knowledge of the principles of genetics will be of practical value in helping the breeder to understand his results in F_1, F_2 and later generations and in guiding his selection of F_2 individuals for further testing. These principles are discussed in Chapters V to X. It is the purpose of this chapter to present some specific results of the increased vigor so commonly observed in F_1 hybrids. This increased vigor, or *heterosis*, as it has been termed by Shull, may manifest itself in greater size, more rapid growth, larger productivity, greater hardiness, drouth resistance, etc. The theoretical explanations of heterosis have been discussed in Chapter XII. In the present chapter we shall consider only the utilization of the principle that hybridization of closely related varieties or species usually results in heterosis. As the methods used with plants grown from seed differ from those which can be used with vegetatively propagated plants, the two groups will be considered separately.

Increased Production in F_1 Maize Hybrids.—This phase of corn breeding has come into considerable prominence in recent years. Although it has not yet become an important factor in corn growing, it presents interesting and important possibilities in the way of increased production. The most significant results have been obtained by growing F_1 hybrids between species, sub-species, commercial varieties, local strains of commercial varieties and closely inbred strains or biotypes. The earliest recorded experiments on increased production are stated by

Collins to be those of Beal (Michigan, 1878–1882), Ingersoll (Indiana, 1881), Sanborn (Maine, 1889), and of Morrow and Gardner (Illinois, 1892). All of these crosses were made between commercial varieties and in each case the hybrids outyielded one or both parents. Then came the work of Shull and of East (1908) with inbred strains and the crosses between them, both investigators obtaining an increase in yield in the hybrids over that of the original stock. Following this the United States Department of Agriculture conducted experiments on an increasingly extensive scale and included work with the most distinct types as well as commercial varieties and inbred strains. More recently various experiment stations have conducted similar investigations.

Crossing inbred strains or biotypes produces the most striking results because the rate of increase in vigor in the F_1 hybrids over the inbred strains is enormous (as much as 250 per cent. over the average of the parents). Of course it is much greater in some cases than in others because of the inherent differences between different biotypes. East worked with biotypes of four different varieties and secured an average increase of 73 per cent. in all crosses. The data on inbreeding the Leaming dent variety are summarized by East and Hayes in Table LI. It will be noted that two of the strains were not grown as second inbred generations

TABLE LI.—EFFECT OF INBREEDING IN STRAINS OF LEAMING DENT MAIZE

Yield in bushels of shelled corn per acre and years in which grown (*After East and Hayes*)

Parent variety	Strain number	Generations inbred					
		1	2	3	4	5	6
88.0 (1905)	6	59.1 (1906)	95.2 (1908)	57.9 (1909)	80.0 (1910)	27.7 (1911)	
	7	60.9 (1906)	59.3 (1907)	46.0 (1908)	63.2 (1910)	25.4 (1911)	
				59.7 (1909)	68.1 (1910)	41.3 (1911)	
	9	42.3 (1906)	51.7 (1908)	35.4 (1909)	47.7 (1910)	26.0 (1911)	
	12	38.1 (1906)	32.8 (1907)	46.2 (1908)	23.3 (1909)	16.5 (1910)	2.0 (1911)
					28.7 (1909)	9.5 (1910)	2.0 (1911)

until 1908 and in that year "the general environmental conditions were much above normal. For opposite reasons, poor soil and badly distributed rainfall, the yields of 1909 are somewhat too low and the yields of 1911 are very much too low." With these facts in mind an examination of the table shows that the strains became more and more differentiated as to yield as inbreeding progressed. "The first strain, No. 6, is a remarkably good variety of corn even after five generations of inbreeding. It yielded 80 bushels per acre in 1910. . . . In the field, even in 1911, the plants were uniformly vigorous and healthy and were especially remarkable for their low variability. The poorest strain, No. 12, is partially sterile, never fills out at the tip of the ear and can hardly exist alone. . . . When two of these inbred strains are again crossed, the F_1 generation shows an immediate return to normal vigor. The plants are earlier and taller, and there is a greater total amount of dry matter per plant. For example, in 1911 the average height of all the strains of inbred Leaming dent was 84 inches while the average height of the 16 hybrid combinations was 111 inches and the height of the shortest hybrid combination was 1 foot greater than that of the tallest inbred strain." In general it seems that the combinations into which strain No. 7 was introduced were the best while those in which the poorest strain, No. 12, was used were the poorest. However, a cross between these two strains in 1911 yielded 60.2 bushels per acre. The F_2 generation from a number of the crosses was grown and in every case there was a decided falling off in production. This would be expected as a matter of course under conditions of random mating in F_1 inasmuch as some homozygous combinations would be formed among the F_2 zygotes. Fig. 148 shows types of ears and comparative yields in strain No. 9 after 4 generations of inbreeding, strain No. 12 in the fifth inbred generation, and the F_1 and F_2 hybrids, all grown in 1910.

FIG. 148.—Inbred strains of Leaming dent corn compared with F_1 and F_2 hybrid generations. The yields per acre were as follows: No. 9 (at the left) 47.7 bu.; No. 12, 16.6 bu.; (12 × 9) F_1, 117.5 bu.; (12 × 9) F_2, 91.5 bu. (*After East and Hayes.*)

Theoretically the maintenance of superior near-homozygous strains and annual crossing of the best for production of F_1 seed for sale to growers is a practicable method of corn breeding. This plan was first suggested by Shull. It is certainly a desirable method not only because of the high degree of heterozygosity produced on crossing such strains, but because continuous inbreeding has a similar effect to growing the plants under adverse conditions. It tends to eliminate all but the strongest individuals and is thus an effective method of selection. However, as a more practicable method, East suggested that combinations of the various commercial varieties be tested until the most profitable combination is found. There has been considerable investigation of both methods, but it is impossible at present to say which will be used more extensively. One of the most valuable features of this method of inbreeding followed by crossing of superior strains, as compared with ordinary ear-to-row selection, is the saving in time. For example, in the production of high-yielding strains of corn which differ in chemical composition of the grains, Emerson and East point out that ear-to-row selection from open pollinated plants will, if carried on long enough, produce a strain of the desired type. It will be sufficiently homozygous to insure comparative constancy as regards oil, protein or starch content. At the same time a sufficient number of factors for other minor characters will be heterozygous to insure a fairly vigorous strain. But, on the other hand, by self-pollination, together with the same sort of selection, several practically homozygous strains of the desired type, high oil for instance, "could almost surely have been produced in much less time." These strains would doubtless have been unlike for many other characters, so that if degree of vigor is dependent upon degree of heterozygosity, the crosses between them would doubtless have been abundantly vigorous. Or if physiological vigor is conditioned by specific factors, then crosses between some of the selected strains would doubtless have effected the most favorable combinations for maximum vigor. In either case the result is the same. "While a few years' time may not be an important consideration where the character in question can be determined at sight, or by mere weighing or measuring, in breeding work requiring costly chemical analysis it is extremely important that the desired results be obtained in as few years and, therefore, with as few analyses as possible."

Method of Comparing Yields.—The importance of accuracy and fairness in comparing the yields of F_1 hybrids with their parents has been determined by Collins. We give his conclusions verbatim:

"So large a proportion of first-generation maize hybrids have been found to give increased yields and the increase is frequently of such magnitude that the utilization of this factor of productiveness becomes a practical question. It is, therefore, highly desirable to understand the reasons why some crosses give favorable results and others give little or no increase over the yield of the parents. A necessary step in this direction is to develop a reliable method of measuring the effect of crossing, apart from other factors that influence yield.

"The development of satisfactory methods of comparing the yield of first-generation hybrids with that of their parents has been retarded by (1) a failure to fully appreciate the importance of individual diversity in hybrids, (2) the abnormal behavior of self-pollinated maize plants, and (3) the difficulty of securing for comparison hybrids and parents with identical ancestry. It is believed that the method here described avoids these difficulties and affords more accurate means of comparing first-generation maize hybrids with their parents.

"The method is illustrated by an experiment in crossing two varieties of sweet corn in which it was found that the progeny from one hybrid ear yielded nearly double that of the other hybrid ear involved in the experiment. To have taken either ear alone would have led to entirely erroneous conclusions regarding the increase secured as a result of crossing. The increase in yield due to crossing as measured by the method here proposed was 31 per cent."

Collins describes his method as follows:

"To compare the behavior of two varieties, which may be called A and B, with that of a hybrid between them, two plants were selected in each variety, A_1 and A_2 in the one variety and B_1 and B_2 in the other variety. The following hand pollinations were made: $A_1 \times A_2$, $A_2 \times B_1$, $B_1 \times B_2$, and $B_2 \times A_1$. The result is two hybrid ears and one cross-pollinated ear of each variety. It is believed that the mean yield produced by seed from the two pure seed ears gives a fair measure of the effects of hybridization. By making two hybrids involving all the plants used in producing the pure seed ears individual differences that affect the yielding power of the pure seed ears are similarly represented in the hybrids. Thus, in both the parents and the hybrids the average yield represents the mean yielding power of the four parent plants, the only difference being the way in which the individuals are combined.

"To secure the most accurate comparison of the yield of the four ears, one seed from each of the ears was planted in each hill. The different kinds were identified by their relative position in the hill. To place the seeds accurately, a board 4 inches square was provided with a small pointed peg 2 inches long at each corner. These pegs were forced into the soil at each hill, making four holes, one for each of the four kinds, only one seed being planted in a hole. The board was always placed with two sides of the board parallel to the row. It was necessary to exercise extreme care in dropping the seeds to avoid changing the position of the kinds. The best way to obviate mistakes of this kind is to make all the holes of a row in advance and to go down the row with one kind of seed at a time.

"At harvest time the seed produced by each plant was weighed and recorded separately. All hills that lacked one or more plants were excluded and the comparison confined to hills in which all four kinds were represented. The method of handling the yields was to determine the mean yield of the four kinds in each hill and to state the yield of each of the four plants as a percentage of the mean of the hill in which it grew. The percentage standing of each kind in all the hills was then averaged to secure the final expression of the relative behavior of the four kinds.

"This method of comparison is similar to the ingenious plan originated by C. H. Kyle, for use in ear-to-row breeding. Kyle's method is to plant each of the ears to be tested in a separate row and in each hill to plant one seed of a standard, or check, ear with which all ears are compared. Since comparative and not absolute yields are desired in the study of hybrids and with only four kinds to compare, the introduction of a check in the present experiment would have increased the space occupied by the experiment without lessening the experimental error."

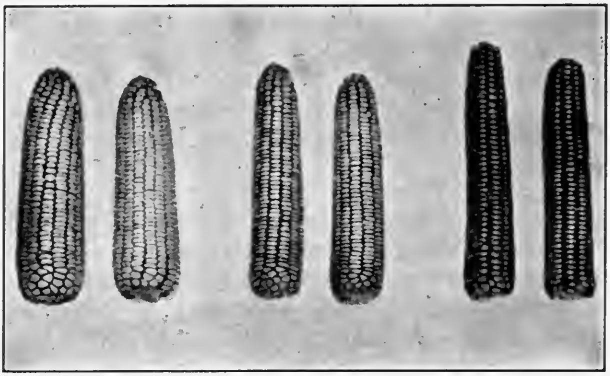


Fig. 149.—Parents and F_1 hybrid between two sub-species of *Zea mays*: Hall's Tyler dent (left), Brewer's flint (right) and hybrid (center). The hybrid yielded 9 per cent. more shelled corn than the dent and 20 per cent. more than the flint and proved the most productive of all varieties and crosses in the 1913 test. (*After Hayes, Conn. A. E. S.*)

Crossing Species, Sub-species, Varieties and Local Strains.—Many experiments have been made to test the increase in productivity of F_1 hybrids between more or less closely related forms of maize. As it is impossible to review them all, we give as an illustration Collins' summary of the results of 16 crosses made in 1908 between corns of diverse types and from widely separated localities. The classification indicated by Collins' descriptions are as follows: *Zea mays indentata* (starchy or dent varieties)—Maryland, Kansas dent, Brownsville, Chihuahua, Mexican dent, Xupha (semi-starch); *Zea mays amylacea* (floury variety)—Tuscarora; *Zea mays everta* (pop)—Cinquantino, Algerian, Tom Thumb; *Zea mays indurata* (flint)—Guatemala red, Salvador Black; *Zea hirta* Bonafous—Hairy Mexican, Huamamantla, Arribeño; Unclassified—Hopi, Chinese (waxy endosperm), Quezaltenango Black, Quarentano. The yields of the 16 crosses and of their parents are given in Table LII.

TABLE LII.—YIELDS OF 16 MAIZE CROSSES COMPARED WITH PARENTAL YIELDS. (*After Collins.*)

Name of hybrid	Yield of female parent, pounds	Yield of male parent, pound	Average yield of parents, pound	Yield of hybrid, pounds	Percentage of increase of hybrid over average of parents, per cent.
Ah_3, Maryland dent by Hopi	1.19	0.74	0.965	1.25	29
Ah_4, Tuscarora by Cinquantino	0.53	0.24	0.385	0.75	95
Dh_1, Kansas dent by Chinese	0.99	0.39	0.690	1.09	58
Dh_2, Chinese by Chihuahua	0.39	0.69	0.540	0.95	76
Dh_3, Hopi by Chinese	0.74	0.39	0.565	1.28	126
Dh_4, Chinese by Xupha	0.39	0.63	0.510	0.54	6
Dh_6, Brownsville by Chinese	0.77	0.39	0.580	1.16	100
Eh_1, Hopi by Algerian pop	0.74	0.34	0.540	0.91	69
Gh_2, Tom Thumb by Quezaltenango black	0.10	0.10	0.100	0.42	(*a*)
Kh_{31}, Brownsville by Guatemala red	0.77	0.31	0.540	0.49	−9
Kh_{62}, Guatemala red by Salvador black	0.31	0.27	0.290	0.33	14
Mh_{13}, Quarentano by Brownsville	0.27	0.77	0.520	0.48	−8
Mh_{15}, Huamamantla by Hairy Mexican	0.40	0.18	0.290	0.31	7
Mh_{16}, Arribeño by Hairy Mexican	0.39	0.18	0.285	0.47	65
Mh_{17}, Hairy Mexican by Chinese	0.18	0.39	0.285	0.61	114
Mh_{25}, Mexican dent by Tom Thumb	0.52	0.10	0.310	0.54	(*a*)
Average percentage of increase of hybrids over average parents	.....	.....	......	.....	53

(*a*) Where the yield of either parent fell as low as 0.10 pound per plant the percentage of increase of the hybrid is omitted. In dealing with these small quantities it is believed that percentages would be misleading.

The superior qualities of first-generation hybrids in maize as set forth by Collins may be summarized as follows: (1) Increased yield. (2) Uniformity equal to that of the parents. (3) Quality intermediate between parents (but Hayes' data indicate complete dominance of low protein over high protein). (4) Increased immunity from disease. (5) Extension of the industry into new territory. Especially strong evidence for this is found in several of the crosses between diverse types. "Almost without regard to the nature of the parents the hybrids remained dark green and vigorous when nearly all the pure strains were giving evidence of the lack of moisture by their curved leaves and yellow color." (6) Less localization of highly bred strains. The importance of local adjustment in highly bred strains is the chief reason for the disappointment which sweet corn growers experience when they purchase carefully selected strains from other localities. "First-generation hybrids are to a great extent independent of this delicate adjustment to local conditions." (7) Increased utilization of the work of experienced breeders. (8) Stimulus to the work of improvement through the possibility of protecting new productions.

More recently Jones and Hayes have made extensive experiments in crossing commercial varieties of corn upon which they report as follows:

> "Fifty first generation corn crosses have been compared with their parents. Eighty-eight per cent. yielded more than the average and of these 66 per cent. yielded more than either parent.
>
> "In time of ripening the first generation crosses were on the average intermediate when compared with their parents. Thus in crosses between varieties differing widely in time of ripening the first generation crosses not only yielded more than the late parent but matured considerably earlier. This increase in the rate of growth is considered to be fully as important under Connecticut conditions as any increase in yield.
>
> "The highest yielding parents gave the highest yielding crosses as would be expected, but a rather unexpected result was obtained in that there was apparently no relation between the yield of the parents and the increase in the yield of the cross. High average yielding parents gave as large increases, when stated in per cent., as low yielding parents.
>
> "There was a tendency for the crosses whose parents differed in their ability to yield to give the greatest increase. This is also shown by the fact that the dent x flint crosses gave greater increases in growth than the flint x flint crosses.
>
> "These facts bear out the assumption that hybrid vigor is not the result of an indefinite physiological stimulation but merely the result of the bringing together of greatest number of favorable growth factors. Crosses between varieties of diverse type therefore possess a greater total number of favorable growth factors than crosses between similar varieties and hence give larger increases when crossed."

The immediate effect of crossing upon size of the grain and hence on yield should not be confused with the increased production of hybrid plants. There is a popular belief that by planting two varieties in alternate rows the yield will be increased. That this idea is supported by scientific evidence was indicated by the earlier work of Correns, Carrier, and Roberts, but it remained for Collins and Kempton to secure the proof of this important fact. These investigators used the ingenious method of pollinating various white seeded varieties with a mixture of their own pollen and pollen from some variety having colored seeds. By taking advantage of the phenomenon of xenia they were able to make direct comparison of the selfed and the hybrid grains from the same ears. The possible invalidity of their results due to more rapid development of hybrid grains and consequent repression of selfed grains was removed through the fortunate discovery of an ear that had been twice pollinated, first with its own pollen and a week later with pollen from a colored variety. "All the white kernels were on the lower portion of the ear, all the colored were on the upper portion. Obviously the hybrid seed could have no advantage in this case. The ear produced 212 white, or pure, seeds and 161 that were yellow, or hybrid. The average weight of the pure seed was 283 gm. per 1000 kernels. The average weight of the hybrid seed was 292.5 gm. per 1000, a difference of 9.5 ± 1.06 gm., or 3.4 per cent." In the experiment itself eleven ears, involving five different varieties, were crossed, giving a total of 1,658 hybrid seeds to be compared with 3,513 selfed or pure seeds. In every instance the size of the seed was materially increased by the foreign pollen, the increase ranging from 2.8 to 21.1 per cent. The fact that the pericarp of the mother plant is not strictly a part of the seed but is of purely maternal origin might seem difficult to harmonize with the results, but Collins and Kempton point out that the necessary increase in size of the pericarp would be comparatively slight and to seek any explanation may be superfluous. The practical value of this evidence is great. As the authors state, "the results afford additional reason for the use of first generation hybrid seed; but even where hybrid seed is not to be used, the planting of two varieties in alternate rows may be found to increase the yields sufficiently to warrant the additional trouble." And further, "as the increased size is evidently a manifestation of vigor, it may be considered as a factor of adaptation, like the vigor of the first-generation hybrid plants. It would seem especially desirable to take advantage of this method of increasing yield in regions which do not produce their own seed corn."

Centralized Seed Corn Production.—Carefully selected strains of maize are liable to prove disappointing when grown under conditions different from those obtaining at the locations where they are produced. But the work of intensive selection requires considerable skill and experience and the farmer can seldom attend to it properly. He should obtain his selected seed corn from a local breeder if possible. The fact that F_1 hybrids in maize are comparatively resistant to local and seasonal conditions which prove detrimental to pure strains indicates that such hybrids may be produced at central points in quite a large territory. When it is known which combination of varieties, or of pure strains of a single variety, is best adapted in certain localities, pure seed of these varieties or strains may be maintained and the crosses made under expert supervision at a central seed farm. On the other hand, a farmer who wishes to produce his own hybrid seed need not hesitate on account of increased cost of production. Collins has shown that even though the cost of raising hybrid seed be double that of ordinary seed, yet "where increases ranging from 5 to 50 per cent. may be expected there are few farm operations that yield such large returns."

A Method of Producing Hybrid Corn Seed.—A grower intending to produce his own hybrid seed each year might do well by beginning with a series of trials with varieties in alternate rows. After determining which varieties are best adapted to the local conditions and give the best results when crossed he will be ready to adopt a simple system of hybrid seed production somewhat like the following. These directions have been sent out by the United States Department of Agriculture to coöperative experimenters. Various other plans could be devised.

Experiments as outlined below involve the use of two varieties and two separate plots. Varieties may be designated as No. 1 and No. 2, the plots as *A* and *B*. The plots should be sufficiently separated to prevent cross-pollination between them.

It should be kept in mind that the increased yield can be expected only for the one year immediately following that in which the cross is made.

Plot *A* is planted with alternate rows of No. 1 and No. 2. The rows planted with No. 2 are to have all plants detasseled. The crop of No. 1 and No. 2 is to be saved separately.

Plot *B* is planted entirely with variety No. 2 and has alternate rows detasseled. The crop from the tasseled and detasseled rows is to be saved separately.

At harvesting there will be the following lots of seed:

1. Plot *A*. Variety No. 1, field-pollinated.
2. Plot *A*. Hybrid between No. 1 and No. 2.
3. Plot *B*. Variety No. 2, field-pollinated.
4. Plot *B*. Variety No. 2, cross-pollinated.

The yields in the year the cross is made should show the comparative value of the two varieties and the effect, if any, of detasseling on the immediate yield.

A comparison of the yield from these four lots of seed the following year should show the yield of the first-generation hybrid as compared with the pure varieties and to what extent the increase, if any, is due to the elimination of self-pollinated seed.

If plot *B* cannot be provided, seed of variety No. 2 should be held for planting the following year in comparison with variety No. 1 and the hybrid seed.

Application in Other Annual Crop Plants.—The increased vigor due to heterozygosis has not yet been utilized in a practical way in annual crops other than corn. Melons and other cucurbits are monœcious, easily crossed under proper conditions and within a single species, and large quantities of seed are produced. Very little is known concerning the value of F_1 hybrids between varieties as compared with parents, but Hayes and Jones report preliminary experiments which indicate that first generation cucumber crosses may frequently be expected to exceed the higher yielding parent in yield. Only one out of four different crosses failed to exceed the average of the parents in any character by an appreciable amount.

In tomato growing Wellington has shown that crossed seed is worth its production as based on the increased value of a single crop without reference to origin of new varieties. He states that, while desirable results have been obtained by crossing plants indiscriminately, "better results would undoubtedly have been obtained if high-yielding mothers had been selected for one or two generations previous to the first crossing." Tomatoes are normally self-fertilized and, the high-yielding strains or pure lines having been isolated, they can be maintained and the crosses may be repeated from time to time. This is a very important consideration for the grower who wishes to put the same grade of product on the market from year to year. "As tomato seed remains fertile from 3 to 7 years, a grower does not need to make his crosses oftener than once in 3 years. The seedsman, as well as the farmer, can profitably raise F_1 generation seed, provided a guarantee is not given for more than one generation, for the buyer, to maintain his quality of product, will have to purchase seed every year." Wellington thinks the best results with tomatoes can be obtained by keeping within a species and crossing distinct varieties or strains. Dominant characters, that will certainly appear in the fruits of F_1 plants if present in either parent are rough or irregular shape, dark red color as contrasted with pink or yellow and pink as contrasted with yellow. Size and season of ripening in F_1 will be intermediate between the parental characters.

Jones and Hayes report results of similar experiments which corroborate Wellington's conclusions. Of two different crosses one (Stone x Dwarf Champion) gave an appreciable increase in both size and number of fruits and the total yield was thereby increased. It even exceeded the better parent by 15 per cent. Moreover, the increase above the latter parent was uniform throughout the four years of the test. The other cross (Lorillard x Best of All) exceeded slightly the better parent in average weight of fruit but it did not excel in total yield. "These results show that not all combinations of tomato varieties give the vigor usually derived from crossing, but when a desirable combination is found it can be counted on to give the increase in yield every time the cross is made. Vigor due to crossing as measured by increased yield was not appreciably greater in crosses between artificially selfed strains than in crosses between ordinary commercial varieties. These results are in agreement with the fact that the tomato is naturally almost completely self-fertilized. The cross of Stone x Dwarf Champion which gave a significant increase in yield also showed a hastening of the time of production. It not only gave a 15 per cent. larger yield than the later parental variety but was earlier in its time of production than the earlier parent. Hence its value to market gardeners was increased."

Similarly, in tobacco, Selby and Houser claim that the culture of first-generation hybrids will prove both profitable and practicable. Since the added cost of producing hybrid seed should not exceed 50 cents per acre and the crossing need not be repeated oftener than once in 3 years, the financial consideration is negligible. In regard to uniformity of crop they find that F_1 hybrids between pure varieties or fixed hybrids show no essential difference in uniformity from the parent varieties and for commercial purposes only such parents should be used. As for yield their results in 1909 showed the average of the hybrids to be about 185 pounds more per acre than that of their parents. The maximum increase obtained was 492 pounds per acre. By selecting seed from the highest-yielding F_2 plants it is possible to produce even higher yields in F_3 and F_4. But such high-yielding selections are not fixed and under conditions of commercial culture the yield and uniformity would undoubtedly decrease rapidly. It appears that the growing of F_1 hybrids offers the one chance of commercial production of the highest possible yields combined with uniformity in size and shape of leaf. The matter of quality of cured leaf is more difficult of solution since this is a complex character and is easily affected by environmental conditions. Until further investigations have been made it seems that the only safe procedure is to choose as parents only varieties or strains that produce leaf of high quality.

Application in Vegetatively Propagated Plants.—In this class of plants the stimulus due to heterozygosis has been extensively utilized, but this has been the result of the method of propagation rather than the conscious use of the principle. In potatoes and strawberries, for example, the commercial varieties are all hybrids. The crosses having been made, the best plant of the first generation became the source of a new variety. There are many opportunities for further application of this principle in the bush and tree fruits, not only for vigor but for excellence of quality as well; also in asparagus, rhubarb, hops, pineapples, sugar cane, sweet potato and many ornamental plants.

It is thought by some horticulturists that the greatest possible improvement in fruits can only be secured by preparing for hybridization by several generations of inbreeding. Thus Jones, proceeding on the assumption that increase of vigor in hybrids is due to heterozygosis, recommends the general adoption of inbreeding in order to secure homozygous strains which can then be utilized in the production of the most vigorous F_1 hybrids. But it is to be remembered that only a portion of the homozygous strains could be expected to produce superior F_1 hybrids. It is, therefore, a serious question whether this method would be as economical in the long run as the crossing of existing varieties.

The use of F_1 hybrids as rootstocks for vines, tree fruits and nuts is of recognized importance. The Royal and Paradox Walnuts, which were named by Burbank from specimens which he produced, furnish a striking illustration. The Royal type of hybrid is produced by crossing the Black Walnut of eastern states (*Juglans nigra*) with the California Black Walnut (*J. californica*); while the Paradox type comes from crossing the walnut of commerce (*J. regia*) with either of the above named black walnuts. Hybrid seedlings commonly appear in the seed beds planted with seed from trees standing near trees of other species. As they are easily distinguished by their larger size while still quite small, all that the nurseryman has to do is to select the hybrids for budding or grafting.

Sterility or partial sterility is frequently associated with increased vigor in first-generation hybrids between species. The large flowers and luxuriant growth of some of the sterile tobacco hybrids render them promising subjects for use as ornamentals. Partial sterility, when manifested by a lessened production of seed, may not be accompanied by any decrease in yield of fruits. In such cases therefore it is a positive advantage if the plant can be propagated vegetatively.

Rapid-growing timber and ornamental trees of a number of different species have been produced by crossing distinct forms. Henry mentions the following valuable trees which, on account of their vigor, botanical characters and non-occurrence in the wild state, are presumably first-generation hybrids: black Italian poplar, London plane, Huntingdon elm, cricket-bat willow and the common lime (*Tilia vulgaris*). According to Henry the pioneer work on hybridization of trees was done by Klotzsch at Berlin in 1845. He crossed two species each of pine, oak, elm and alder. He "claimed that by hybridization, both the rapidity of growth and the durability of timber of forest trees could be augmented considerably; but no further experiments were made, and his pioneer work fell into oblivion." The art of breeding trees was renewed by Burbank's work with the walnuts about 1890. Henry reports results with F_1 hybrids in Populus, Fraxinus, Alnus, Ulmus and Larix. He points out that one of his most vigorous hybrids (*Populus generosa*) was "derived from two parents so little related that they are placed in two distinct sections of the genus." At the same time, "a cross between two races of the common alder shows considerable vigor, though the parents are so closely allied that they can only be distinguished by the most trivial characters." Thus it appears that prediction as to the outcome of species crosses in trees is quite as impossible as in other classes of plants. There is great need for further experimentation. In planting wind-pollinated species provision can easily be made for natural hybridization by mixing groups of different species. It has been found that the quality of the timber in rapid growing F_1 hybrids is equal or superior to that of the parents.

Increased resistance of F_1 hybrid plants to insect pests and diseases is doubtless often merely another manifestation of their increased vigor. But in this connection it is to be remembered that disease resistance is generally a heritable character, so that in a particular instance its appearance in F_1 will depend on the factorial composition of the parents and the relation of the factors in inheritance.

CHAPTER XXI

MUTATIONS IN PLANT BREEDING

Discontinuous heritable variations have appeared very frequently in cultivated plants under conditions such that they could not be attributed to hybridization. The selection of these variations has produced new varieties in the same way that the early color varieties of the sweet pea arose. By means of breeding experiments many such variations have been proved to follow the Mendelian principles of inheritance. The general conformity of varietal crosses with the Mendelian principles is sufficient reason for asserting that the vast majority of cultivated varieties arise either directly or indirectly through factor mutations. A few have originated through chromosome aberrations, but, so far as is known, none which are of importance to agriculture. It is especially clear that in self-fertilized species the production of new varieties from single plant selections is made possible by the occurrence of factor mutations. The successes of Le Couteur, Shirreff and Hallet, and the achievements of Vilmorin, Nilsson, Hays and Johannsen with individual plant selections find their explanation in the existence of genetically diverse forms within the species or varieties with which they worked. These pure lines must have originated through changes in specific factors. Similarly with the genotypes of maize and other cross-fertilized species, although new combinations of factors are continually arising through natural intercrossing, yet entirely new factors can arise only by means of changes in existing factors. These factor mutations do not necessarily induce profound somatic changes, and slight morphological variations may hardly be distinguished from modifications due to environment. When physiological characters alone are affected, as is sometimes the case, the most careful tests of many individuals may be required to discover a desirable mutation. But once a mutation arises, the normal range of fluctuation in the character or characters affected is different from that of the parent form, and new material has been provided for man's selection if he desires to use it and can isolate it. When these facts are realized the fundamental importance of mutations to breeding will be appreciated.

Bud mutations, especially when strikingly different from the parental type, have long been known. Bailey states that Carriére in 1856 enumerated over 150 bud-varieties or sports of commercial importance in France and he estimated that no fewer than 300 named horticultural varieties grown in this country in 1895 had a similar origin. There is no reason to suppose the number has decreased and it is probably larger. There is good evidence (see Chapter XIV) to show that bud sports arise through factor mutations and that they occur in as great diversity as do seed sports. Sometimes striking morphological or substantive changes are produced but probably the somatic effect is often slight and hence not easily detected (Chapter XXIII).

Mutations in Crop Plants.—Johannsen has reported two mutations in his pure lines of beans. The careful statistical analysis of his successive pure line families revealed the first mutant in 1903 and Johannsen thinks it appeared as a bud sport. It was characterized by its large size and relatively narrow shape. As it was constant from the first it must have originated in homozygous condition. The second mutant bore seeds which were relatively broad in shape. It could be traced back to 1907 when it existed in heterozygous condition. Later it was obtained in pure line. Very recently mutations of great commercial value occurred in the Florida Velvet Bean, *Stizolobium deeringianum*. The old variety was limited to Florida and the Gulf Coast on account of lateness. About 1,000,000 acres were grown in 1915. We are informed by Piper that early varieties originated by mutation at at least three different places, the first in 1906. These resulted in the crop being adapted to the entire cotton belt and in a very rapid increase in acreage since 1915. In 1916 about 2,650,000 acres were grown and in 1917, about 6,000,000 acres.

Hayes describes a number of mutations in tobacco which is normally self-fertilized. The first was found in a homozygous strain of the Connecticut Cuban shade variety of commercial tobacco (*N. tabacum*). This strain bears from 14 to 25 leaves per plant, the mean number for 1910 and again for 1914 being 19.9 leaves. In 1912 the Windsor Tobacco Growers Corporation grew about 100 acres of this strain and during the clearing of the field three plants were found that had not yet bloomed and which bore a number of uncut leaves. One of these was transplanted to the greenhouse of the Connecticut Agricultural Experiment Station. It produced 72 leaves on the main stem and blossomed about January first. All the seedlings grown from this plant came true to the new type which differs from the parent strain "in having leaves of a somewhat lighter green shade, in a partial absence of basal suckers, and in a practically indeterminate growth" (see Fig. 150). The quality of leaf seems as good as the Cuban and an increased yield per acre of approximately 90 per cent. has been obtained, but it is yet too soon to know how satisfactorily the new variety will conform to trade requirements. Several similar mutants have been found in plantations of the Connecticut Havana variety. This variety has been grown in Connecticut for over 50 years and is uniform in habit of growth.

On one of the farms the same mutation has recurred several times. Hayes believes that these mutations cannot be explained as the result of accidental crosses. For in the large series of crosses that have been made in the Connecticut station in no case have new forms exhibiting this tendency to indeterminate growth been obtained.

FIG. 150.—The Stewart Cuban variety of tobacco, a very promising mutation. Plants from seed sown under glass in December and transplanted to the open in May were twelve to fourteen feet tall in September and had produced eighty leaves per plant. (*From the Journal of Heredity.*)

Nilsson-Ehle discovered that in pure lines of oats occasional grains appear that are aberrant either in color or in morphological characters. The variations tested by him either bred true at once or after one or two generations practically all of the progeny would breed true for the new characters. Surface and Zinn consider this sufficient evidence to make it "almost certain that similarly inherited variations may occur in respect to physiological characters such as yield." That they were justified in making this inference is shown by the success of their experiments on pure line selections for yield.

Other self-fertilized crop plants in which mutations have been reported are barley, wheat, tomato and potato.

In maize the sudden appearance of new characters in established varieties or strains has been reported by a number of investigators. The remarkable diversity between inbred strains as discovered by Shull and by East indicates the extent to which germinal variations occur in this plant. Each author obtained one strain which was so nearly sterile as to be in danger of complete extinction while other strains appeared to be capable of maintaining fairly good annual yields indefinitely. Abundant evidence of the occurrence of factor mutations in maize is also found in the numerous pairs of contrasted characters which are inherited in Mendelian fashion. Besides those referred to in earlier chapters we may mention multiple stems (suckers) as dominant over single stems (no suckers), normal stature (tall) as dominant (usually) over dwarf stature, normal green leaves as dominant to striped leaves, presence and absence of aerial roots, hairy and glabrous stems, branched and unbranched tassel, normal ear and branched ear, normal anthers and fasciated anthers, presence of normal reproductive organs and absence of the same (barrenness). Most of these allelomorphs behave as unit characters. Various quantitative differences such as stature, ear-length and number of rows to the ear are either conditioned by several pairs of factors or by single pairs of factors which are subject to a wide range of variability in expression. Constitutional vigor and productivity are doubtless conditioned by the interaction of very many factors and a mutation in a single one would alter the end result. In short the inherent individuality of corn plants, which makes possible the successful application of selection methods, must be referred to factor mutations.

Sugar beet improvement, particularly increase in sugar content of the roots, depends directly upon the occurrence and selection of mutations, according to Pritchard. As a result of statistical investigations of variation, correlation, inheritance and selection in the sugar beet, he concludes that although sugar beet improvement has been accomplished, continuous selection is not necessarily the determining factor in attaining the present high sugar content of the best varieties. His statistics show that the best roots transmit no better qualities than do the mediocre roots because the differences are merely "fluctuations" (modifications). The real differences between sugar beet families are usually very slight and are greatly exceeded by their "fluctuations."

Both the best and the poorest families transmit average qualities, so that continuous selection is not an efficient means of improvement. The isolation of mutants, on the other hand, is thought by Pritchard to offer promise of improvement, but if the mutation method is to be used, it is deemed essential that more efficient experimental methods be devised to reduce the effects of soil differences and thus make it possible to distinguish real differences more clearly (see Chapter XXV).

Other normally cross-fertilized crop plants in which mutations are known to have occurred are cotton, hemp, rye and the sunflower.

The Search for Mutations.—It has long been thought that the two most effective methods of inducing heritable variations in plants are hybridization and change of environment. Regarding the importance of the first there is of course no question, and there is evidence that very radical changes of environment such as Tower applied to his beetles and White to his tomatoes may induce germinal variation. But the idea that mere change of location from warmer to cooler climates or from poorer to richer soils, or *vice versa*, is very effective in "breaking the type" finds very little to support it. This notion that culture induces germinal variation doubtless finds its explanation in the fact that sooner or later after a plant is subjected to intensive culture and close observation new heritable variations appear. But why conclude that these variations are induced by culture? During the first season of garden cultivation of a species of tarweed two mutations were discovered. One was a change in the color of the stamens, the other was petallody in the ligulate flowers. It seems very probable that these variations would have occurred had the plants been growing in the wild. They were found because the plants were closely inspected. But is their not fair evidence that cultivation of the same species in different regions gives rise to different mutations? There is danger of befogging the issue by this question unless we distinguish clearly between the origin of *mutations* and the origin of *varieties*. To consider only one of many possible illustrations: the native sorghums of South Africa, the Sudan, Egypt, Arabia and Persia, India, and Manchuria are a diverse lot of forms; yet sorghum undoubtedly originated in Africa and spread thence to the various regions where it now exists as distinct varieties. It must be admitted that different varieties have developed in different regions, but does this necessarily indicate that geographical differences actually caused the original *germinal* alterations which resulted in the different varieties of sorghum? Such a conclusion seems unwarranted in view of what is actually known concerning the occurrence of mutations under both natural and artificial conditions. Moreover, it is not improbable that the progenitors of existing varieties of sorghum all originated in Africa, although geographical differences may have been the determining factor in the survival of those mutations which gave rise to existing varieties. Factor mutations conform in their manner of occurrence with de Vries' mutation theory; they arise suddenly, they occur in all directions, they are heritable, and *some of them* are advantageous to the species and are preserved by natural selection. When so preserved they give rise to new forms or races, and when fostered by man they make possible new horticultural varieties of plants or new breeds of animals. But as yet we have no ground for asserting that factor mutations are caused by geographical differences or by any specific elements of the environment. From his study of variation in tobacco Hayes reached the conclusion that while environment is of great importance in breeding tobacco as well as in growing the commercial product, yet change of environment "does not cause a breaking up of type, and whatever variations occur due to environment appear alike in all plants of a particular type." Thus it appears that mutations arise quite independently of conditions of culture, and it is probable that they are somewhat more frequent than has generally been supposed. It is certain that mutations which are undesirable for agricultural purposes are quite as apt to occur as are desirable ones. For this reason neglect of seed selection has caused the "running out" of many good varieties. The breeder who would improve the best existing varieties which are adapted to a given location must either resort to hybridization between the varieties or else search for the most desirable biotypes within each variety. Even though hybridization is clearly necessary from the first, it may well be preceded by a systematic search for the best forms within the varieties to be crossed.

One of the most successful attempts to take advantage of the desirable mutations which had occurred within cultivated varieties was carried out by Surface and Zinn at the Maine Experiment Station in their experiments on oat breeding. Oats being self-fertilized, they assumed that any new characters which had originated would breed true. The two most desirable improvements in the commercial varieties of oats cultivated in Maine are increase in yield and in strength of straw. Accordingly individual oat plants were selected with these two points in mind. This work began in 1910 when 460 plants were chosen from 18 different commercial varieties. Of these only 188 were selected for planting in 1911 and on the basis of the results obtained 80 were continued for testing in duplicate 1–2000 acre plots in 1912. Of these pure lines 34 were sufficiently promising to be continued into field tests in 1913. Thirty-one of these were again tested in 1914. In 1915 all of these pure lines were discarded except 12 and these were tested in quadruplicate plots in 1915. In each of the 3 years 1913–15 these pure lines were grown along with a number of the best commercial varieties obtainable. In 1914–15 the pure line plots alternated in the field with commercial variety plots.

After correcting the yield of individual plots for differences in soil fertility (see Chapter XXV) it was found that the 12 pure lines averaged to yield 80.8 bushels per acre against 75.2 bushels for the 11 commercial varieties. "Only 4 of the commercial varieties gave a better yield than the poorest of the pure lines. In all cases the average yield of the pure lines selected from a given variety exceeded the yield of the parent variety." Of the 18 commercial varieties with which they started only 3 are represented among the 12 pure lines. It was found that these pure lines closely resemble their respective parents in morphological characters and concluded, therefore, that mutations in the physiological characters which result in higher yield are not necessarily associated with changes in morphological characters of the plant or grain.

Even more striking results in some respects have been obtained by Clark by means of head-to-row selections of Ghirka spring wheat in North Dakota. Starting with 300 individual plant selections in 1909, in spite of the destruction of all the cultures by hail in 1912, after 5 years' work two pure lines were found, one of which was superior to unselected Ghirka in all characters except crude protein content and the other in all characters except volume of the baked loaf.

In all such work the importance of beginning with large numbers must be emphasized. Other things being equal as the number of selected individuals increases the chances of locating the desired variants increase. The same holds true when attempting to locate aberrant individuals by inspection of young seedlings, nursery stock, etc.

Propagation of Mutations.—The question of how to preserve and proppagate a desirable mutation becomes a problem only in plants which are normally cross-fertilized. In self-fertilized species the new form exists as a pure line and need only be isolated. Similarly in plants that are propagated vegetatively usually there is no difficulty in multiplying a new variety. This method has been applied to such crop plants as alfalfa with great success. But in a cross-fertilized plant in which vegetative propagation is impracticable the method of procedure will depend upon circumstances. If in a given species the plants are self-fertile the appearance of only a single plant of a new form makes it possible to test its genetic constitution and if it is a mutation to multiply it. If it is heterozygous for the factor conditioning the new character or characters it will of course be necessary to select the best individuals from the next generation. This situation will confront the breeder only in the case of mutant factors which are dominant or partially dominant when in the heterozygous condition. When the mutant factor shows partial dominance in a heterozygote but segregates as a Mendelian recessive there will be no difficulty in establishing a pure strain, but should it segregate as a Mendelian dominant it becomes necessary to test a number of the seedlings exhibiting the new characters. In cross-fertilized species, in which individual plants are self-sterile, where a mutation appears in only one plant, several successive crosses may be necessary in order to produce a strain which breeds true for the new type. It must be crossed back on the parental form to begin with. If the change from the parental type is conditioned by a single factor the number of hybrid generations to be raised will depend on whether that factor segregates as a dominant or a recessive. In the latter case a true breeding strain should be obtained in the second generation but in the former it will require three or more hybrid generations depending on the extent to which the new characters depend upon environmental conditions for their expression.

CHAPTER XXII

GRAFT-HYBRIDS AND OTHER CHIMERAS

A graft-hybrid, as its name implies, is a shoot or plant which is produced by grafting one kind of plant upon another and whose characters are intermediate between the characters of the two components. None of the so-called graft-hybrids are really hybrids at all; they are merely mixtures of tissues from two kinds of plants which can live in unison. But each kind of tissue is distinct in its every cell, *i.e.*, there has been no fusion of cells or blending of germ plasm as in the case of sexually produced hybrids. Some difference of opinion still exists regarding a single case which will be referred to again, but the above statement certainly applies to all other graft-hybrids that have been investigated. As Buder says, a graft-hybrid is nothing else than a special form of graft-symbiosis. Thus all graft-hybrids are chimeras (p. 271). A conception of how chimeras originate naturally may be gained by learning how graft-hybrids have been produced experimentally.

Tomato-nightshade Graft-hybrids.—Some members of the nightshade family are easily grafted even though they belong in different genera. Thus it is possible to double work nightshade on tobacco on tomato. Reciprocal grafts of tomato and potato are easily made and Heuer has grafted tomato on egg plant and tomato on bittersweet. In recent years Winkler has produced four different chimeras and another form which he considers a true hybrid by grafting tomato on nightshade or *vice versa*. The four Solanum chimeras are shown in Fig. 151. Winkler's method is to graft on a scion by one of the ordinary methods and soon after it has united with the stock to cut it off taking pains to make the cut pass through the united tissues of stock and scion as shown in Fig. 152. Most of the adventitious buds pushed out are either nightshade or tomato. But occasionally a bud will be formed on or near the line of union. In such cases either one of two combinations of the graft-components may result depending on the relations of the two kinds of callous tissue. If the two masses meet as in *a* of Fig. 153, the young shoot will consist of sectors of nightshade and tomato, but should one of the cell-masses grow over the other tissue producing the condition shown in *b*, the young shoot in this case will be composed entirely of tomato inside but will have an envelop of nightshade cells surrounding it. The first type is termed sectorial and the second periclinal. A third type has been recognized by Winkler in which the vegetative cone is a mosaic of unlike cells. This type he named hyperchimera. Coit has reported the case of a Valencia orange tree which from its consistent instability appears to have been propagated from a mixed bud and hence belongs in this class of chimeras.

All of Winkler's Solanum chimeras are periclinal and the degree of resemblance of such a graft-symbiont to the parent whose tissue comprises the inner portion of the shoot seems to depend upon the number of layers of cells from the other parent which envelop it. Thus the form *tubigense* (Fig. 151, *D*) which closely resembles the nightshade has all the inner portion of *S. nigrum*, with just an epidermal layer, one cell thick, of *S. lycopersicum*. But *proteus* (Fig. 151, *C*), whose leaves are much more like tomato leaves, has a double layer of tomato cells overlying the nightshade body. Similarly, *Kœlreuterianum* (Fig. 151, *B*) is really a tomato with nightshade epidermis, while *Gærtnerianum* has a tomato body covered with two layers of nightshade cells. These graft-hybrids were discovered only after much patient work in the course of which Winkler made 268 grafts which produced more than 3000 shoots. All four were propagated from cuttings and by this method they have been obtained and grown by the New York Botanical Garden.

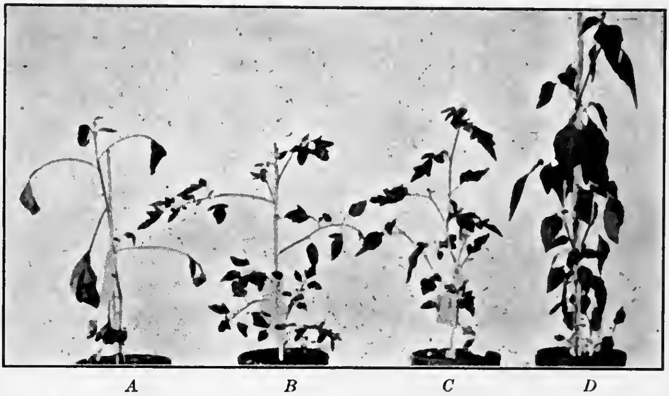


FIG. 151.—*Winkler's Solanum chimeras.* Produced by grafting tomato on nightshade (and vice versa). From left to right, *Solanum Gaertnerianum, S. Koelreuterianum, S. proteus,* and *S. tubigense.* The second resembles the tomato parent most closely; it has a tomato body with nightshade epidermis (a single layer of cells). The fourth is most like the nightshade parent and it has a nightshade body with tomato epidermis. The first has a tomato body covered with 2 layers of nightshade cells and the third, a nightshade body covered with two layers of tomato cells. Such combinations are called periclinal chimeras. (*From Journal of Heredity.*)

It has not been possible to compare these forms with true sexual hybrids because no one has yet succeeded in crossing the tomato and the nightshade. But sufficient evidence of their mixed composition is found in the character of their progeny and from the study of chromosome numbers made by Winkler. In *tubigense* the fruits are almost identical with those of the nightshade and the seeds produce only pure nightshade plants. The reason for this is clear when it is remembered that this form is really nightshade with a single epidermal layer of tomato cells, since

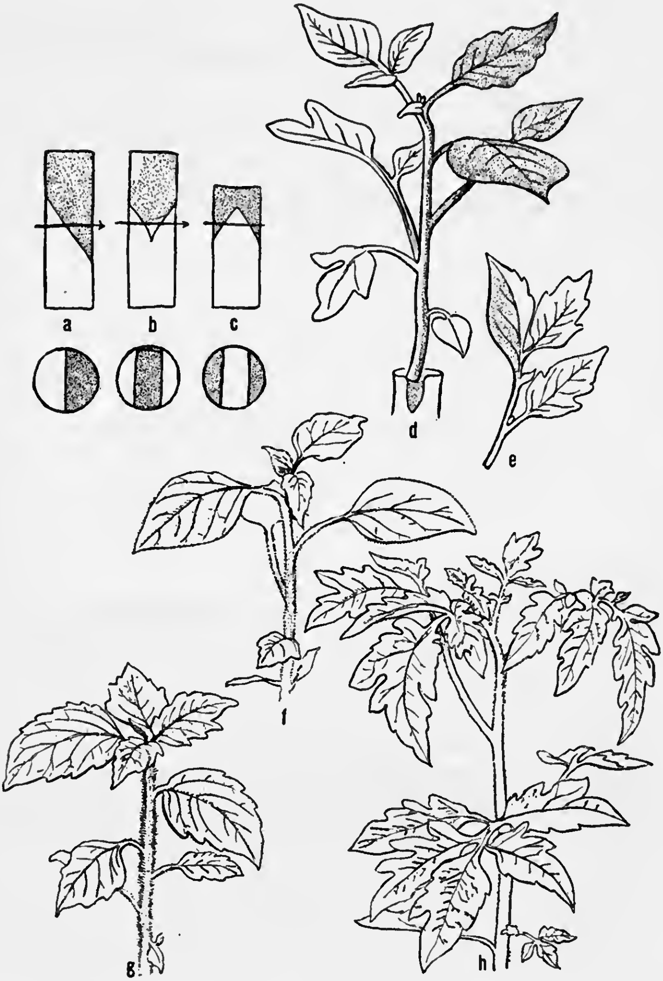


Fig. 152.—Diagrams showing methods of grafting used in producing the tomato-nightshade chimeras and some of the results; shaded portions represent scion tissue, unshaded, stock tissue. *a*, Splice graft; *b*, cleft or wedge graft; *c*, saddle graft; *d*, sectorial chimera (shaded portion, nightshade; unshaded portion, tomato tissue); *e*, chimera leaf, part nightshade, part tomato; *f*, nightshade; *g*, periclinal chimera, *Solanum tubigense*; *h*, Tomato. (*After Winkler from White.*)

the germ cells arise from the sub-epidermal layer. The seedlings of *Gœrtnerianum* are also pure nightshade because, although this form consists of tomato tissue within, it is enveloped by two layers of nightshade cells. Similarly with *proteus*, which is a nightshade except for its two outer layers of tomato cells, the fruits resemble tomatoes and from the seed pure tomatoes have been raised. The other form, *Kœlreuterianum*, fails to produce fruits. The chromosome numbers are 24 for the tomato and 72 for the nightshade. If a fusion of nuclei involving diploid numbers had occurred the cells of the supposed hybrids should contain 96 chromosomes, but the only counts obtained by Winkler in the four chimeras were 24 and 72. Thus it appears that in each graft-symbiont the two kinds of tissue maintain their identity. Yet there is a combined effect on the morphological characters. The physiological interactions too are such as to cause reduced vigor. This effect is least noticeable in *Kœlreuterianum* which is sterile. The fifth new form, which Winkler claims is a true graft-hybrid, was named *Darwinianum*. It appeared on one of the shoots from a decapitated graft. Winkler claims the chromosome number of this form is 48 and that certain if not all of the tissues of this plant are composed of cells derived from the actual fusion of tomato with nightshade cells which involved nuclear fusion. If this is actually the case *S. Darwinianum* is a hybrid in the strict sense and the only one known to have been produced by vegetative means. However, Baur points out that Winkler bases his claim for this number on the ground that he found 24 chromosomes in the pollen mother-cells which arise from the sub-epidermal layer. Baur thinks that Winkler's interpretation is unwarranted. He believes it much more probable that *S. Darwinianum* is a periclinal chimera with a nightshade epidermis, then a sub-epidermal layer of tomato cells and the adjoining inner tissues of nightshade. Then the number found, 24, is the diploid number of the tomato and the reduction division, according to this explanation, is omitted in the tomato pollen mother-cells which, in this chimera, are bounded on both sides by nightshade tissues; or else it occurs at an unusually late stage in development. "I cannot admit," says Baur, "that the existence of real graft-hybrids in the strictest sense of the word is proven."

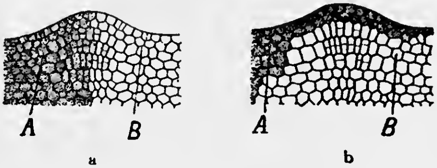


FIG. 153.—Diagram to show formation of adventitious buds arising at the point of union of the two graft-components *A* and *B*. *a*, represents a sectorial combination; *b*, a periclinal combination. (*After Buder.*)

Since the true nature of Winkler's chimeras has been made clear a number of historical cases of graft-hybrids have been investigated. The results of this work have been summarized by Buder whose list appears in Table LIII. Most of these cases have been fully discussed in other works. Typical leaves of the two types of Cratægomespilus and of the two parents, the whitethorn and the medlar, are illustrated in Fig. 154.

TABLE LIII.—LIST OF THE MOST IMPORTANT PERICLINAL CHIMERAS PRODUCED BY GRAFTING. (*Adapted from Buder.*)

Name and origin	Used in grafting		Composition
	As stock	As scion	
Laburnum (*Cytisus*) *Adami*, arose spontaneously in 1826 from an unsuccessful graft.	*Laburnum vulgare* (Shower of Gold).	*Cytisus purpureus* (Purple Broom).	According to *Buder* only one outer layer of *C. purpureus*, all within being *L. vulgare*.
The Cratægomespili of Bronvaux, originated spontaneously many decades ago at Bronvaux in Metz from places where stock and scion had overgrown on grafts nearly a century old.	*Cratægus monogyna* (Whitethorn).	*Mespilus germanica* (Medlar).	According to Baur and H. Mayer both forms have a Cratægus body which is covered by a Mespilus mantel:
(*a*) *Cr. Asnieresi* (resembling whitethorn)..............	....	....	In (*a*) of one layer of cells.
(*b*) *Cr. Dardari* (resembling medlar)..................	....	....	In (*b*) of two layers of cells.
The Cratægomespili of Lagrange, apparently complete analogues of the two forms. from Bronvaux.			
The pear-quince "hybrid" of Frère Henri, originated about 1903 in Rennes.	Cydonia (Quince).	Pyrus (Pear).	Probably consists of pear tissue within a layer of quince cells.
The peach-almond graft hybrid of Daniel and Delpon, arose spontaneously in 1908 at Mas-Grenier (Tarn and Garonne).	*Amygdalus communis* (Almond).	*Amygdalus persica* (Peach).	Evidently a mixture of sectorial and periclinal chimeras.
The tomato-nightshade "hybrids" of Winkler, produced experimentally in 1907–9.	*Solanum lycopersicum* (Tomato).	*Solanum nigrum* (Black nightshade).	According to Winkler: Outer layers Inner tissue
(*a*) *S. tubigense*............	....	....	1 of *S. lycopers.* *S. nigrum*
(*b*) *S. proteus*..............	....	....	1 and 2 *S. lycopersicum* *S. nigrum*
(*c*) *S. Kœlreuterianum*.......	....	....	1 of *S. nigrum* *S. lycopers.*
(*d*) *S. Gœrtnerianum*.........	....	....	1 and 2 *S. nigrum* *S. lycopers.*
(*e*) *S. Darwinianum*.........	....	....	"An actual hybrid" (but see text).
The tomato-eggplant and tomato-bittersweet "hybrids" of Heuer, produced experimentally in 1910.			
Form I.....................	*Solanum lycopersicum* (Tomato).	*Solanum melongena* (Egg plant).	Probably only the epidermis is egg plant, tomato within.
Form II....................	*Solannm lycopersicum* (Tomato)	*S. dulcamara* (Bittersweet).	Epidermis of tomato, inner portion bittersweet.
The populus "hybrid" of Baur, produced experimentally in 1911.	*Populus canadensis.*	*P. trichocarpa.*	Only the epidermis of *P. trichocarpa*, within *P. canadensis*.

In addition to the above there are the Bizarria as they have been termed. These are periclinal chimeras (some of them perhaps also sectorial chimeras) between different species of Citrus: *Pomeranze, Citrone, Cedrate, Limette.* The earliest record of these dates from Florence, 1644. They aroused interest in their day because of the manifold sectorial and periclinal chimera combinations in their fruits. Although most of these forms are now forgotten, several are still in cultivation, but they have not received close study (but see COIT, "Citrus Fruits").

Baur's Investigation of a Natural Chimera.—The key to the explanation of Winkler's artificially produced chimeras was furnished by Baur's discovery of the difference between the white-edged and solid green varieties of geranium (*Pelargonium zonale*). From his study of seedlings of the white-edged variety he had come to realize that the color of the leaves on a seedling depends entirely upon the nature of the cells composing the vegetative cone or plumule. This led him to examine the cells in white-edged and green leaves and he found that in a white-edged leaf there is an extra layer of colorless cells in addition to the true epidermis (see Figs. 155, 156 and 157). He concluded that a plant bearing all white-edged leaves must have a complete peripheral layer of the colorless cells just below the epidermis as shown in Fig. 157, a, and that a plant differing in this respect from a normal green plant should be considered a periclinal chimera. He had observed sectorial chimeras among his geranium seedlings and found that occasionally a plant having some of its leaves entirely green and some of them entirely white would produce a shoot bearing white-edged leaves. He found that such shoots arose near the

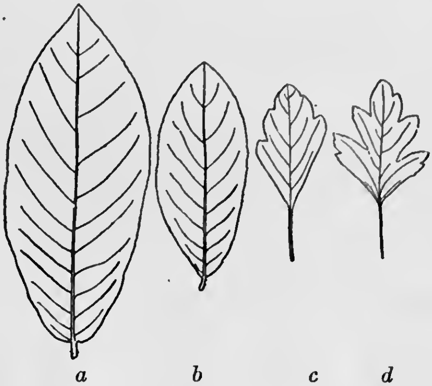


FIG. 154.—Leaves of the Cratægomespili of Bronvaux and their components. *a*, Mespilus germanica (Medlar); *d*, *Cratægus monogyna* (Whitethorn); *b*, *Cratægomespilus Dardari*, with two outer layers of medlar cells; *c*, *Cratægomespilus Asnieresi*, with one outer layer of medlar cells. (*After Buder.*)

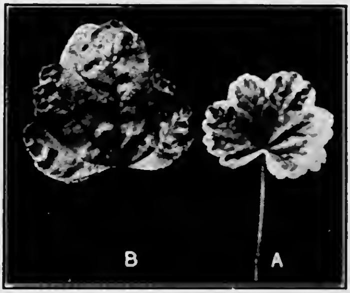


FIG. 155.—Leaves from periclinal chimeras of the white-edged geranium; *a*, from a plant with two white peripheral cell-layers; *b*, from a plant with only one epidermal layer of colorless cells. (*After Baur.*)

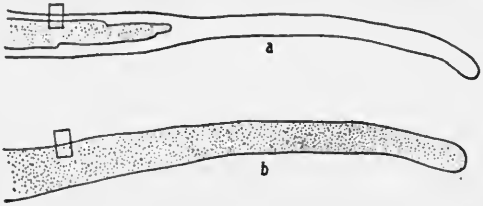


FIG. 156.—Sections through edges of the two leaves shown in Fig. 155. Green tissue indicated by stippling. For much enlarged views of the portions enclosed by the small rectangles see Fig. 157. (*After Baur.*)

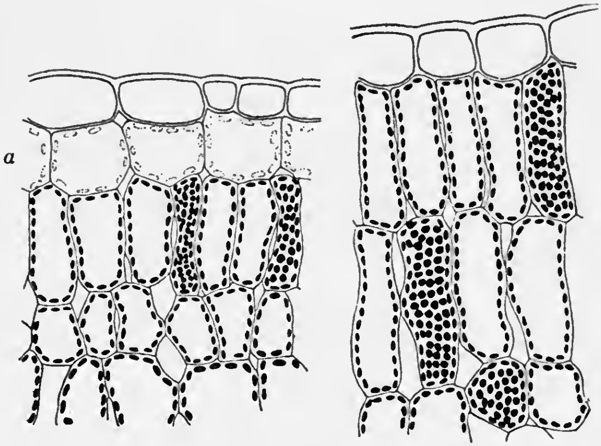


FIG. 157.—Microscopical views of those portions of the cross-sections in Fig. 156 represented by the small rectangles. Colorless chromatophores are indicated in outline, green in black. (*After Baur.*)

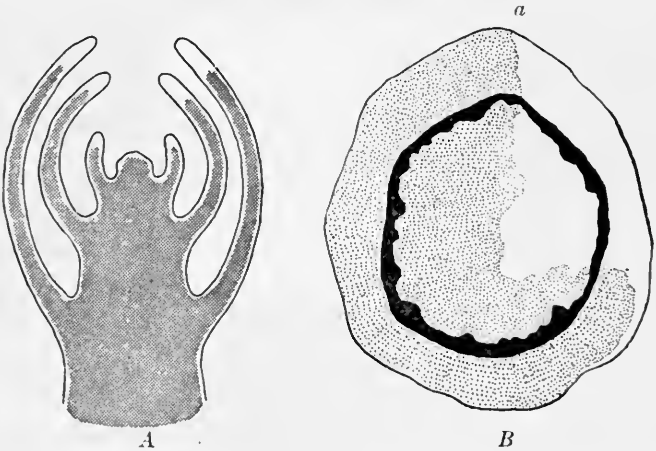


FIG. 158.—*A*, Diagram of longitudinal section through a young shoot of a plant bearing white-edged leaves—a periclinal chimera. *B*, Cross-section of stem of a sectorial chimera. A bud pushing out at *a* would produce a sectorial chimera, while one arising at *b* would form a periclinal chimera. (*After Baur.*)

boundary line between the green and the white tissue of the stem. Hence he concluded that in order to have a periclinal chimera arise from a sectorial chimera the relation between the two kinds of tissue would have to be as shown at *b* in Fig. 158. A bud pushing out at such a point would have an envelope of colorless cells in addition to the colorless epidermis.

Without doubt this structural principle explains the origin of all natural chimeras. But this principle holds only when there are groups of normally homogeneous tissues in the same stem or bud which have come to differ with respect to one or more characters. In graft-hybrids such diverse tissues come from different plants. The question of the natural origin within the same plant of morphological and physiological differences causing somatic heterogeneity where homogeneity is the ordinary condition is a problem of far greater fundamental importance. It has already been shown that probably all such diversities within single individuals arise as factor mutations (Chap. XIV).

Other Natural Chimeras.—Sectorial chimeras caused by mutations in color factors are the most common natural chimeras. They occur very frequently in citrous fruits, especially in the orange and lemon (see Fig. 161). Other chimeras in these fruits are caused by factor differences affecting thickness and texture of rind and frequently associated with these are differences in color and flavor of the pulp. Color chimeras are also fairly common in apples and pears and they have been found in grapes, olives and tomatoes, as well as in gladiolus, poppies, sunflowers, dahlias, and doubtless many other flowers. Many valuable variegated forms of ornamental shrubs are mixtures of sectorial and periclinal chimeras with normal green vegetative parts. Some striking examples are the Variegated Black Elderberry (*Sambucus nigra variegata*), the Variegated Deeringia (*Deeringia celosioides*) and the variegated forms of the Japanese Spindle Tree or Strawberry Bush (*Euonymus japonicus*). Variegated foliage which is caused by factor mutations causing complete or partial chlorophyll reduction are also fairly common among herbaceous plants.

Two Categories of Variegation.—The variegated plants mentioned above, like the white-edged geranium, can be propagated asexually and it is known that in the geranium, snapdragon, four-o'-clock, maize and other plants the variegated character can be transmitted to sexually produced offspring. However, certain variegated plants cannot transmit variegation through the seed although it is transmissible by means of vegetative propagation. Baur has shown that in the latter class, variegation results from a pathological condition and by double working susceptible and immune stocks he determined that it must be caused by a toxin produced by the diseased cells. The long familiar cases of "graft infection" among the Malvaceæ are thus explained. It seems that all cases of "infectious chlorosis" in this family can be traced back to a single variegated specimen of *Abutilon striatum* Dicks., which was introduced into Europe in 1868 and named *Abutilon thomsoni.* Miss Reid has shown, however, that among the flowering maples (Abutilon) the variegated forms can be grouped into two classes: "those with a mottled variegation which is infectious and those with a non-infectious variegation with the white cells at the periphery. Both types are of importance in horticulture, especially for use as bedding plants; both types are of special scientific interest."

The Physiological Behavior of Graft-hybrids.—Although chromosome counts and progeny tests indicate that the cells of each graft-symbiont maintain their identity independently of the close proximity of foreign cells, yet the intermediate characters of graft-hybrids indicate that the components have a mutual influence upon each other. This influence is especially notable in the manifestation of physiological activity involving the whole plant. None of the Solanum graft-hybrids are as vigorous as either component under normal conditions. In fact, it is with considerable difficulty that they are maintained by means of cuttings, except in the case of *Koelreuterianum.* This lack of vegetative vigor may not be characteristic of all graft-hybrids but it seems to be common to most of them. Lack of vigor exists in many natural chimeras also, especially in those involving chlorophyll reduction.

In the Solanum graft-hybrids the germ cells of the two components are not equally susceptible to the effect of adjacent foreign cells. In both *tubigense* and *Gaertnerianum* the fruits contain fertile seeds which produce only pure nightshade plants. But in *proteus* only part of the seeds are viable and these produce tomato seedlings, while in *Koelreuterianum* the flowers are entirely sterile. Similarly, in *Cytisus Adami* the "hybrid" (intermediate) flowers are sterile.

Graft-hybrids offer many interesting possibilities as a means of studying the physiology of development as influenced by the reciprocal relations between the components. This method of attack has been utilized much more extensively in the study of development in animals than in plants. Crampton, for example, grafted together the pupæ of different species of moths thus producing double monsters. From the specific effects upon pigmentation in some of the graft symbionts it was concluded that the pigmental colors in some species are derived from the haemolymph by processes of drying and decomposition which are regulated by some specific internal factor. Crampton mentions several other investigators who performed similar experiments on animals. Buder has suggested the reciprocal grafting of male and female plants in diœcious species as a means of investigating the physiology of sex determination in plants. This suggests the whole field of reciprocal effects between scion and stock, concerning which there has been considerable investigation in recent decades.

Modification of One Graft-symbiont by the Other.—The repressing or stimulating effects of certain scions on certain stocks is well known. Excellent examples are found in the various "dwarf" rootstocks used in the culture of the pome and citrous fruits. Besides the dwarfing effect of the stock upon the scion, there is often a reciprocal stimulating effect of the scion upon the stock which causes the latter to increase in diameter faster than the scion. A mutually stimulating effect is sometimes observed, as in the almond and the peach when used as graft components. The importance of selecting stock of about the same vigor, when grafted, as the scion has long been recognized by nurserymen. The fact that grafts usually exhibit a certain amount of modification according to the kind of stock used has given rise to many reputed cases of deleterious effects and extreme modifications due to grafting.

A matter of considerable economic importance involving this question concerns the culture of wine grapes. After the introduction of American vines and their hybrids into the phylloxera-infested districts of France there was widespread concern over the possibility that the quality of the French wines would be injured by grafting on the new stocks. Many investigations were carried on. Although in the earlier stages of the work some very definite effects of stock on scion were reported, the evidence as a whole is considered by leading investigators as indicating merely that the stock may either increase or decrease the capacity of the scion according to the combination used. It has been concluded that where due account is taken of affinity of stock and scion, if other conditions are favorable, grafting has caused no deleterious effect on yield or quality.

A specific case of supposed deleterious effects attributed to the influence of stock on scion was observed by Paelinck. A dark-red variety of cherry, Early Rivers, was grafted on mahaleb stock. The resulting tree bore fruit which was yellowish white in color, of smaller size and which matured 8 days later than Early Rivers. Scions from this white-fruited tree were grafted on mazzard stock which has small black fruit "to see whether the white fruits would revert to the dark color." The result as one would expect was negative. Undoubtedly this was a case of bud mutation.

Other reputed extreme effects of graft-symbionts involve the supposed transfer of characters from the one to the other. Baur asserts that after reviewing the accounts of many grafting experiments he has reached the conclusion that most of the reciprocal effects between stock and scion can be explained on the basis of modification in nourishment. Moreover, where this explanation does not hold there is a more probable cause than the notion of transfer of characters. For example, in the case of Daniel's eggplant which, when grafted on tomato bore tomato-shaped fruits, Baur states that there are varieties of eggplant which occasionally bear tomato-shaped fruits even when not grafted, and that Daniel probably used such a variety. Again Daniel and Elder have reported experiments tending to show that the seedlings of scions exhibited an influence of the stock. Baur is inclined to think that accidental cross-pollination must explain such cases. But Daniel has recently reported similar results when working with different varieties of beans. In this case, however, there is the possibility that the seedlings of the scions and the seedlings used for comparison, which were from ungrafted plants, belonged to different pure lines. Thus in some such simple manner all the supposed cases of transference of morphological characters may be explained.

Regarding the actual transference of the chemical constituents of the tissues from stock to scion and *vice versa*, the results of experiments differ with respect to different plant ingredients. Thus, according to Guignard, glucosids do not pass from one graft component to the other when the two contain different kinds of glucosids, and the glucosids present in plants are apt to differ unless the plants are closely related. In graft-symbionts whose components belong to different species, Guignard thinks that each component tends to retain its own chemical properties. On the other hand, Meyer and Schmidt found that alkaloids such as nicotine will pass from a tobacco scion into a potato stock. This is a promising field for future investigation.

CHAPTER XXIII

BUD SELECTION

The efficacy and practicability of bud selection is a subject of considerable interest especially among horticulturists. During the past decade it has received more and more attention from investigators until now there are under way a number of comprehensive projects which, in future years, should furnish definite information concerning the more important vegetatively propagated crop plants. If it is determined that bud selection is an effective method of improving certain varieties either by securing increased yield or by the discovery of superior strains, its importance to horticulture will have been demonstrated. It will still remain for horticulturists to decide as to the practicability of introducing systematic bud selection in the commercial propagation of those plants in which it has been proved to be an effective method of improvement. The efficacy of bud selection depends upon the nature of bud variation.

Bud Variation in Plants.—There are two kinds of bud variations, viz., modifications and mutations. Modifications are common to all plants and are easily detected even in dormant buds. On deciduous trees, for example, the buds formed during one season's growth usually show considerable variation in size. Such variations do not necessarily represent inherent differences between the buds. They are usually due to differences in the particular combinations of conditions which exist during development of the buds. Phytomers exhibit fluctuating modifications in all other characters as well as size in response to the varying conditions of nourishment, light, temperature and other elements of the environment. These modifications are not transmissible and selection of such bud variations alone could never change the average output of an orchard or establish an improved strain.

Bud mutations, on the other hand, although comparatively rare, are of general occurrence and the new characters induced by them are transmissible. Hence in considering the efficacy and practicability of bud selection in a horticultural variety the first thing to be determined is the nature and frequency of somatic mutations in that variety. There is only one way in which this question can be answered completely and definitely and that is by extensive tests of vegetatively propagated offspring. Such tests must be made under controlled conditions especially as regards the nature of the rootstock on which the tested scions are propagated. Careful inspection may reveal a certain number of chimeras and bud sports. Both, in fact, are comparatively common in some varieties, such as the Boston Fern and the Washington Navel Orange, and they sometimes give rise to superior new biotypes. Yet inspection alone is not sufficient. A new fern sport must be propagated in order to test its constancy when multiplied vegetatively. Similarly a supposed orange sport must be propagated and the progeny must be tested in order to ascertain whether the selected phytomer is really a mutation and a desirable one at that.

Having discovered a new type which originated by bud mutation, the question arises: Will there be any practical difficulty in maintaining this new form by means of vegetative propagation? Are additional somatic mutations likely to occur in sufficient number to endanger the preservation of the selected form? It will be remembered that sometimes bud mutations in the Boston Fern produce ever-sporting varieties that have little or no commercial value. Similar inconstant forms have arisen in other ornamentals. Nevertheless it has been practicable to propagate vegetatively many valuable bud sports and hybrids, including some that are highly variable. One such product of composite hybridization is the cultivated Coleus. This ornamental foliage plant is commonly used for beds and borders in summer and as a conservatory plant in the colder months. The foundation stock was produced in England about 1867 by hybridizing four different exotic species. Hundreds of named varieties have been produced, some having appeared as bud mutations, but the majority being seedlings. Some of the varieties now in cultivation are characteristically variable. In one such variety Stout has investigated the variations in leaf color pattern and leaf shape in a series of 833 plants, all descended by vegetative propagation from two similar plants.

Bud Selection in Coleus.—The two plants with which Stout began had a definite pattern of leaf coloration consisting of a green mid-region and yellow border with blotches of red in the epidermis (Fig. 159). The green and yellow pigments exist in the sub-epidermal layers. The vegetative offspring from the two original plants were kept separate and the simple habit of branching in this plant made it possible to indicate the particular branch as well as the individual plant from which a cutting was taken. In this way Stout was able to trace the pedigree of any plant to its original source. During the course of the investigation 16 new color patterns were obtained. There also appeared the laciniate form of leaf which is seen in the younger leaves of the plant on the left in Fig. 159. Of the 16 new color patterns 15 arose by somatic mutations which produced bud sports either directly or, in some cases, indirectly from chimeras. The other new pattern arose solely as a fluctuating variation.

Fig. 159.—Two Coleus plants which descended from the same branch, which at the time it was propagated was uniform as to leaf shape and bore leaves having the same general type of color pattern, viz., green mid-region and yellow border with red blotches on the epidermis. The right hand plant resembles the original plant although it represents the fourth vegetative "generation." The left-hand plant shows the laciniate type of leaf which appeared several times as a bud mutation. (*From Stout.*)

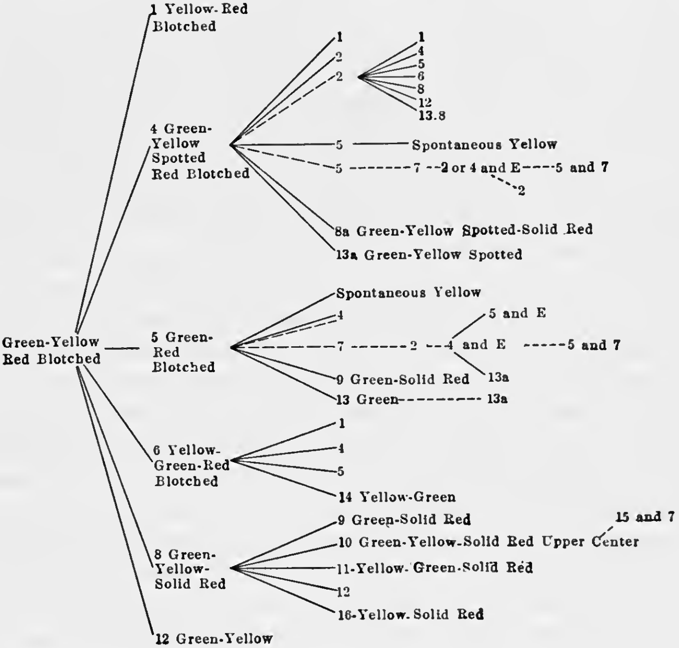


Fig. 160.—Diagram showing derivations of color patterns in Coleus. The descriptive name of a color pattern is given only where it first appears in a line of descent. A continuous line indicates origin by bud mutation and a dotted line indicates fluctuating variation. (No. 2 = original form. No. 7 = laciniate-leaved form. *E* = entire leaves.) (*From Stout.*)

It consisted of absence of yellow and decrease of red in the younger leaves of a few plants. Six of the 15 patterns that arose as bud mutations also appeared more or less frequently as fluctuating variations on certain plants. The derivations of the various color patterns are shown by the diagram in Fig. 160. It will be noted that the original pattern, No. 2, is described as green-yellow-red blotched which means green center, yellow marginal border and red blotches on the epidermis. In the same way the description of pattern No. 4 is interpreted as green center, yellow-spotted marginal border and red blotches on epidermis.

The frequency with which these various bud mutations occurred is shown in Table LIV. Here are indicated under "Plants" the number of plants in which each type of change might have occurred, under "Frequency," the actual number of bud mutations that did appear, and, finally, the ratio of bud mutations to constant buds. This ratio is obtained by assuming that on the average each plant produced 200 buds.

TABLE LIV.—FREQUENCY OF BUD MUTATIONS PRODUCING NEW COLOR PATTERNS AND LEAF-SHAPES IN COLEUS. (*After Stout.*)

Type of change	Plants	Frequency	Ratio
Increase of yellow and decrease of green	827	27	1: 6,130
Decrease of yellow and increase of green	740	50	1: 2,960
Reversal of positions of green and yellow	450	8	1:11,250
Increase of epidermal red to solid red	770	8	1:19,250
Decrease of epidermal red, complete loss	815	19	1: 8,580
Decrease of epidermal red, all cases	815	21	1: 7,760
Appearance of the laciniate character	765	13	1:11,770
Entire leaf from laciniate leaf	68	1	1:13,600

Stout remarks that these data indicate the tendencies of the bud variations and give a clew to the behavior of the characters in question. Thus, decrease of yellow occurred twice as often as increase of yellow, and loss of red 2.2 times as often as increase of red. Although these data indicate a tendency toward loss rather than gain of the two colors, the fact that the number of mutations involving gain is about half as large as the number involving loss has considerable interest. It has been generally considered that mutations involving addition of a character are exceedingly rare. While this may be the case in many pure species, it would appear from the above evidence that among the progeny of species hybrids such mutations may be relatively frequent.

The manner of appearance of these bud mutations was typical of somatic factor mutations. Stout says, for example, "the loss of yellow, loss of green, and gain and loss of red all occurred in single branches and in sections of branches. Frequently two quite different changes occurred on the same plant." After citing a case of modification in degree of pigmentation in Coleus by the use of artificial light, Stout declares: "In marked contrast to these results it may be noted that the bud variations that I have reported give more marked changes than those induced by Flammarion and that these appear suddenly and in a sector of a bud in a manner that suggests internal readjustments rather than external environmental influence."

Stout tested the seed progeny of two of his plants, obtaining in all 45 plants from selfed seed. As would be expected in such a case of composite ancestry, there was a wide range of variation in size as well as shape of leaves and in leaf coloration every gradation between pure yellow plants that died within a few weeks and pure green. No better evidence could be offered that these highly variable characters are actually conditioned by specific factors which segregate and recombine in sexual reproduction.

The history of Coleus as reviewed by Stout also contains some interesting facts about the origin of the characters under discussion. The four original species that furnished the foundation stock, from which the modern Coleus has been developed, contained no yellow coloration whatsoever. They were characterized by green leaves overlaid with different shades of red, purple or chocolate. The first appearance of yellow occurred in a leaf sport, *i.e.*, in one-half of a single leaf the green was exchanged for a decided yellow tint. "The bud at its base was propagated and gave the new variety." However, it does not appear that this sport was used in hybridization work. "Yellow coloration also appeared as a new or spontaneous development" among the second lot of hybrids raised at the gardens of the Royal Horticultural Society about 1869. Again in regard to the laciniate-leaf character, as early as 1856 a variety of *Coleus blumei* (which was the first species introduced into Europe and was originally described in 1826) was described as being "somewhat more richly colored but differing chiefly in having the leaves deeply and doubly lobed." While there is no record of the origin of this variety, it is certain that it appeared before *C. blumei* had been hybridized with any other species. It is very probable, therefore, that it arose as a bud mutation. Thus it appears that two of the three characters whose presence, absence or partial development figure conspicuously in Stout's "bud variations" actually originated by factor mutations during the early horticultural history of this plant.

Regarding the efficacy of selection in maintaining the new forms that arose by bud mutation, Stout's results show clearly that even in such a highly variable plant as a horticultural variety of Coleus, bud selection is very effective. Stout describes his methods as follows:

> "The series of plants considered under any type pattern are in large measure a selected stock. When cuttings were made for the perpetuation of the pattern

in a new generation, they were made from the plants most typical and constant for the pattern concerned. When a bud variation appeared, if the conditions were favorable, the parts possessing it were allowed to develop until there were several branches from which cuttings could be taken simultaneously. In such cases the selection of branches for the new type was a simple matter, as it depended on the taking of branches sharply distinct from the main part of the plant. . . . When further cuttings were made for a new generation to perpetuate the type they were made from plants most uniform and constant (determined from the records) for the pattern in question. Usually but three cuttings were taken from a plant and these were taken from branches most uniform and clearly conforming to the type."

The relative numbers of "constant" plants and of plants showing either clear-cut bud mutations or "fluctuations" are of considerable interest in connection with this matter of maintaining strains. These proportions are given in the tabulated summary of the main clones that were derived from one of the two original plants Table LV. Clones 11 and 12 were derived from two branches that had the same color pattern, yet it seems that they possessed "quite different potentialities for constancy and for bud variations. Even more marked differences than these developed among the various subclones. A study of pedigrees shows that in all patterns and in all main clones there were certain lines of progeny much more constant than many others. These could not be detected by any other than a pedigree method." These facts have a definite bearing on the maintenance of vegetatively propagated varieties or strains. If similar diversity as regards degree of variability exists in other cultivated plants, as it undoubtedly does, careful bud selection must be of prime importance in keeping varieties true to type or at least in preventing deterioration through the accumulation of undesirable bud mutations. In Coleus at least it is certain that bud selection is effective and necessary in maintaining strains true to type. If it is equally potent in its effect on other vegetatively propagated plants, bud selection should be given far more attention by nurserymen than it has generally received.

TABLE LV.—GENERAL SUMMARY OF CLONES DERIVED FROM PLANT NO. 1

Clone	Total number of plants	Plants constant	Per cent. of plants constant	Number of bud variations	Ratio of frequency
11	211	132	62	49	1: 860
12	192	87	45	21	1:1,830
13	138	75	54	4	1:6,900
14	155	80	51	18	1:1,720
117	91	54	59	31	1: 590
111	34	29	85	4	1:1,700

Bud Selection in Horticultural Practice.—The probable importance of bud selection to American pomology was recognized by Munson in 1906. He advocated its practice in the following words: "Select through successive generations buds, that is cuttings or scions, from branches which bear fruit most nearly approaching the ideal." Two years later Webber presented the subject of "clonal or bud variation" to the American Breeder's Association and also recommended bud selection. At this time, however, there was but little evidence that could be cited as proof of the practical value of bud selection. Working with violets Galloway and Dorsett were able to produce disease-resistant and floriferous strains. The Boston Fern sports were beginning to attract attention. But it was still generally supposed that bud sports were of comparatively slight importance as far as pomological practice was concerned. About this time two of the pioneer citrus growers of California, E. A. Chase and J. P. Englehart, became interested in the numerous variations among their orange and lemon trees and the latter began to experiment with bud selection. He first recognized and propagated the Golden Nugget Navel Orange, a sport from the Washington Navel. He soon convinced himself that many of the variations in fruit characters which he observed could be perpetuated by budding. In 1910 Coit emphasized the fact that through the unintentional propagation of undesirable sports a gradually increasing proportion of the trees in the citrous orchards of California were developing into drones or worthless types and that the only way to prevent this was greater care in choosing the buds used in propagating nursery stock. Meanwhile, Shamel had begun an extensive series of experiments on the improvement of citrous fruits through bud selection. During his preliminary investigation in 1909 Shamel found what he took to be distinct types of Washington Navel Oranges and the observations and experiences of certain growers seemed to indicate that trees producing small annual yields and poor quality of fruit could be top-worked with scions from trees known to be annual high producers of superior fruit to the very great advantage of the citrous fruit growers. Accordingly an elaborate system was devised for recording the performance of individual orange, lemon and pomelo trees.

Performance Records as a Basis for Bud Selection.—This study of the performance of individual citrous trees has emphasized the fact that there may be inherent differences with respect to quality and yield between different trees of the same commercial variety. Already these tests have been supplemented by demonstrations in top-working low-producing trees with scions from fruitful individuals. As a result of the systematic campaign which the government representatives have conducted throughout the citrous fruit districts of California and Florida, many of the growers are keeping records of the annual yields of part or all of the trees in their orchards.

Bud Mutations in Citrus.—What has been accomplished through bud selection in citrous fruits has been made possible by the relatively high frequency with which bud mutations occur. A dozen distinct types of Washington Navel orange are now known to occur more or less frequently in California orchards (Fig. 161). This fact is of especial significance in the light of the history of the Washington Navel orange which, as it originally existed in Southern California, consisted of only a few trees (possibly only two) which were propagated from navel orange trees that were introduced from Brazil by the U. S. Department of Agriculture. According to Coit the evidence from early California horticultural literature indicates that the Washington Navel variety was recognized as a distinct and at least fairly uniform type of orange. That a strong tendency to mutation characterizes this variety is evidenced by the frequent origin of new forms or reappearance of old ones as bud sports. In some cases the aberrant type differs not alone in fruit characters but also in habit of growth or leaf-shape and frequently in yield. In fact high yield is said to be correlated with superior fruit at least in some types. Similarly in the Eureka lemon the so-called "shade-tree type" makes

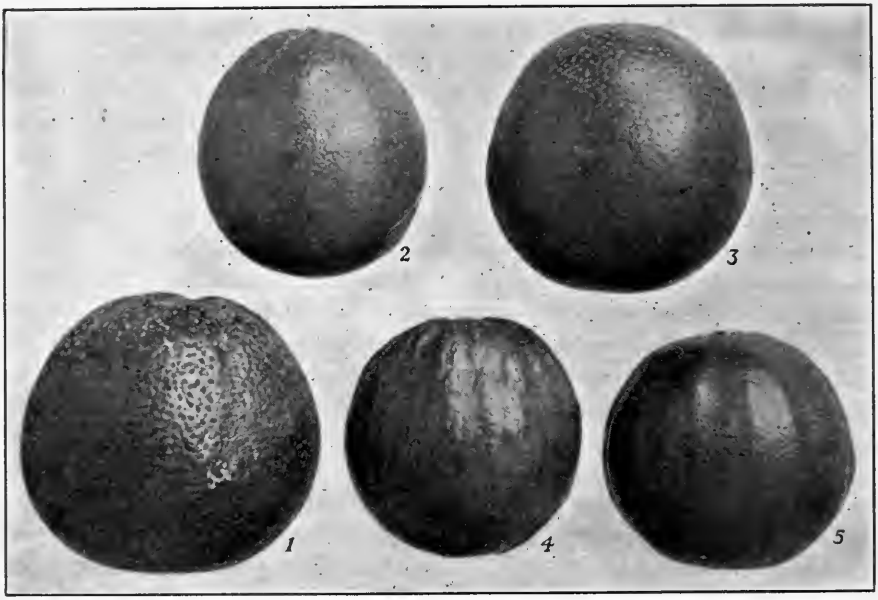


Fig. 161.—Fruits of the Washington Navel orange (1), and four forms that have originated from it by bud mutation; (2), Thomson Navel; (3), Yellow Navel; (4), Corrugated; (5), Ribbed. *(Courtesy U. S. Department of Agriculture.)*

rank growth and low yields, and such trees have been successfully top-worked with scions from fruitful types.

Deciduous Tree Fruits.—The efficacy and practicability of bud selection in other species than the citrous fruits is not yet determined. But there is considerable evidence that in certain varieties at least it is possible to find distinct types which remain constant when propagated vegetatively. In the apple and peach bud sports are known and they may be more frequent than has been supposed. Dorsey mentions four varieties of apple which originated in this manner and reports the discovery of another sport. It is possible that certain varieties have a greater tendency to sport than others. The Baldwin apple may be such a variety. It is claimed by some authors that the many variations occurring in this variety are purely environmental, while others assert that they have propagated such variations successfully. But in the apple and most other deciduous fruits there are plenty of good varieties which are adapted to conditions in the regions at present devoted to fruit growing. Here, as with citrous fruits, new varieties are not needed so much as profitable orchards. Will it pay to keep performance records as a basis for bud selection in deciduous fruits? That is the critical point, and it is not yet settled. Both favorable and adverse evidence has been presented. The Virginia Station kept a record for four years of the yields of 1245 trees in the same apple orchard (variety or varieties and age not known). Of these 375 yielded an average of four barrels to the tree and produced 60 per cent. of the crop, while 215 trees averaged less than one barrel per tree and were kept at a loss. The Dominion Experiment Station, Ottawa, Canada, has kept records of yields of different trees in the same orchard covering a period of 18 years. The most productive tree of McMahon-White yielded 1250 gal., and the least productive, 882 gal. Of Patten Greening the most productive tree yielded 974 gal., and the least productive 586 gal., while in the case of McIntosh Red one tree yielded 1219 gal., and another 670 gal. Clearly there are wide differences in the productivity of individual apple trees. Much of this variability in production is probably due to soil differences. It is claimed by Powell, however, that one cause of the marked decrease in the number of apple trees in New York State is the absence of profits due to low-producing trees. The true condition can be determined only by keeping performance records on an extensive scale. Even though many healthy but low-producing trees may be found, there still remains the question whether or not it will pay to top-work these low-producers with scions from high-producers. It has not yet been determined whether any of the wide differences in the productivity in individual apple trees are due to bud mutations.

Next to yield, uniformity of fruit is perhaps the most important commercial consideration. But there are marked differences in varieties in respect to uniformity and in the extent to which this feature is transmitted to vegetative offspring. The experience of Tyson Brothers in Adams County, Pa., illustrates this point. They propagated 8000 trees with scions from two old trees of York Imperial apples which had been noticed because of their productivity and the uniformity in shape of their fruit. Unfortunately no scions were taken from average or poor trees, and hence there is no basis for comparing productiveness in the young orchard. Furthermore it is possible that these trees will exhibit less variation in form of fruits with increased age. But, as yet, so far as uniformity of fruit is concerned, the experiment seems to have been decidedly inconclusive. Progress with a similar experiment on the Ben Davis variety has been reported by Whitten. Scions were taken from an exceptionally poor tree and from another tree which produced the largest and best apples of its kind on the station grounds. Examination of the third year's crop showed no perceptible difference in size, color, grade or quality of the fruit from the two lots of trees. In fact the average yield per tree was somewhat higher in the lot propagated from the poor tree than in the lot propagated from the superior individual. There appeared to be as much variation between individual trees in each plot as between the two plots.

"Pedigreed" Nursery Stock.—In response to the growing interest in bud selection many nurserymen have taken advantage of the idea of value which is commonly associated with pedigree. The more conscientious ones have selected their scions from trees which they believe to be superior, but a certificate of source is not a pedigree. This term, it must be admitted, has been used in scientific investigations of vegetatively propagated plants, where careful records were kept for a relatively large number of asexual "generations," as in Stout's work on Coleus. But no nursery stock now on the market is entitled to be known as pedigreed and even though such stock may be produced in future years, the danger from misrepresentation, either intentional or unintentional, will be as great as ever. Coit has suggested that stock propagated from tested trees be known as *recorded* stock and recommends a simple plan by means of which Deputy County Horticultural Commissioners may officially seal and record each tree when it is budded.

Bud Selection in the Potato.—No one doubts the occurrence of bud mutations in the potato. Numerous instances of the origin of new varieties as bud sports are on record. Yet there is considerable difference of opinion regarding the relative frequency of bud mutations in this species. Numerous investigations have been made on the improvement of the potato by means of tuber and hill selections. The most important papers have been reviewed by East and, more recently, by Stuart. East observed over 700 named commercial varieties during a period of 3 or 4 years and found 12 bud mutations. Changes were noted in the color, shape and habit of growth of the tubers and in the depth of the eyes. But as for the bearing of bud mutations on origin of new varieties East reached the conclusion that, while isolated cases of improvement might be due to selection of bud mutations, yet comparatively few (probably less than 0.5 per cent.) of our present varieties arose in this manner. This evidence on the origin of varieties has led East to adopt the view that probably all bud mutations are so exceedingly rare in the potato that few, if any, cases of "running-out" or "degeneration" in varieties are to be explained on this basis. He believes the principal factor in such deterioration is disease, and that in numerous experiments on potatoes, in which it is shown that successive selections have raised the average yield over that of the unselected tubers, the results are entirely due to the elimination of diseased tubers.

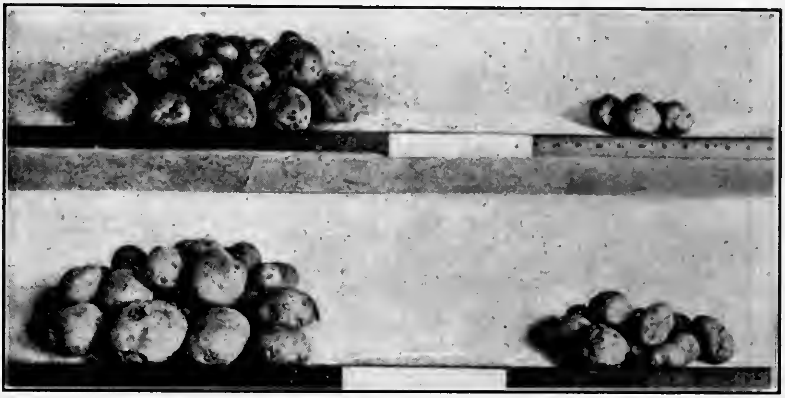


FIG. 162.—Variation in yield between tuber-units from the same hill. Above, the progeny of two tubers from hill selection No. 35; below, that from hill selection No. 4. (*After Stuart.*)

While the elimination of diseased tubers or of tubers that were weakened by disease in the leaves or stem does undoubtedly explain the success of many selection experiments it may not account for all of them. Tests of individual tubers of almost any commercial variety apparently reveal inherent differences in the tubers. Although the plant is very susceptible to environmental conditions and some tuber characters such as shape and size are very unstable, yet sometimes the product of two closely similar tubers which came from the same hill when grown under closely similar conditions will differ widely (see Fig. 162). The most satisfactory method of testing individual tubers is the tuber-unit method which was introduced by Webber. Each tuber which is to be tested is cut lengthwise into four equal pieces which are planted at equal distances from each other. The four hills thus comprise a tuber-unit.

Stuart in 1911 conducted a tuber-unit experiment with some 150 standard commercial varieties of potatoes.

"The seed used was grown in Burlington, Vt., in 1910, on land which had not grown a cultivated crop of any kind for at least 35 years. In addition to this the seed was selected from the most promising hills at the time the crop was harvested. The tubers as a whole were remarkably uniform in size and there could, therefore, have been little difference in the size of the seed pieces used. Any variation, therefore, which occurred between the plants of the various tubers which were planted would seem to be due to some inherent tendency in the tuber itself. The remarkable dissimilarity between the growing plants of the individual units of a variety planted contiguously in the row was so surprising that some three dozen units were photographed and when these were harvested the tubers were also photographed (see Fig. 163). It was found that the divergency in yield was just as great as in the size and vigor of the plants. In 1912 five units were planted from both strong and weak plants, and it was found in practically every instance that the low-yielding 1911 plants gave poor germination, a feeble vine growth and a still lower yield than in 1911."

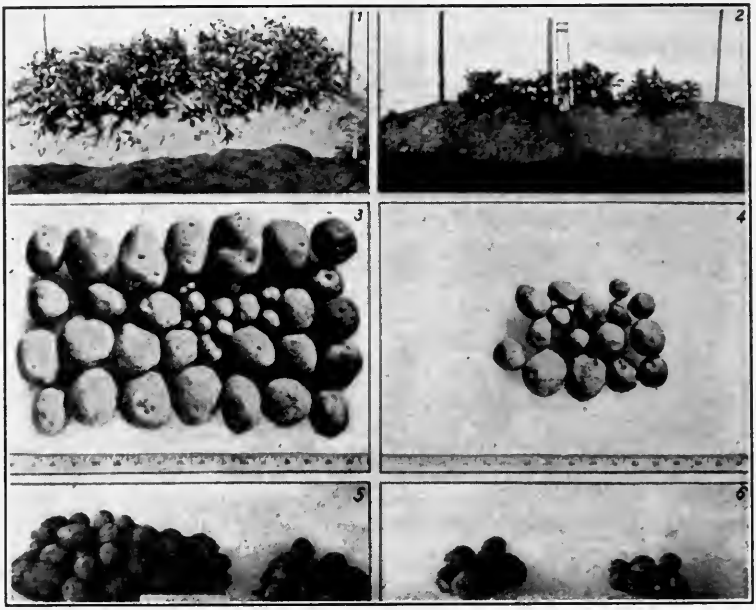


FIG. 163.—Strong and weak tuber-units of the Gold Coin variety of potatoes. Nos. 1 and 2 represent strong and weak tuber-units in 1911; Nos. 3 and 4 represent yields from tuber-units 1 and 2; Nos. 5 and 6 represent yields in 1912 from 5 tuber-units of Nos. 3 and 4. (*After Stuart.*)

There have been many experiments similar to the one above described and they certainly indicate that a certain proportion (from 5 to

10 per cent. according to Stuart) of weak, diseased or unproductive plants are to be found in all unselected varieties. It is equally certain that in the vast majority of cases in ordinary field practice these are unrecognized and the resultant effect upon yield is unnoted. Even though lack of vigor and low yield is entirely due to disease and hill or tuber selection does nothing but eliminate these undesirables, it will be well worth doing. But other characters, as well as yield and vigor, should be kept in mind in attempting to produce an improved strain of potatoes. The ideal market tuber is of medium size, round or oblong in outline and somewhat flattened. The eye should be shallow. The eating quality should not be overlooked, but varieties and tastes differ greatly in this respect. In addition to these, adaptability to local conditions and disease resistance should receive attention.

> "The selection of a large number of high-yielding hills which are then thrown together for mass planting the ensuing year is not likely to result in any marked improvement except by the elimination of the diseased or unproductive plants. The only certain method of securing a superior strain is to plant each selection separately. . . . Every progressive farmer should have his selection plot, in which to grow his yearly selections; and, in addition, he should have his increase plot, where the promising selections may be increased for the field-crop planting" (Stuart).

Certified Seed Potatoes.—The certification of seed potatoes based on official inspections during the growing season and after harvesting has been adopted in some states. According to Milward the summer inspection considers stand, vigor of vine, specific and non-specific diseases and varietal purity; and bin inspection looks after conformity to type, diseases, market condition, quality and yield. In view of the increasing importance attached to disease in the degeneration of potato varieties some such system of inspection and certification should be adopted in every state where potatoes are extensively grown. But it must be borne in mind that complete protection against failure or loss is by no means assured even under a system of seed certification. Stewart has recently reported several instances of sudden degeneration of prolific strains, at the Cornell University Experiment Station, through the invasion of some obscure disease of which there are a number that infest the potato. In some cases only the larger tubers in a hill are affected while the smaller tubers are apparently healthy. Stewart's conclusions follow:

> "(1) Neither normal foliage nor high yield is a guaranty of productivity in the progeny of the following season. Degeneration may occur quite suddenly. (2) It is unsafe to select seed potatoes from fields containing many degenerate plants. Even the normal plants from such fields are liable to produce worthless progeny. (3) Mosaic threatens to become an important factor in the production

of seed potatoes. It is transmitted through the seed. (4) It is doubtful if any method of seed selection will prevent the "running out" of seed potatoes under certain conditions."

Other Crops in Which Bud Selection May Apply.—It is claimed that many desirable varieties of roses, carnations, chrysanthemums, violets and other plants which are cultivated for their flowers originated as bud sports. The best florists are very critical regarding the characteristics of their stock and sports are soon discovered. The importance of propagating from typical, healthy plants is generally appreciated. Many of the roses used for forcing winter blooms produce two types of shoots which are known to the horticulturist as blind and flowering wood. For some years the Bureau of Plant Industry conducted experiments on the selection of buds from the two types of shoots, but it became apparent that the diversity among individual plants in regard to their flowering habits, whether propagated from blind or from flowering wood, was greater than the diversity between the progeny of flowering wood plants as compared with the progeny of blind wood plants. As a result of fertilizer experiments with the variety, My Maryland, Blake inferred that there was a real basis for production of improved strains by bud selection. But he points out that it would require time and much care in selection and that the average florist can hardly attempt to do more than to note the relative vigor of his plants at various stages and propagate from the best producers that are not especially favored by particular environmental conditions.

The strawberry is so important commercially and comes into bearing so soon when propagated from offsets that if bud selection were effective in producing improved strains it would be of tremendous practical value. But the results of experiments indicate that the individual differences so frequently observed in strawberry plants are merely modifications. Whitten reports that bud selection of strawberry plants during a period of 15 years has given no gain in the total productiveness of the plots which originated from high-productive plants over the plots which originated from low-productive plants of the same variety. The experiment began by selecting six plants that yielded four times the amount of fruit of six low-producing plants all of the Aroma variety. Each succeeding year selections in the high-yielding plot were made from the highest plants and in the low-yielding plot from lowest-yielding plants. It is possible that in some varieties of strawberries bud mutations occur more frequently than in others. But in order to find a high-yielding plant whose high-producing character would be maintained among its vegetative offspring it would probably be necessary to test hundreds of individual high-producing plants. Hybridization offers much greater promise in the production of high-yielding strains of strawberries.

Limitations of Bud Selection.—The efficacy of bud selection as a means of improving the type is dependent upon the occurrence of bud mutations; its practicability, upon their frequency. As a method of plant improvement bud selection will always be handicapped because recombinations of factors are possible only in sexually reproduced individuals. Moreover, it appears that in some vegetatively propagated crop plants desirable bud mutations, which can be detected without resorting to statistical methods, are so rare that bud selection can never become a generally used method of producing new varieties, even though it may occasionally be used effectively for that purpose. On the other hand, it is highly practical to give careful attention to the selection of scions from such plants as are known to be healthy and typical of the variety. Such bud selection is a means of preventing the propagation of worthless or undesirable mutations and it should be practised by every nurseryman as a matter of course.

CHAPTER XXIV

BREEDING DISEASE-RESISTANT PLANTS

The term, plant disease, has been restricted by some authors to those disorders and abnormalities caused by fungous parasites only. Other authors have employed the term in a more general sense, including thereunder all abnormal conditions of structure and function which are caused by the different elements of the environment. We shall use the term in this more general sense and for the purpose of this discussion it may be defined as follows. Plant diseases include all the ailments and injuries which can be traced to specific causes or agencies as well as certain functional disorders the causes of which are obscure or difficult of analysis. In order to discuss profitably the breeding of disease-resistant plants it is necessary to consider more fully the various categories of causes.

The Causes of Plant Diseases.—In general the diseases of plants are caused either by unfavorable conditions among the inanimate elements of the environment or by the invasions of other organisms. While every case of disease must be considered as the result of interrelated causal agencies, yet it is usually possible to discover specific agents that are primarily responsible for the pathological condition. It is then possible to determine the nature of disease resistance in particular instances with more or less definiteness according to the nature of the specific causes.

The most important non-living elements of the environment affecting the health and vigor of cultivated plants are the soil, the water supply and the temperature and humidity of the atmosphere. These environmental factors influence plant development in so many ways that the opportunities for maladjustment between plants and their environment are practically endless. Such conditions as excess of alkali or lack of sufficient moisture in the soil or the combination of excessively high temperature and low relative humidity are typical and important illustrations of specific environmental conditions which induce disease in plants.

The living organisms of chief importance in causing plant diseases are insects, fungi and bacteria. Injurious insects may be roughly classified according to their ways of feeding under two heads, viz., sucking and biting insects. The first class includes the plant lice, phylloxerans and scale insects which obtain their nourishment by sucking it from the living plant. The second class includes all moths and butterflies whose larvæ devour living plants as well as beetles and other insects that obtain their food in similar fashion. Pathogenic fungi and bacteria are wholly or partially parasitic. Bacteria which cause plant diseases are those capable of establishing themselves and multiplying in number within the living tissue of the host. A few of the important plant diseases caused by bacteria are "fire-blight" of pears and apples, crown gall of many fruit trees, grapes and other plants, and the black rot of the cabbage. Some fungi, such as rusts and smuts, are strictly internal obligate parasites (as distinguished from those obligate parasites which are wholly or partially epiphytic), *i. e.*, they cannot exist outside the body of a particular host plant or plants except in the spore stage. In such cases the relation between parasite and host is symbiotic. The specific relations between parasites and their hosts vary from a condition of tolerance of the parasite without serious injury to the host to one in which the destruction of the host finally ensues. Many fungi, such as the powdery mildews, are epiphytic although they derive their nourishment from the living plant tissue by means of haustoria. Between the epiphytes on the one hand and the internal parasites on the other are many types of endophytic fungi in which various proportions of the parasite's life cycle are spent within the host plant.

Thus there are many agencies, some non-living as well as many living things, which threaten the normal development of cultivated plants. Even among the parasitic fungi themselves there are many devices for invading the host plant and many instances of specific physiological relationship between parasite and host.

The Nature of Disease Resistance in Plants.—Disease resistance in a plant may be defined as the ability to develop and function normally under conditions such that other plants of the same species fail to develop or are destroyed. Resistance is always either partial or complete. The avoidance of disease by such means as precocious or delayed maturity is hardly to be considered as true disease resistance. Since there are so many agencies which may cause disease in plants it is evident that the ability to resist disease may depend on any one of many characters or it may involve every function of the plant. In either case this ability is a manifestation of the physiological individuality of the plant and hence it may be inherited. Nowhere is this more strikingly shown than in the disease resistance of certain natural species.

Disease Resistance in Natural Species.—The nature of disease resistance in a particular instance is indicated by the nature of the cause of the disease. In the case of non-living causes resistance on the part of certain plants can be explained only as a manifestation of the inherent properties of the protoplasm. Thus the alkali resistance of salt grass, the Australian salt bushes, the common beet and asparagus is a heritable character. If it were not so these species could not perpetuate themselves on soils which are too strong in alkali content for most plants. Similarly with many plant troubles that are referred to adverse soil conditions, such as chlorosis and die back, it has been found that some species are much better able to resist such conditions than other species and within a particular species certain varieties may be more resistant than other varieties. This holds true in the case of other non-living agencies such as excess and deficiency of moisture and heat. For every plant there is a set of optimum conditions and these conditions are very different in different species and among varieties of the same species. For example, rice flourishes in standing water while maize requires well aerated soil. But there are thousands of varieties of rice, each one adapted to the conditions peculiar to a certain locality and there are many varieties of maize which make possible the culture of this species under conditions varying from the humid corn belt to the arid regions of northern Mexico, Bolivia and central China. Similarly in other field crops and in fruits, in various parts of the world there exist species and varieties which are adapted to certain local conditions that would be inimical to normal development of related species and varieties. Agricultural exploration coöperating with systematic seed and plant introduction has already made available for the plant breeder a large number of distinct forms of economic plants which in course of time may revolutionize many productive and manufacturing industries.

Turning now to the phenomena of resistance to the attacks of animal or plant parasites, we find that natural species are characterized by as great diversity in this respect as was observed in the case of resistance to alkali, drouth and other physical elements of the environment. A few specific examples will serve to illustrate this general principle. The relation of different species of the grape to the phylloxera, *Peritymbia vitifoliæ* Fitch (*Phylloxera vastatrix* Planchon), is representative of a great number of reported instances of insect parasitism on vegetation. Also in their general aspects the phenomena of variation in phylloxera resistance among species of the vine are representative of the facts of disease resistance in general. Moreover, on account of the great economic importance which this particular vine disease assumed in Europe some forty years ago, and later in California, there has been a large amount of investigation on the culture of grapes in phylloxera infested regions. The life cycle of this insect includes both leaf-feeding and root-feeding forms. The extent of the injury caused by the warty galls on the leaves is comparatively insignificant. It is the root-feeding form which inflicts serious damage to susceptible vines. On the roots of such vines the characteristic symptoms are of two distinct kinds, viz., small galls or "nodosities" near the tips of young rootlets, and larger swellings or "tuberosities" occurring upon the older rootlets and roots (Fig. 164). The root-tip galls or nodosities are commonly found even on resistant species if phylloxera are present. The principal difference between resistant and susceptible vines as regards reaction to phylloxera attacks is found in the number, size and penetration of the lesions on the larger roots. This phylloxeran is a native of eastern North America and the species of Vitis which are native to this region all exhibit some resistance to its attacks. This resistance of species native to the habitat of a disease-causing parasite is a general fact of great significance to agriculture on account of its potential value in both plant and animal breeding.

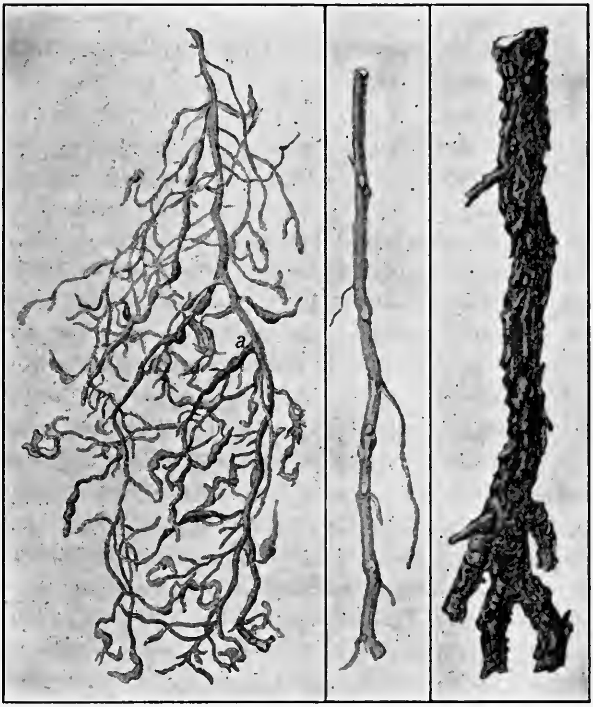


Fig. 164.—Effects of phylloxera on vine roots. On left affected root tips or nodosities; in same figure incipient tuberosities are shown at *a*. Center, non-penetrating tuberosities on an American vine. Right, penetrating and confluent tuberosities on *V. vinifera*, the most serious form of the disease. (*After Viala and Ravaz.*)

The phylloxera was introduced into France through the importation of American vines and it soon became a most serious obstacle to the culture of the choice wine, table and raisin grapes of the Mediterranean region, all of which varieties belong to a single species, *Vitis vinifera*. In fact, every member of this large and valuable plant group has been found to be susceptible to phylloxera thus making impossible its culture as a direct producer, *i.e.*, on its own roots, in a phylloxera infested region. After striving in vain to exterminate the insect in all infested areas, European vineyardists gradually adopted the only other practicable method of grape growing, viz., the grafting of *vinifera* varieties upon resistant roots. The problem of determining which species of Vitis were both highly resistant to phylloxera and well adapted to the soil and climatic conditions of various European localities required extensive investigations. Eighteen native American grapes have been tested as well as several Asiatic species, but the latter were all less resistant than the most susceptible American species. The American vines which have come into most prominence on account of their proven value in the reconstitution of phylloxera devastated vineyards may be listed according to relative resistance about as follows, if the maximum or absolute immunity be taken as 20.

18–19. *V. rupestris.*
18. *V. riparia* and *cordifolia.*
17. *V. berlandieri.*
16. *V. cinerea.*
14–15. *V. æstivalis, linsecomii* and *candicans.*

All of the above species belong to the sub-genus or section, Euvitis. Two of these, *rupestris* and *riparia,* together with certain hybrids between these and between these and *vinifera,* are now considered the most valuable resistant stocks. Another American species belonging to the section *Muscadinia,* viz., *rotundifolia,* has been found to have a resistance of 19 or higher inasmuch as the insect has never been observed on its roots. It is also free from the common fungous diseases of the vine, but the difficulty of propagating it from cuttings and its slight affinity for grafts of other species make it a valueless species for the reconstitution of vineyards. On the other hand, the American species, *labrusca,* has become of great economic importance since it is the parent of the Concord, Isabella, Niagara and many other cultivated varieties. Yet its resistance to phylloxera is ranked at 5, and when grown in California it is no more resistant than is *californica* when used as a rootstock for producing vines, and the resistance of the latter is ranked at 4. Yet the *labrusca* derivatives are extensively grown in the northeastern states and in other northern temperate regions. This is explained by the fact that the phylloxera itself does not thrive below a certain minimum temperature. Thus we find that resistance to phylloxera in the species of Vitis varies all the way from zero in *vinifera* to practically absolute resistance in *rupestris, rotundifolia* and certain hybrids and that the existence of highly resistant forms which are also suitable for vineyard culture has made possible the preservation of an important agricultural industry.

The question of the nature of the cause of resistance to phylloxera has received rather wide attention among investigators, but it has not yet been definitely answered. According to Ravaz, a chemist has thought to measure resistance by the amount of resinous principles in the roots; a physician by the relative duration of the roots; an anatomist by the relative thickness of the medullary rays; but all these explanations have failed to withstand investigation. Foëx states that resistance was first thought to be due to great vigor, large root development and ease of production of new roots but that this was insufficient since some vines of small vigor, like *Vitis monticola*, are resistant while others of great vigor are susceptible. Foëx, himself, traces a relation between the thickness and succulence of the bark of the root and susceptibility. There is also a theory, which originated in Italy, that resistance is due to acidity of the sap and the degree of acidity is highest in seedling plants and in clones which have recently come from seedlings, the acidity decreasing with the age of the variety. But this is contradicted by the fact that *vinifera* seedlings are quite as susceptible as their parents. Variability in resistance of several varieties of grape when grown in different infested localities is accepted by Grassi as evidence of the existence of "benignant" and "malignant" races of phylloxera. But this does not explain the high resistance or immunity of some American species. Having in mind the fact that the phylloxera sucks its nourishment from the leaf or root by inserting its prolonged rostrum into the living tissue, it seems most probable that resistance is to be explained as absence of response to a specific stimulus. The many remarkable instances of hypertrophy in vegetative tissues due to wounds inflicted by insects can be explained satisfactorily only by assuming that the insect injects something into the wound which causes abnormal functioning of the affected parts. If this occurs in the case of phylloxera then resistance consists in failure of the wounded tissue to respond to the foreign element injected by the insect. Such failure of response might be due either to the absence of a particular substance which reacts so as to stimulate growth or to the presence of a specific anti-body which counteracts the effect of the insect's poison. The latter seems the more probable condition in view of what is now known concerning immunity in general. The complete susceptibility of *V. vinifera* would then be due to absence of the anti-body. But the absolute resistance or complete immunity of *V. rotundifolia* may be caused by the presence of a substance which is actually repellent to the insect itself. At any rate, the fact that we are dealing here with distinct natural species makes it reasonably certain that resistance and susceptibility to phylloxera infestation are somatic expressions of genotypic diversity.

Another important case of variation in disease resistance among species of the same genus is found in the relation of various chestnuts to the very destructive bark disease caused by the fungus, *Endothia* *parasitica.* The parasite is a native of eastern Asia where it is parasitic upon native species of chestnut, to which it appears to do relatively little harm. In other words these species are highly resistant to the parasite. However, when the fungus was introduced into America, presumably in nursery stock some 25 years ago, it found in our native species, *Castanea americana,* a very susceptible host (Fig. 165). The parasite has already caused the destruction of the American species throughout the northern Appalachian region and is strongly threatening its complete extinction as a timber tree. Investigations have determined that the European chestnut is also susceptible to the attacks of this fungus, so that the future existence of this species is also jeopardized. The American chestnut is one of our most valuable forest trees and its destruction will entail an enormous loss. A very promising Chinese species is known provisionally as *C. mollissima.* While it is scarcely a timber tree as compared with our native species, yet it may thrive in our climate. As the nuts are of good quality and the tree has shown marked resistance to experimental inoculations on plants already established in this country it is hoped that it will prove to be a successful substitute for the vanishing American species. Even the culture of the American species for commercial nut production in western North America will be constantly threatened. Hence it is fortunate that breeding experiments with the

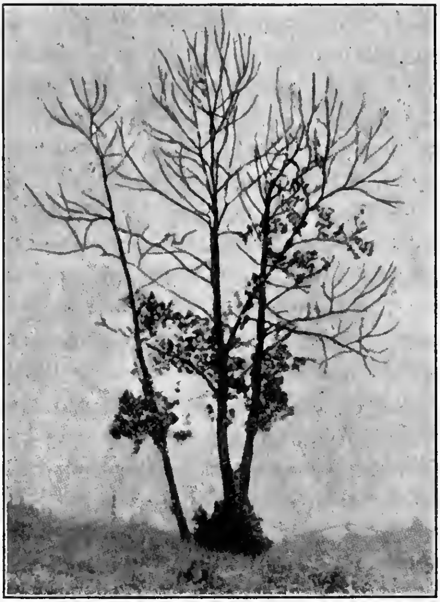


FIG. 165.—An advanced stage of the chestnut bark disease, caused by *Endothia parasitica,* a virulent pathogenic fungus from China. (*From the Journal of Heredity.*)

chestnuts have already been under way some 20 years. To these we shall refer again.

A bacterial organism which finds similar wide diversity in the resistance of possible hosts is the fire-blight pathogene, *Bacillus amylovorus*. Being indigenous in eastern North America, this organism must have maintained itself on the native species of apples and related genera previous to the introduction of European apples, pears and quinces since it cannot survive long even in the dead tissues of the host. The disease is spread naturally by insects that visit infected plants; it may also be carried on pruning tools. Fire-blight is the most widely destructive of all pomaceous fruit diseases; but the pathogene manifests different degrees of virulence in different species. Its most susceptible hosts are the commercial varieties of the pear, which are all derivatives of the European species, *Pyrus communis*. In several regions naturally well adapted for pear growing the culture of this fruit has been abandoned on account of the destructiveness of pear-blight. Even the more resistant varieties of *communis* as well as certain hybrids between *communis* and other species, such as the Kieffer, a supposedly resistant pear, have all proven to be susceptible to the disease when grown in the humid climate of the southern States. Therefore in discussing the problem of blight-resistance in pears it must be remembered that the pathogene itself is very susceptible to environmental conditions and that a particular host which is known to be resistant under one set of conditions will not necessarily prove to be generally resistant. Hence the breeding of blight-resistant pears should be carried on in a region ideal for pear culture in every respect except that it is ideal for the fire-blight organism also. Such conditions exist in southern Oregon where Reimer has made a complete collection of the known species of pears and has conducted scientific tests of their resistance to blight by means of inoculations with pure cultures of the bacillus. The results to date indicate that the following species are highly resistant: *Pyrus sinensis*, *P. ovoidea* and *P. variolosa*. Under *P. sinensis* he finds there are several distinct species which will be classified after they have fruited, but they are all resistant. The birch-leaved pear, *P. betulifolia*, which is used as a stock in China, proved susceptible when the inoculations were made on 1- and 2-year old trees. But it is probable that older trees will show greater resistance and the same may be said of the 16 other species in which inoculation established the disease and which might be considered as susceptible varieties. However, varying degrees of susceptibility were exhibited by these species. Hansen reports the birch-leaved pear as quite resistant to blight in South Dakota where it has grown for over 20 years.

We have now considered one plant disease which may be considered typical of each of the three great classes of disease-causing organisms and in each we find the same diversity among natural species as regards disease resistance. It is unnecessary to multiply instances further. In all likelihood the resistance of the Chinese chestnut to *Endothia parasitica* and of the Chinese Sand Pear to the fire-blight bacillus is due to some specific quality of the protoplasm probably something in the nature of an antitoxin. That this quality is heritable will be seen from the results of hybridization experiments.

Breeding Disease-resistant Varieties by Hybridization.—Allusion was made in Chapter XX to the fact that first generation maize hybrids are often more drouth resistant than either parent. Presumably this is merely one manifestation of heterosis. Hybridization is a very important means, however, for the production of improved varieties which are better adapted to specific adverse elements of the environment. Witness the important results already secured in the production of cold-resistant varieties of fruits, grains and forage plants, by Hansen, Patten and Saunders and at the U. S. Agricultural Experiment Stations in Alaska.

At one stage in the anti-phylloxera campaign in France and California viticulturists held definitely to the ideal of securing through hybridization "a vine that, while resisting the phylloxera, the two mildews, the black rot, etc. (all of which diseases are natives, and which the American vines resist more or less well), will give *without grafting* a grape that has size and the quantity and quality of the *Vitis vinifera*." With this object in mind many crosses were made but they have produced no hybrids between *vinifera* and American species that can be substituted for the choice *vinifera* varieties. It, therefore, became necessary to utilize resistant species and hybrids as stocks on which to graft the producing varieties. However, it is still possible that, by growing large numbers of F_2 and F_3 seedlings from some of the most promising F_1 hybrids, the dream of the viticulturist might be realized. It seems that no grape breeders have carried out extensive tests of hybrids beyond the first generation from the cross. This is not strange inasmuch as grape breeding for phylloxera resistance was at its height during the latter part of the 19th century and before the importance of testing for several generations after a cross was generally appreciated. That phylloxera resistance and susceptibility are conditioned by specific genotypic elements is evidenced by the results of Rasmuson who tested F_2 seedlings from several crosses between certain American species and between American species and *V. vinifera*, as well as crosses between different varieties of *vinifera*. The latter, he reports, yielded only susceptible offspring while the crosses between different American species gave both resistant and susceptible offspring, the latter being in the minority. Resistance appeared to be dominant and susceptibility recessive in the progeny of crosses between American species and *vinifera*. The data are not given but he believes the observed numbers of resistant and susceptible vines favor the assumption of two factors that condition immunity when either is present alone or when both are present together.

FIG. 166.—*a*, Sandcherry, *Prunus besseyi*; *B*, Wyant plum, *P. americana*; *C*, *D*, F_2 hybrids from Sandcherry × Wyant. (*After Beach and Maney, Iowa A. E. S.*)

Resistance to aphis in the stone fruits is thought to be a heritable character from the result of crosses made at the Iowa Experiment Station (Fig. 166). The data permit no reliable conclusions regarding the genotypic relation of aphis resistance and susceptibility in these plants, but the indications are that these characters are conditioned by a single factor difference. Another interesting case of the inheritance of resistance to aphis was observed by Gernert in F_1 hybrids between teosinte and corn. Both the corn root-aphis, *Aphis maidiradicis,* and the corn plant-aphis, *A. maidis,* were involved, and both the teosinte and the hybrids were completely resistant while the corn was badly infested. The desirability of securing aphis resistant varieties of maize will be apparent when it is realized that most of the corn growing regions of North America are infested with these insects and that the loss in reduction of yield caused by them is enormous.

The work of Van Fleet on hybridizing various species of chestnuts was begun 10 years before the terrible bark disease had worked havoc with the chestnut trees near New York City, which is the oldest known center of infection. Hence many crosses were made with either the American or European chestnut as one parent, but in 1907 these were all destroyed by the Endothia. Fortunately however numerous controlled pollinations were made on the bush or Virginia chinquapin, *Castanea pumila,* using pollen of a Japanese species, *C. crenata,* as well as other Asiatic chestnuts. It is asserted that the Asiatic species and the chinquapin-Asiatic hybrids are highly resistant, because few have shown any appearance of infection although surrounded by diseased trees, and that even when infection takes place the injury is quite local in character. Van Fleet adds that second generation seedlings of chinquapin-*crenata* crosses show no disease although constantly exposed to infection (Fig. 167). Thus a beginning has been made in what promises to be an important branch of nut breeding, and the orchard production of commercial chestnuts has been insured against future encroachments by a deadly disease through the timely efforts of a zealous and far-sighted plant breeder.

Fig. 167.—In the center is a nut produced by a cross between the American bush chinquapin, *Castanea pumila,* (right), and the Japanese chestnut, *C. crenata,* (left). Although intermediate in size the hybrid nut is disease resistant and of good quality. (*From The Journal of Heredity.*)

In an attempt to breed blight-resistant pears of horticultural value Hansen has produced and distributed for trial thirty-nine first generation hybrids between various commercial varieties and either the Chinese Sand Pear or the Birch-leaved Pear. Should these hybrids prove to be unsuitable as commercial varieties they may be used as foundation stock in further efforts to produce a hardy, blight-resistant variety. Although the Kieffer and the Le Conte are presumably F_1 hybrids between *sinensis* and *communis*, they have not been used by Hansen because they are not hardy in the north. For lower latitudes however these two partially resistant varieties should be utilized not only by raising seedlings from them but also by an extensive series of crosses especially with other partially resistant *communis* derivatives of high quality such as the Seckel. The work of Reimer and of Hansen indicates that perfectly resistant stocks may be developed which are adapted for each important pear-growing region. If to this achievement may be added the creation of fairly resistant varieties of really excellent quality, the worst difficulties in pear production will be removed and the world's supply of this delicious fruit will be practically assured.

Creating Rust-resistant Commercial Wheat by Crossbreeding.—The grain rusts are the most important of all fungous plant diseases. The annual losses they entail for the grain crops of the world must be estimated in the hundreds of millions of dollars. Although prevention of wheat rust to some extent is now possible by giving careful attention to the water and soil relations of the wheat plant and by early seeding or the planting of early varieties which sometimes escape attacks by rust, yet these diseases still remain a serious menace to the maximum production of wheat. Hence, the creation of rust-resistant varieties has become a very important problem. The diversity among varieties of wheat as regards resistance and susceptibility to rust fungi was recognized by Knight in 1815 and the desirability of creating new varieties which should be resistant to rust as well as highly productive and of good milling quality was fully realized by such breeders as Pringle, Blount and Farrer. Although they were not familiar with the Mendelian principles of segregation and recombination of characters, these breeders of wheat, a self-fertilized annual crop plant, were naturally led to persist in their efforts beyond the F_1 generation. The work of Farrer especially was thorough and reliable. He found that he could not secure absolute resistance to the black stem-rust, *Puccinia graminis* Pers., combined with good milling quality in his wheat crosses even when rigorously selected in the F_2 or "wild" generation as he called it. Most of the soft bread wheats are very susceptible to rust and, when crossed with the resistant durums, poulards and spelts, they give rise to strains which are either poor bread wheats or are rust susceptible. Biffin discovered in 1903 that resistance to the yellow rust, *Puccinia glumarum* Eriks. & Henn., in his cross between Rivet, a slightly susceptible wheat and Red King, a very susceptible variety, was recessive in the F_1 generation but appeared in approximately one-fourth of his F_2 population. Tests of later generations proved that this character bred true. Eriksson tested Biffin's work and found only slight variations in the F_2 ratio and in the intensity of the resistance. However, it appears that resistance of the wheat plant to other species of rust fungi may be inherited as a dominant character. Vavilov reports that he crossed Persian wheat, *Triticum vulgare* var. *fuliguosum* Al., which alone out of 540 varieties was immune to mildew, *Erisiphe graminis* DC., but which was susceptible to brown rust, *Puccinia triticina* Eriks., with other varieties of common bread wheats and secured F_1 hybrids which were immune to both diseases. Thus it is clear that the inheritance of rust resistance is dependent upon the specific relation existing between the parasite and the host.

The practical aspects of breeding rust-resistant cereals is greatly complicated by the fact that resistance in a single variety of wheat, for example, is likely to vary geographically. While this is due in part to the responsiveness of the wheat plant to radical changes in environment, it is probably more often due to physiological variations in the rust fungi. The virility of a given parasite appears to vary not only with the host but with the geographical location. A striking example of this was observed by Mackie in the behavior of Kubanka, a durum wheat of Russian origin. Although this wheat is remarkably rust resistant in the northern Great Plains region, yet when grown on the west coast of Mexico it succumbed completely to the stem rust (*Puccinia graminis* var. *tritici*) which it had resisted successfully in the Dakotas. The explanation of this failure of a supposedly resistant wheat is found in the existence of local physiological races of the species *P. graminis*. Thus Freeman and Johnson found *P. graminis* var. *tritici*, which is supposedly confined to wheat, attacking barley and rye as well. The same results were obtained with oat stem rust, *P. graminis* var. *avenæ*, which readily attacked barley but was less virulent on wheat and rye. The stem rust of barley was found to be most readily transferred to the other cereals. In addition to the barberry numerous wild grasses serve as hosts of the stem rusts which fact still further complicates the problem of breeding for rust resistance. Starkman and Piemeisel have investigated the rusts of about 35 species of grasses and have found six distinct biologic forms of this species of rust, one of which came from an isolated area. Among other important discoveries, they found that more than one biologic form may occur on the same host in nature, sometimes even on the same plant; that these biologic forms can be distinguished from each other morphologically as well as parasitically; that different strains of the same biologic form sometimes differ in degree of virulence on the same host; and that all gradations in susceptibility occur among the hosts, from complete immunity to complete susceptibility to various biologic forms.

Finally, it must be remembered that but little is yet known about the nature of rust resistance. That it is in no wise dependent upon morphological characters appears to be well established. Carleton has pointed out that biochemical investigations are needed in connection with this problem. The recent investigations of Wagner on hydrogen ion concentration and natural immunity in plants representing four genera including the potato resulted in the conclusion that the variation in hydrogen ion concentration in plant tissues is a phenomenon of reaction to the injection of pathogenic bacteria. Also that the course and end results are related to the susceptibility of the plant in question and to the character of the disease as acute or chronic. An investigation now in progress at the University of California (by W. W. Mackie) seems to indicate that there is positive correlation between degree of acidity as indicated by the concentration of hydrogen ions and degree of resistance to *P. graminis* in wheat. A similar investigation of the species of Bromus in relation to the physiological races of the Corn and Grass Mildew, *Erysiphe graminis* DC., as reported by Salmon would be highly desirable. Whatever the nature of the resistant quality may be, there is no question regarding its heritability. But in view of the complicated nature of the problem which we have briefly outlined it would appear to be inevitable that the utilization of resistant varieties of wheat must be confined to limited areas in which adequate tests have proven their adaptability.

Inheritance of Disease Resistance in Other Plants.—The conclusions we have reached in respect to rust resistance hold good in a general way for other parasitic plant diseases. In addition to the typical cases already described brief reference may be made to other notable examples of the successful creation of disease resistant varieties by hybridization and subsequent selection. The next case, however, will be considered somewhat in detail because it serves as an excellent model in method of procedure. The ravages of a group of wilt diseases caused by closely related fungi of the genus Fusarium have been checked through the successful efforts of the United States Department of Agriculture. As reported by Orton these are the cotton wilt, *Fusarium vasinfectum* Atk., the cowpea wilt, *F. tracheiphilum* Erw. Sm., and the watermelon wilt, *F. niveum* Erw. Sm. It is clear that these fungi possess a high degree of adaptation to the parasitic mode of existence. Also that, while the cause of resistance in certain varieties of the host species is not fully established, yet the resistance itself is a physiological quality. No constant morphological differences have been detected between immune and susceptible plants; neither are there observable differences in time of germination, rate of development or period of maturity. Furthermore, the resistance is specific; varieties that resist the wilt may be susceptible to bacterial blight and *vice versa.*

That wilt resistance is a heritable character was strikingly demonstrated by Orton's creation of a wilt-resistant edible watermelon, *Citrullus vulgaris.* All watermelons appear to be very susceptible to the disease. Extended tests in 1900 and 1901 failed to show any basis for selection among the 120 or more varieties tested. Recourse was had, however, to an inedible form of *Citrullus vulgaris* known as citron or stock melon which was immune to wilt. From a cross between this citron and the Eden variety of watermelon F_1 hybrids of "wonderful vigor and productiveness" were raised. The fruits were intermediate in character, having the oval form and stripes of the watermelon and the hard flesh of the citron. The F_2 population was extremely variable in every respect,

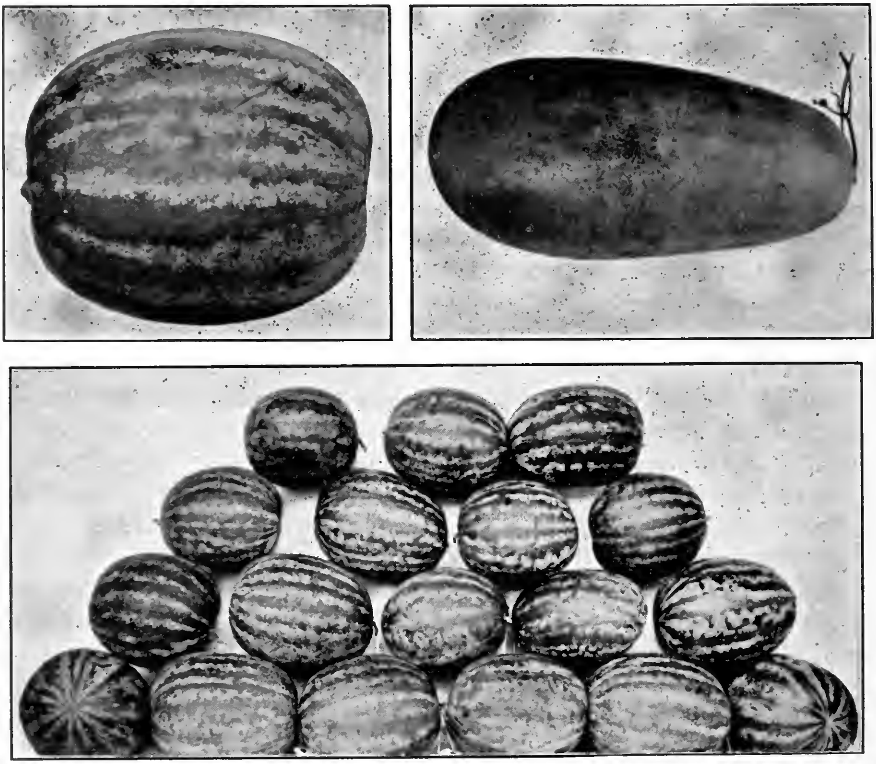


FIG. 168.—Parents and product of third generation offspring of the watermelon-citron hybrid. (*After Orton.*)

the various citron characters appearing to be dominant in the majority of plants. From among 3000 or 4000 plants ten fruits were selected on the basis of resistance and quality and the seeds were planted the following year, 1904, in isolated, infected plots. Of these ten plots two were found to bear melons of uniform appearance and quality one of which resembled the Eden parent. These were sesquihybrids from the F_1 pollinated by Eden. Again all the best melons were selected and planted separately the following year and further variations were found. After five more years of selection a variety was obtained which had great uniformity and disease-resistance while the fruit had a thin, tough rind which enables it to endure long railway shipments. The flesh is so juicy that the melons are heavier than Eden melons of the same size; the quality and flavor are good although not equal to the finest (Fig. 168). These qualities have been preserved and resistance maintained at a distance of 740 miles from the place of origin, but on the Pacific Coast the resistance was not maintained.

This failure of the supposedly resistant variety when grown in a far distant locality is not strange when we remember that the wilt fungi are highly specialized in their adaptation to hosts. According to Orton *Fusarium niveum* attacks no other living plant than the watermelon and "in this respect, coupled with their close morphological resemblance and their common geographical distribution, they seem to be analogous to the biological strains of Puccinia and Erisyphe." In combating all such diseases the importance of developing locally adapted varieties must not be overlooked.

The specific nature and heritability of disease resistance is also evidenced by the results of numerous other experiments among which may be cited the following. In the tomato wilt resistance was found by Norton to be recessive to susceptibility and varieties of Fusarium-resistant tomatoes from Tennessee were found to be susceptible in Maryland. Stuckey found that cherry, pear and currant tomatoes were immune to the blossom-end rot, a functional disease and, when crossed with commercial varieties, they transmitted resistance as a dominant character. Resistance to leaf blight in the cantaloupe was found by Blinn to be inherited as a dominant character. Jesse B. Norton when breeding for resistant varieties in combating the asparagus rust, *Puccinia asparagi* DC., found resistance dominant in all the F_1 offspring in his crosses between the female plants of the rust-susceptible American varieties and a rust-resistant European asparagus. The resistance was somewhat variable but was fixed by selection in succeeding generations. These few cases, taken almost at random, together with the typical illustrations already discussed, amply justify the recommendation that the breeding of disease-resistant varieties of economic plants by hybridization and subsequent selection should receive more attention from plant pathologists and horticulturists in the future.

Breeding Disease-resistant Plants by Selection.—Selection alone is a powerful means of improving plants with respect to disease resistance when used either in variety tests or in the improvement of a single variety. The testing of varieties for disease resistance is an exceedingly important service which can be done most satisfactorily by experiment stations and commercial seedsmen in connection with their routine work. However, the geographical variability in many parasitic organisms and the importance of local adaptation of varieties in many economic plants make it imperative that each important agricultural region should have its own station for variety testing.

The diversity between varieties in respect to disease "resistance" is sometimes due to morphological or anatomical peculiarities which prevent the invasions of parasites. For example, pubescence or waxy excretions on the surface sometimes prevent disease; the number of stomata or the arrangement of cells beneath them may condition fungus infection. Also some varieties escape certain diseases by virtue of their seasonal adaptation or because of precocity. Thus certain grains are less troubled with smut than others because they germinate more quickly. A difference of 2 days in time required for germination may be the deciding factor in smut infection. Certain varieties of potatoes are able to form a corky layer in about 6 hours after being cut while others require 3 or 4 days. Bacteria require from 12 to 24 hours to commence putrefaction through enzyme action. In addition to these and many other varietal differences there is always the possibility of real immunity which is due to some specific physiological character of the variety. A probable instance of considerable importance is the immunity of milo to the smut fungus which is infectious to all other sorghums.

Although there are numerous valuable reports on the disease relations of certain varieties of our important crop plants, much remains to be done in the way of both extensive and intensive testing. The following citations merely illustrate the kind of information that is now available. Recent observations at the Kansas Station on 119 varieties of winter wheat showed infection with orange leaf rust, *Puccinia rubigo-vera tritici* Carleton, varying from 5 to 90 per cent. According to Orton there are varieties of the potato which are partially resistant to late blight and probably also to scab, a matter which has received considerable attention abroad but very little in this country, although there are undoubtedly great possibilities in this work. Orton's success in producing wilt resistant varieties of cowpea was made possible by the discovery of one immune variety, the Iron, which was apparently of chance origin. In future breeding work much time and effort might be saved if agronomists and horticulturists would insist on accuracy with respect to the specific diseases observed in all records of disease resistance or immunity.

The selection of disease-resistant strains is a simple but effective method of improving commercial varieties of many crops. Of course the efficacy of this method in autogamous species is dependent upon the occurrence of mutations or natural hybrids. This is the reason why selection for rust resistance within a variety of wheat is usually wasted effort. But in the majority of crop plants there is more or less crossing and consequently more or less likelihood of picking desirable combinations of disease-resistant factors. As a result of efforts to find a wilt-resistant Sea Island Cotton several strains were obtained by planters and by the U. S. Department of Agriculture, all of which are resistant enough to grow on the worst infected land. Upland cottons are even more susceptible to wilt, but varieties are now grown which are very resistant to wilt and of excellent productiveness (Fig. 169). All of these improved varieties of cotton have been secured by continuous selection beginning with resistant individuals. As a result of his experience in improving varieties of flax for wilt resistance, Bolley has emphasized the importance of continually subjecting the select strains to conditions favorable to the disease but otherwise optimum for the plant. Spragg isolated a strain of alfalfa resistant to leaf-spot by selecting from a few resistant plants

FIG. 169.—Breeding field of upland cotton planted with progeny rows each from the seed of an individual plant. Note difference in resistance to wilt disease. (*After Orton.*)

which were discovered in the 1913 nursery, the result presumably of a mutation. Johnson reports the results of 2 years' experiments on the relative resistance of selected strains of tobacco to the root rot, caused by *Thielavia basicola* (B & Br.) Zopf. A strain of White Burley tobacco has been developed which possesses a high degree of resistance. The Wisconsin Station has successfully combatted the "yellows" and the black rot of the cabbage by selection. Both are very destructive diseases, the first being caused by a fungus and the second by a bacterium. Starting with a commercial variety that is resistant or immune to the "yellows" a strain which is also highly resistant to black rot has been developed. "A stand of from 95 to 99 per cent. of the rot-proof type was obtained on some fields where both the imported Danish and Puget Sound seed failed to give more than 15 to 20 per cent. of a crop." The practical value of such simple selection as the elimination or roguing of all diseased or weakly plants, an ancient practice, must not be overlooked. As was pointed out in Chapter XXIII, much of the value of hill selection in potatoes doubtless lies in the elimination of diseased tubers.

Finally it must be remembered that some diseases or "off-type" states in plants are caused by environmental conditions to overcome which it would probably be impossible to select resistant strains. A case in point is Yellow-berry in wheat which is described as the appearance of yellow or white, mealy or half-mealy, or spotted grains, otherwise without apparent blemish. Its occurrence is believed by Headden to indicate "that potassium is present in excess of what is necessary to form a ratio to the available nitrogen present advantageous to the formation of a hard, flinty grain." He concludes that it is entirely within the control of the grower through employment of proper cultural methods. However, the universal occurrence of Yellow-berry on the Pacific Coast points to something more profound than the potash-nitrogen ratio as the determining cause. If this general factor is climatic, wheat breeding projects on the Pacific Coast should be organized with reference to it in the fundamental tests of commercial varieties and of the various species and sub-species of wheat for the purpose of planning more promising hybridization experiments. Attempts at improvement of existing varieties for resistance to Yellow-berry by selection would appear unwarranted. Especially is this the case if the disease can be counteracted by cultural methods. The need for resistant varieties is also less imperative in the case of many destructive diseases for which methods of control have been successfully devised. Yet it is obvious that an enormous saving to agriculture would come from the production of such varieties. There is a vast field here for the combined efforts of the pathologist and the geneticist.

CHAPTER XXV

PLANT-BREEDING METHODS

In no phase of agriculture is there greater need of scientific planning with reference to economy of time and resources as well as efficiency of method than in plant breeding. In annual species the individual plant is of small intrinsic value as compared with a domestic animal, and generations follow each other in rapid succession. These facts tend to encourage methods that are wasteful or inefficient, or at any rate methods that fail to accomplish all that might be accomplished in a given time. In work with perennial species the need of a scientifically planned system of breeding is even more urgent because of the greater intrinsic value of the individual plant and the longer time required to obtain results.

Pedigree Culture Methods.—The pedigree culture was first used in a systematic manner by Vilmorin in breeding wheat. Later it was adopted by Hays of Minnesota and by Nilsson in Sweden. The essential feature of the pedigree culture consists in rearing successive generations of organisms under such conditions that the ancestry of each individual is known. Its purpose is to insure absolutely accurate knowledge of ancestry. To attain to this ideal many precautions are necessary, and some sources of error, due principally to accident, cannot be entirely eliminated. However the same accident is not liable to happen twice to the same culture and when an accident does occur sometimes the culture can be repeated. Any material whose pedigree is in doubt should be eliminated at once or, if rare or valuable, relegated to the class of unknown until its own behavior in breeding indicates its genotypic nature.

Seedage methods in pedigree culture work with plants are very important. Handling seeds and seedlings requires quite as much care as does castration and pollination especially with very small seeds and this work should be done by the person in charge if possible. However, the work of transplanting and field planting can usually be performed by a person especially adapted and trained for it. The work of taking notes, collecting seed and recording data, on the other hand, should be done by the investigator or breeder. The original label should be collected with the seed and preserved until the permanent records are made; then it should be carefully copied and compared with the written notes before being discarded. As a rule it is well to count the seeds in each bag inasmuch as hybrid seed may prove to be partially sterile or may exhibit delayed germination or other abnormalities.

Planting pedigree cultures involves some of the most difficult problems especially in handling small seeds. Larger seeds such as wheat, corn, peas and beans are handled satisfactorily by planting a single seed in a paper planting pot containing thoroughly sifted soil. If more than one seedling of the species planted should appear in a single pot, it should be discarded. These individual plants should then be set out at equidistant points in the rows and each row labeled. Also at the time of planting a memorandum should be made of the plan of the plot with the position or number and contents of each row as a safeguard in case of loss of labels. Small seeds like tobacco, petunia, primula and even those like the strawberry should be planted in sterilized soil in order that any seeds of the same species that happen to be in the soil will be destroyed. The most satisfactory method of sterilizing soil for seedage is to steam it under pressure. The soil is placed in the clean earthenware pots or seed pans, in which the seeds are to be sown, and these go directly into the autoclave, where they should remain under pressure of 15 pounds to the square inch for at least 1 hour. Where gas is not available for heating the autoclave an alcohol blast lamp may be used. If it is not convenient to prepare the sterilized soil fresh each day as needed, the pots not intended for immediate use should be covered before being sterilized with a piece of fine-meshed fabric which is securely tied below the flange of the pot. This covering is left in place until the pot is used. The manipulator should have clean hands, clothes and utensils and should handle only one lot of seed at a time using due precaution between each lot to avoid mixing. Each lot should be labeled as soon as sown. The seed pots or pans are then moistened by setting them in a vessel containing water, care being taken not to let the water overflow into the seed vessels. All subsequent watering should be by means of sub-irrigation rather than surface watering when dealing with small seeds, or if this is not practicable the water used in sprinkling should be filtered or strained. When ready to prick out, the little seedlings may be transplanted into unsterilized soil provided they are set at uniform distances so that any foreign seedlings that appear later can be distinguished with certainty. This is easily accomplished by selecting a board the same size as the flat and ruling it into squares, then driving tenpenny nails through the corners of the squares. With this tool the holes are made for a whole flat of seedlings at once and they are uniformly spaced. If the seedlings are minute it is a wise precaution to mark each as it is pricked out by sticking a tooth pick into the soil close to it.

Protection of cultures also involves problems which are highly important in pedigree plant breeding but difficult to discuss without entering into considerable detail. The danger may appear in the form of curious or ignorant persons who do not understand the importance of keeping hands off. Or a strong wind may succeed in forcing into the greenhouse seeds of the same species as the one undergoing investigation. Or pests of various sorts may appear—damping off, insect pests, snails, slugs, mice, and in the breeding garden birds, gophers, moles, rabbits, etc. In this connection it may be sufficient to say that eternal vigilance is the price

Fig. 170.—Birdproof cereal breeding garden at the University of California.

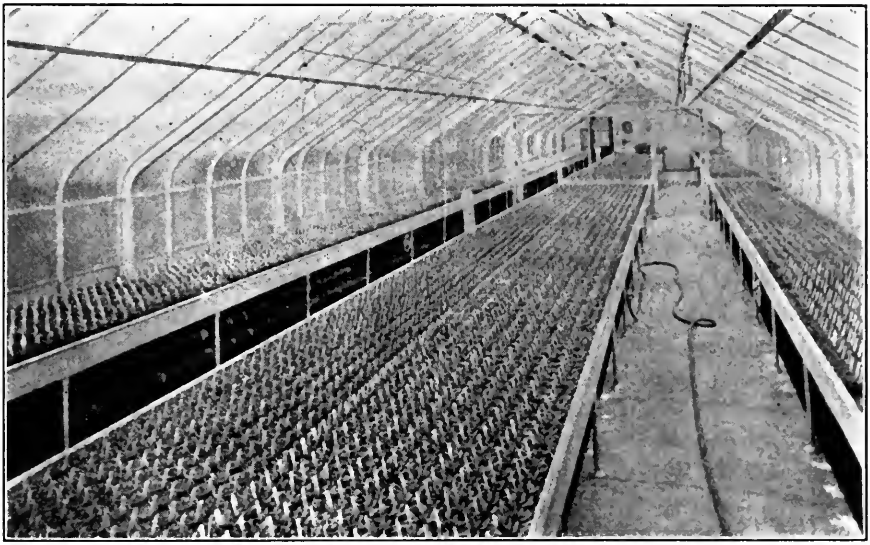
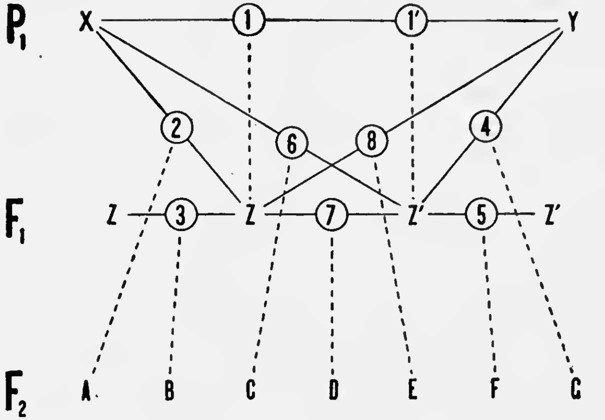


Fig. 171.—Pedigree cultures of Bursa in greenhouse of the Department of Botany, Princeton University. *(Photo from G. H. Shull.)*

of success. Anyone with ordinary ingenuity will usually be able to provide the necessary protection. The important thing is to realize its need in time to prevent loss or contamination of cultures. If the breeding garden is located in or near cities the English sparrow will work havoc with developing seeds, especially of cereals. This menace can be completely overcome only by enclosing the threatened cultures with something that will keep out the birds and at the same time cut off the minimum amount of light. We have found 1-inch mesh poultry netting satisfactory (see Fig. 170). Many plants used in genetic investigations can be handled most satisfactorily in the greenhouse. Fig. 171 shows a greenhouse filled with pedigree cultures of a single species.

A systematic method of recording and preserving data is *sine qua non* for the pedigree culture. It is absolutely unsafe to trust to memory if any degree of accuracy is to be attained. For work on a small scale a serial number (using Arabic numerals) for each culture is satisfactory. This number then becomes the permanent designation of the given culture, each plant in the row receiving a subscript number. Thus plant No. 5 of culture No. 3 would be designated as $3P_5$. If this plant is selected for further testing with self-pollinated seed, its progeny in the next generation will be labeled $3F_1\ P_5\ P_1$, $3F_1P_5P_2$ and so on down the row of plants. However, this method is rather cumbersome and for work upon a large scale the "annual-note-book-page" method first described by Shull is much more satisfactory. In this system each culture of a given year is numbered chronologically receiving the number of the page in the note book for that year on which it happens to be recorded. The label bears this number preceded by the distinctive numerals of that year. Thus the particular culture recorded on page 1 of the 1918 note book will be labeled 181 or 18.1. The use of the decimal point is a convenience especially if one is working at an institution where serial numbers are in use in another department. In addition to the annual note book a set of permanent index cards should be arranged each year, including of course only those actually grown in a given year. By writing the current year number in one corner and the corresponding number for the preceding year in the other corner one has a convenient system for securing the complete pedigree of a given culture. To complete this method some designation is necessary for the individual plants selected in any year. This may be a number in parentheses, a subscript, a letter, or, where plants are set at equal distances from a given base line and each plant is thus numbered automatically, the letter P with subscript is satisfactory. Whatever the individual designation may be, it becomes the name of the particular plant for the remainder of its existence but its progeny will receive a new number when the seed is sown.

A system of labeling and recording that will be at once concise and definitely descriptive of the individuals and the nature of the matings has obvious advantages. Pearl has devised a system which is especially useful in crossbreeding experiments and in work with self-sterile plants; it can be adapted for any material. By the use of letters to denote individuals or types of individuals that are brothers and sisters and numbers to denote types of matings a perfectly general set of terms is provided



TYPES OF MATING IN F_2

F_2 individuals mated	Number of mating	F_2 individuals mated	Number of mating	F_2 individuals mated	Number of mating	F_2 individuals mated	Number of mating
A × X	10	B × Z'	46	C × F	51	E × E	19
A × Y	12	B × B	13	C × G	53	E × F	45
A × Z	40	B × C	37	D × X	22	E × G	47
A × Z'	42	B × D	29	D × Y	24	F × X	30
A × A	11	B × E	55	D × Z	52	F × Y	32
A × B	33	B × F	57	D × Z'	54	F × Z	60
A × C	25	B × G	59	D × D	17	F × Z'	62
A × D	35	C × X	18	D × E	43	F × F	21
A × E	61	C × Y	20	D × F	31	F × G	49
A × F	63	C × Z	48	D × G	27	G × X	34
A × G	65	C × Z'	50	E × X	26	G × Y	36
B × X	14	C × C	15	E × Y	28	G × Z	64
B × Y	16	C × D	39	E × Z	56	G × Z'	66
B × Z	44	C × E	41	E × Z'	58	G × G	23

FIG. 172, Table LVI.—Illustrating a system of labelling F_1 and F_2 individuals resulting from any type of mating. (*Adapted from Pearl.*)

Order of precedence: female named first in every cross; X ♀ × Y ♂ = mating (1); Y ♀ × X ♂ = mating (1'); in back-crosses *later* generation ♀ × *earlier* generation ♂ ranks first, thus Z ♀ × X ♂ = mating (2), X ♀ × Z ♂ = mating (2'), etc.

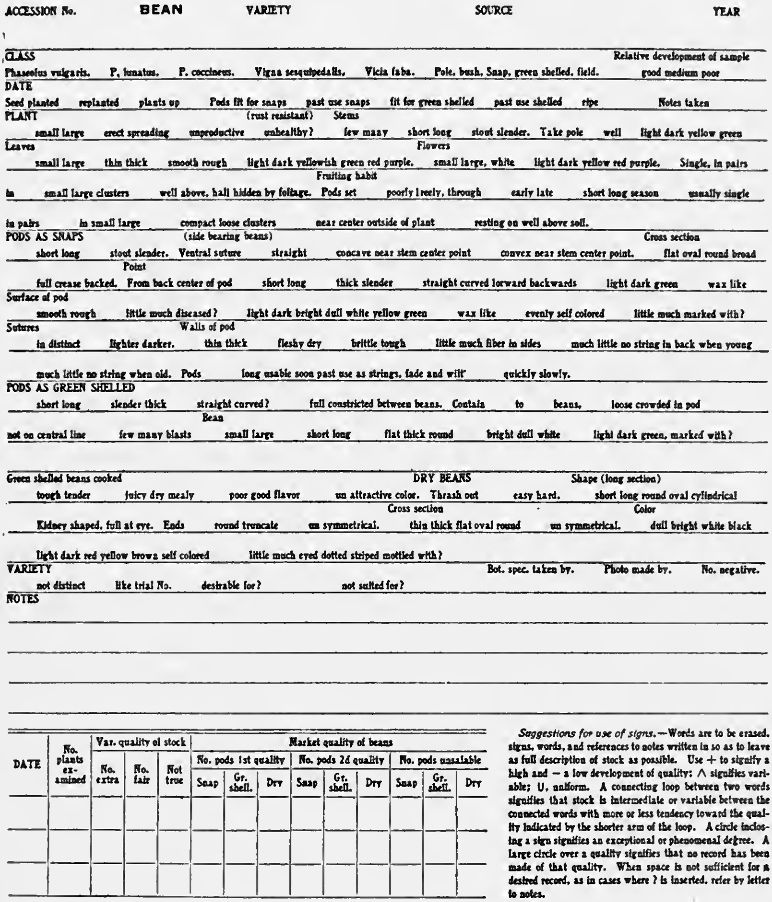
which can be used to describe any pedigree. The scheme described below is essentially Pearl's system with some minor changes. In the diagram (p. 423) solid lines with circles containing numbers indicate matings between the individuals represented by the letters which they connect. Dotted lines lead from the matings to the individuals produced. The order of precedence in nomenclature may be varied to harmonize with the former practice of the investigator. Table LVI indicates every possible combination of F_2 individuals to produce F_3. By priming the mating numbers reciprocal back crosses can be indicated and the kinds of individuals produced may be similarly distinguished. For example, following the order of precedence suggested below the diagram, $Z \times Y$ is mating 8 and produces E but $Y \times Z$ is mating $8'$ and produces E' while E or $E' \times X$ is mating 26 and produces, let us say, N and $X \times E$ or E' is mating $26'$ and produces N'. The order of mating in intra-fraternal crosses will be immaterial except in the case of sex-limited characters when individuals may be distinguished by subscripts. Pearl explains the arrangements of mating numbers in the table as follows:

A word should be added in regard to the system by which the numbers have been assigned to the matings. It might at first sight appear as though the arrangement were an entirely haphazard one. It is not. On the contrary the numbers will be found to conform to the following general principles, which seem likely to be of aid in practical work, as tending to make it easy to recall from a number just what its particular pedigree looks like.

1. All even numbers refer to back-cross matings.
2. All odd numbers refer to co-fraternal or intra-generation matings (not back-crosses).
3. Matings below 2 are of parental generation individuals; between 2 and 8 inclusive are of F_1 individuals; matings over 10 are of F_2 individuals.
4. Even numbers from 10 to 36 inclusive designate back-crosses of F_2 individuals with their *grandparents*, or individuals of the grandparental generation.
5. Even numbers from 40 up designate back-crosses of F_2 individuals on F_1 individuals.
6. In the case of the odd numbers from 11 up it is, *in a general way*, true that the smaller the designating number of a mating the more closely related to each other are the two individuals entering that mating likely to be. This principle of assigning the numbers could not be so precisely followed as the preceding five, but still is perhaps worth a little.

In using such a system it is of course necessary to have the basic table always at hand. The diagram is quickly drawn and the typewritten tables may be pasted in note books or both diagram and table may be printed on cardboard for use in breeding pens or plots.

The Svalöf System.—At the Swedish Institute for the Improvement of Field Crops, Nilsson has worked out a very complete and efficient system of plant breeding. Gradually, as increased appropriations of funds have permitted expansion, a corps of experts has been employed, each investigator concentrating on one or two species, and thereby training himself to distinguish all the different forms so as to judge of the relative value of different combinations of characters. Furthermore a definite course of procedure has been developed as a result of many years of experience during which time marked success has been achieved in the inprovement of Swedish field crops. To begin with the work consisted mainly of variety testing and extensive effort at improvement through mass selection. These methods still find a place in the routine work, but they are of insignificant value as compared with the coördination of intensive methods which makes the Institute's system a model which institutions engaged in similar work may profitably follow. From Nilsson's description we find that the Svalöf system may be briefly outlined under three heads, viz., *genotype selection, strain tests* and *hybridization.* In all this work the methods of pedigree culture are followed so that the original source and performance record of each form grown at the station or distributed for trial can be accurately stated. Genotype selection in all plants except the self-sterile species is accomplished by the pedigree method of testing the progeny of single individuals. In wheat, barley, oats, peas and vetches, which were the first crops chosen for improvement at Svalöf, this means of course the isolation of pure lines from the beginning, and the more recent work with rye, clover, forage grasses, beets, etc., has determined that allogamous species are composed of biotypes which are analogous to the pure lines of autogamous species and which can be segregated from one another by continued inbreeding, exactly as inbreeding in maize has been found to isolate biotypes. Although inbreeding must be continued for several years before these biotypes or strains acquire a satisfactory degree of purity and stability, yet it has been shown already according to Nilsson that this method can be used to bring about the same practical results as have been secured in wheat and other autogamous plants. In connection with this preliminary selection of promising forms the intensive study of the specialists at Svalöf has made each member skilful in detecting different forms in the species with which he is working and in judging the relative value of the characters displayed. Having separated from the population some of the biotypes of which the "variety" is composed, it next becomes necessary to subject all these strains to comparative tests in order that the few superior forms may be discovered and propagated more extensively. This requires long years of careful work and the overcoming of certain difficulties which will be discussed later. The handling of thousands of cultures each year (in 1912 there were over 9500 numbers in the trial plots) has required the devising of many practical arrangements to insure exactness and order. Each distinct strain that has been retained for more extensive trials is regarded as an established variety. Hybridization of cereals had been started at Svalöf upon rather an extensive scale previous to 1900 but it had not given encouraging results. After the announcement of Mendel's discovery this phase of the work was greatly enlarged, particularly with wheat and oats by Nilsson-Ehle. Through the application of Medelian principles new varieties of these cereals have been produced which combine general good qualities with cold-resistance or earliness which makes them better



ACCESSION No. **BEAN** VARIETY SOURCE YEAR

CLASS Relative development of sample
Phaseolus vulgaris. P. lunatus. P. coccineus. Vigna sesquipedalis. Vicia faba. Pole, bush, Snap, green shelled, field. good medium poor
DATE
Seed planted replanted plants up Pods fit for snaps past use snaps fit for green shelled past use shelled ripe Notes taken
PLANT (rust resistant) Stems
small large erect spreading unproductive unhealthy? few many short long stout slender. Take pole well light dark yellow green
Leaves Flowers
small large thin thick smooth rough light dark yellowish green red purple. small large, white light dark yellow red purple. Single, in pairs
Fruiting habit
in small large clusters well above, half hidden by foliage. Pods set poorly freely, through early late short long season usually single
in pairs in small large compact loose clusters near center outside of plant resting on well above soil.
PODS AS SNAPS (side bearing beans) Cross section
short long stout slender. Ventral suture straight concave near stem center point convex near stem center point. flat oval round broad
Point
full crease backed. From back center of pod short long thick slender straight curved forward backwards light dark green wax like
Surface of pod
smooth rough little much diseased? light dark bright dull white yellow green wax like evenly self colored little much marked with?
Sutures Walls of pod
in distinct lighter darker. thin thick fleshy dry brittle tough little much fiber in sides much little no string in back when young
much little no string when old. Pods long usable soon past use as strings, fade and wilt quickly slowly.
PODS AS GREEN SHELLED
short long slender thick straight curved? full constricted between beans. Contain to beans, loose crowded in pod
Bean
not on central line few many blasts small large short long flat thick round bright dull white light dark green, marked with?

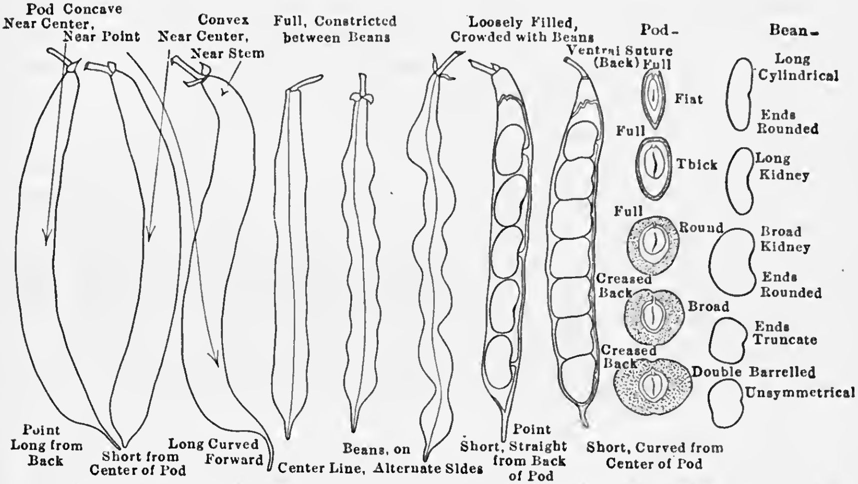
Green shelled beans cooked DRY BEANS Shape (long section)
tough tender juicy dry mealy poor good flavor un attractive color. Thrash out easy hard. short long round oval cylindrical
Cross section Color
Kidney shaped, full at eye. Ends round truncate un symmetrical. thin thick flat oval round un symmetrical. dull bright white black
light dark red yellow brown self colored little much eyed dotted striped mottled with?
VARIETY Bot. spec. taken by. Photo made by. No. negative.
not distinct like trial No. desirable for? not suited for?
NOTES

DATE	No. plants examined	Var. quality of stock			Market quality of beans								
					No. pods 1st quality			No. pods 2d quality			No. pods unsalable		
		No. extra	No. fair	Not true	Snap	Gr. shell.	Dry	Snap	Gr. shell.	Dry	Snap	Gr. shell.	Dry

Suggestions for use of signs.—Words are to be erased, signs, words, and references to notes written in so as to leave as full description of stock as possible. Use + to signify a high and − a low development of quality: ∧ signifies variable; U, uniform. A connecting loop between two words signifies that stock is intermediate or variable between the connected words with more or less tendency toward the quality indicated by the shorter arm of the loop. A circle inclosing a sign signifies an exceptional or phenomenal degree. A large circle over a quality signifies that no record has been made of that quality. When space is not sufficient for a desired record, as in cases where ? is inserted, refer by letter to notes.

Fig. 173.—Variety description blank for beans used by the Bureau of Plant Industry, U. S. Department of Agriculture. (Other face shown in Fig. 174.)

adapted for more northern localities. It has been found, as would be expected, that in breeding for numerous characters at the same time the recombinations in F_2 following hybridization of many select strains are so complicated as to render very illusory the idea of reaching definite results by theoretical calculations. But in spite of this difficulty hybridization offers a means of creating new forms which cannot be obtained otherwise. Thus it is an indispensable supplement to the methods of selection and strain-testing.



Outline Drawing. Check outlines which best illustrate the general form and character of pod and also those showing the characteristics of the beans and their arrangement in the pod.

ACCESSION No. **BEAN** VARIETY SOURCE

Location of trial Section, row to row, inc. Observer Year

SOIL PREVIOUS CROP FERTILIZER USED?
Gravelly, sandy, loamy, clayey, mucky wet dry early late well poorly fitted

AREA
feet of row plants to yard feet between rows samples in trial

CULTURE
from seed in place Cultivation frequent deep thorough Plants sprayed times with?

WEATHER CONDITIONS INSECT INJURY DISEASE DEVELOPMENT OF PLANTS
hot cold dry wet much little none much little none good fair poor

FIG. 174.—Reverse of description blank shown in Fig. 173.

Variety Tests.—The principal purposes of variety testing are first, establishment of varietal types of field crops and vegetable plants, and second, determination of the best varieties for a given locality. In the establishment of varietal types many difficulties are encountered of which we shall consider four.

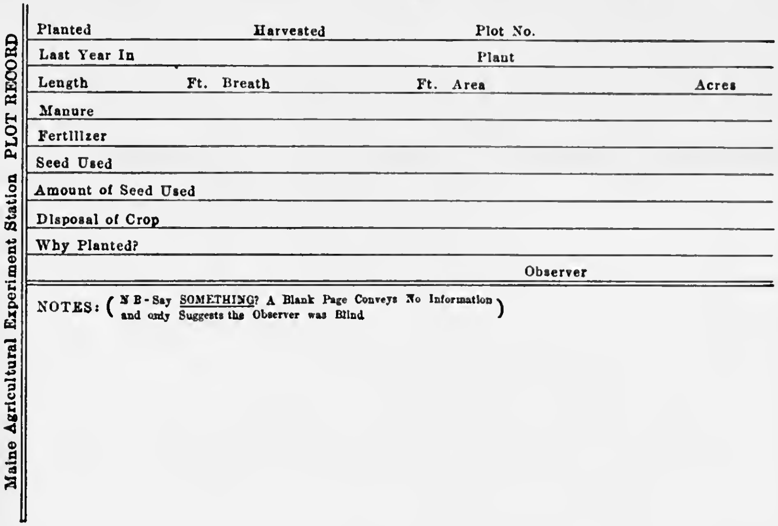
(*a*) *Confusion in Nomenclature.*—Horticultural and agricultural plant nomenclature is in a state of great confusion, a condition which makes it necessary at the outset of scientific variety testing to make taxonomic studies of the known types and to adopt a system of nomenclature which shall be followed consistently throughout the investigations.

(*b*) *Inaccurate Descriptions.*—The type descriptions of many cultivated varieties are either too meager or faulty to be serviceable in critical work or they are wanting altogether. This often makes it necessary to secure seed bearing a given varietal name from various growers to make comparative trials and then to choose the particular lot which may be considered most nearly typical of the variety. Much of this expenditure of time and money could be saved by the general adoption of definite, mechanical methods of describing varieties. The Bureau of Plant Industry of the U. S. Department of Agriculture has advocated for years the wider use of variety description blanks such as the one for beans reproduced in Figs. 173 and 174.

(*c*) *Impurity of Commercial Seed.*—This is one of the most serious difficulties in the way of accurate work in variety testing. Corbett states that practically every sample of seed of any of the turnip-rooted beets will be found to contain 50 per cent. or more of roots resembling more or less closely the form and other characteristics of the variety, but the remaining population will be made up of an admixture of all possible variations of the turnip-rooted beets. The condition in potatoes is also serious according to Corbett and before Stuart undertook by progeny-row and hill-selection methods to establish pure strains of commercial varieties any pretense at variety testing consisted merely in comparing one mixed lot with another mixed lot.

(*d*) *Complexity of Variation.*—The fact that fluctuating variations may be both heritable and non-heritable makes it necessary to use pedigree culture methods in any effort to compare the genetic constitution of varieties.

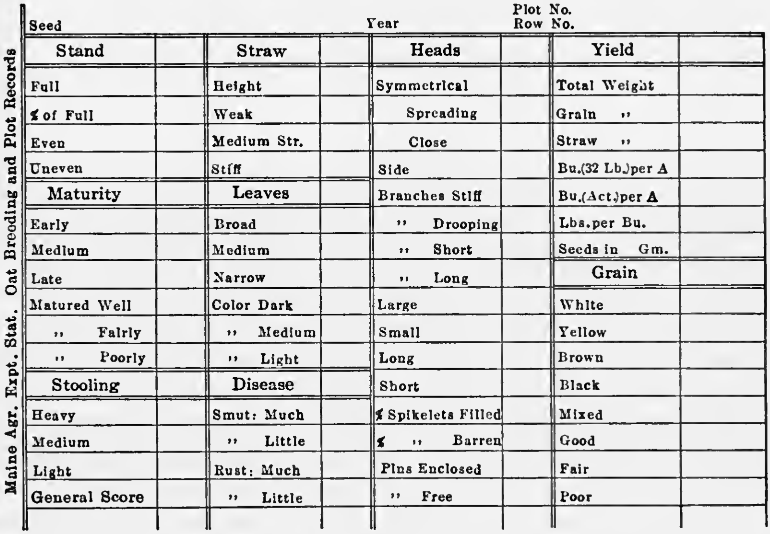
In determining the best varieties for a given location the chief desiderata are yield, quality or chemical composition and uniformity. The chief requisites for success are (1) an adequate system of records; (2) proper interpretation of the results. To facilitate the keeping of accurate notes about each variety the use of loose-leaf printed forms has been found most practicable. Three of the forms used at the Maine Experiment Station are reproduced here. Fig. 175 shows a facsimile of the plot record blank which may be used for any crop and provides for size of plot, fertilization, seed used and general notes. Fig. 176 shows a facsimile of the blank used for recording data on oat varieties. Fig. 177 shows the plot index by which it is possible to trace back the pedigree of any plot culture as plot numbers are never duplicated. This form is used in all the plant-breeding work at that station. These forms illustrate the sorts of records which it is necessary to keep; the sheet for data on varieties would have to be designed especially for each crop plant.


Maine Agricultural Experiment Station PLOT RECORD

Planted Harvested Plot No.
Last Year In Plant
Length Ft. Breath Ft. Area Acres
Manure
Fertilizer
Seed Used
Amount of Seed Used
Disposal of Crop
Why Planted?
Observer

NOTES: (N B - Say SOMETHING? A Blank Page Conveys No Information and only Suggests the Observer was Blind)

FIG. 175.—Facsimile of plot record sheet used in oat variety tests at the Maine Experiment Station. (*After Surface and Barber.*)

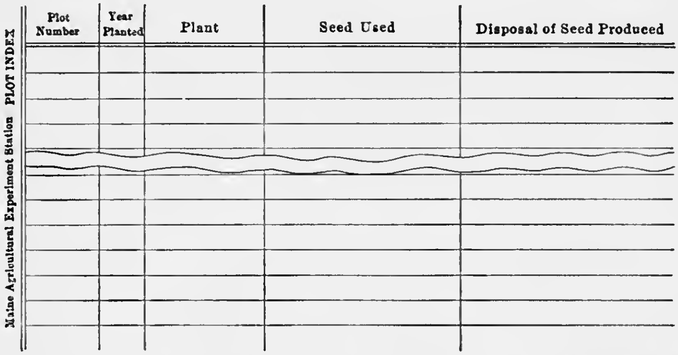

Maine Agr. Expt. Stat. Oat Breeding and Plot Records

Seed Year Plot No. Row No.

Stand		Straw		Heads		Yield	
Full		Height		Symmetrical		Total Weight	
% of Full		Weak		Spreading		Grain ,,	
Even		Medium Str.		Close		Straw ,,	
Uneven		Stiff		Side		Bu.(32 Lb.)per A	
Maturity		Leaves		Branches Stiff		Bu.(Act.)per A	
Early		Broad		,, Drooping		Lbs.per Bu.	
Medium		Medium		,, Short		Seeds in Gm.	
Late		Narrow		,, Long		Grain	
Matured Well		Color Dark		Large		White	
,, Fairly		,, Medium		Small		Yellow	
,, Poorly		,, Light		Long		Brown	
Stooling		Disease		Short		Black	
Heavy		Smut: Much		% Spikelets Filled		Mixed	
Medium		,, Little		% ,, Barren		Good	
Light		Rust: Much		Pins Enclosed		Fair	
General Score		,, Little		,, Free		Poor	

FIG. 176.—Facsimile of oat breeding record used in oat variety tests at the Maine Experiment Station. (*After Surface and Barber.*)

The experimental errors involved in variety testing may be considered under two heads: (1) accidental errors such as incorrect weighing, faulty computation, unobserved variations in field treatment, sampling, etc.; (2) residual errors such as variations caused by soil heterogeneity due to natural conditions or to non-uniform treatment, uneven distribution of soil moisture, etc. The practical questions involved in reducing accidental errors and the experimental determination of the probable error have received considerable attention particularly from English and American agronomists (see papers by Carleton, Farrell, Hall, Hall and Russell, Lyon, Mercer and Hall, Montgomery, Olmstead, Pritchard, Stockberger, Surface and Barber and Wood and Stratton). The need of some suitable mathematical criterion of soil heterogeneity has been pointed out by Harris. The criterion proposed is the coefficient of correlation between neighboring plots of the field. With the method of treatment developed by Harris it has been shown that correlations between the yields of adjacent plots ranging from $r=0.115\pm0.044$ to 0.603 ± 0.029 can be deduced from the data of fields which have passed the trained eyes of agricultural experimenters as satisfactorily uniform. In three out of four cases tested the coefficient was more than 8 times as large as the probable error indicating a relatively large degree of soil heterogeneity. Harris' method in condensed form is as follows:



Maine Agricultural Experiment Station PLOT INDEX

Plot Number	Year Planted	Plant	Seed Used	Disposal of Seed Produced

FIG. 177.—Facsimile of plot index sheet used in all plant breeding work at the Maine Experiment Station. (*After Surface and Barber.*)

Add together the yields of a chosen number of contiguous p plots to form a number m of combination C_p plots. The sum of the squares of p is subtracted from the sum of the squares of C_p and the result divided by $m[n(n-1)]$, where n is the number of ultimate plots in each of the m combination plots. The quotient is reduced by subtracting the square of the mean yields of the ultimate plots p, and the remainder divided by the square of the standard deviation of yields of ultimate plots, σ_p^2. The quotient is the correlation between the yields of the ultimate units, p, of the same combination plot, C_p, the measure of heterogeneity required. If S indicates summation the formula is

$$r_{p_1p_2} = \frac{\{[S(C_p^2) - S(p^2)]/m[n(n-1)]\} - \bar{p}^2}{\sigma_p^2}$$

where n is constant throughout the m combination plots.

Surface and Pearl have devised a method of correcting for soil heterogeneity which when tested by Harris' method was found to give in all cases a very marked reduction in the amount of heterogeneity when the corrected figures were used, and when tested experimentally, it seems that this method leads to results which more nearly represent the truth than do the uncorrected yields. However, this method in its present form is adapted for use only when the plots are arranged in a particular way which is not always practicable with certain crops or on certain areas. It is probable therefore that the older method of check plots or rows together with replicate planting will continue to be used. Following are some of the conclusions reached by Montgomery regarding the reduction of experimental error:

Fig. 178.—Head-to-row nursery (wheat) in which 25 grains from a single head are planted in a row 20 inches long. (*After Montgomery.*)

(*a*) Systematic repetition constantly reduces error as the number of repetitions increases, but with 16-foot row plots 10 to 20 repetitions must be made, depending on the degree of accuracy required.

(*b*) It is probable that the greater the number of strains to be compared the more repetitions will be necessary, because of the greater area they will cover.

(*c*) Small blocks, 5.5 feet square, give results similar to those of the row plots, except that the reduction of experimental error is somewhat greater as a result of repetition. Blocks repeated 8 or 10 times give results apparently about as accurate as rows repeated 15 or 20 times.

(*d*) The rate of planting within certain wide limits, has little influence on yield.

(*e*) There is some competition between adjacent rows, especially when varieties very different in habit of growth are planted side by side. The use of blocks does away with this source of error.

FIG. 179.—Row-plot nursery (wheat) in which the rows are 16 feet in length with a 4-foot alley adjacent, thus making the beds 20 feet in width. (*After Montgomery.*)

(*f*) Block plots and row plots at the usual rates of seeding will probably correlate more closely with results in field plots than in plots where the plants are spaced as in centgeners.

(*g*) Where error is corrected by the system of repetition plots, check plots would be used for the purpose of determining the experimental error. When the variation in checks equals the variation in strains, no possible selection can be made.

Strain Tests.—The chief purposes of strain tests are (1) separation of types within commercial varieties with a view to standardization of varieties and (2) selection of the most profitable strains within a variety. The mixed condition of our varieties of vegetables calls for continual attention on the part of the seedsmen and experiment stations in an effort to bring existing varieties up to some definite standard. One difficulty is found in the widespread use of synonyms, according to Work, who advocates the organization of a recognized board of review which will decide after trial and comparison, whether a submitted sample is worthy of standing as a new variety or simply as a strain or stock. Myers has conducted extensive strain tests of tomatoes and has reached the conclusion that the best way to insure success in procuring high yielding strains of vegetables is to secure seed a year in advance of the time it will be needed and submit it to a preliminary test. The difficulties encountered in selecting the most profitable strains within a variety involve the same sources of experimental error as are met in variety testing. The necessity of distinguishing between heritable and nonheritable variations calls for individual plant selection and pedigree culture methods. Plant-to-row tests and subsequent plot tests of the progeny of individual wheat plants are shown in Figs. 178–181. In all such work the use of loose leaf record blanks is advantageous. Two forms of blanks used in testing pure line selections of oats are shown in Figs. 182 and 183. Plant-to-row strain tests are still generally used with cotton, corn and other cross-fertilized plants, but Hartley has pointed out the importance of reducing experimental error to a minimum in testing corn.

Fig. 180.—Increase plots of one-thirtieth acre each. Selected strains of wheat from the nursery are tested in these plots for 3 years. (*After Montgomery.*)

Factors That Affect Experimental Results.—In discussing the standardization of field experimental methods Piper prepared the following list of factors affecting experimental field work with plants, advising that they be published in connection with any series of field experiments where relative yield is the object sought.

Climatic:

1. Character of season as to rainfall, temperature, etc. (These data are usually available in the Weather Bureau records.)

Edaphic:

2. Character of soil.
3. Preparation of soil.
4. Fertilizers.
5. Cultivations.
6. Irrigations.

Experimental:

7. Size and shape of plots.
8. Error due to marginal effect.

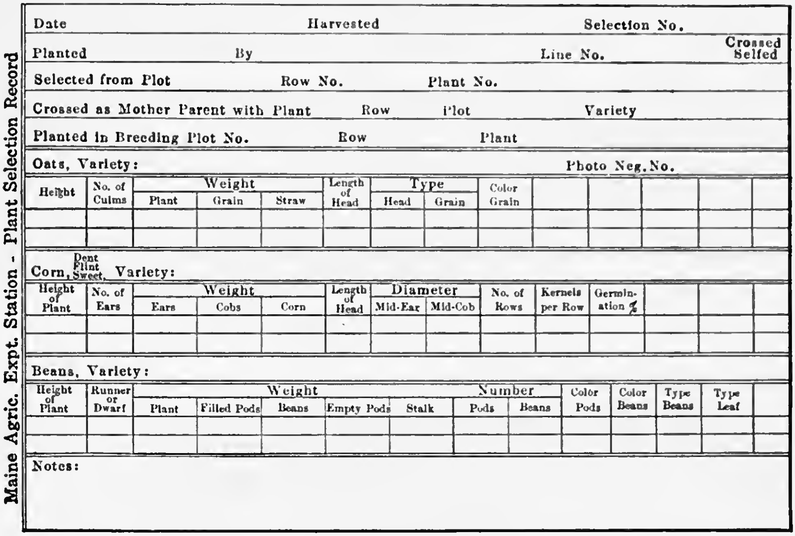
Fig. 181.—Increase plots harvested and ready to thresh. The plots in this field averaged 60 bu. to the acre. (*After Montgomery.*)

9. Method of obtaining yields.
10. Percentage of moisture at time of weighing.

Biological:

11. Variety of plant, including purity and trueness to type.
12. Source of seed.
13. Viability of seed.
14. Preceding crop or crops.
15. Date of seeding or planting.
16. Rate of seeding or planting.
17. Method of seeding or planting.
18. Date of appearance above ground.
19. Percentage of stand.
20. Uniformity of stand.
21. Uniformity of growth.
22. Percentage of weeds.
23. Date of blooming or heading.
24. Date of maturity.

25. Stage and evenness of maturity.
26. Date of harvesting.
27. Damage by disease, animals or weather.



Maine Agric. Expt. Station - Plant Selection Record

Date Harvested Selection No.
Planted By Line No. Crossed Selfed
Selected from Plot Row No. Plant No.
Crossed as Mother Parent with Plant Row Plot Variety
Planted in Breeding Plot No. Row Plant

Oats, Variety: Photo Neg. No.

Height	No. of Culms	Weight			Length of Head	Type		Color Grain					
		Plant	Grain	Straw		Head	Grain						

Corn, Dent Flint Sweet, Variety:

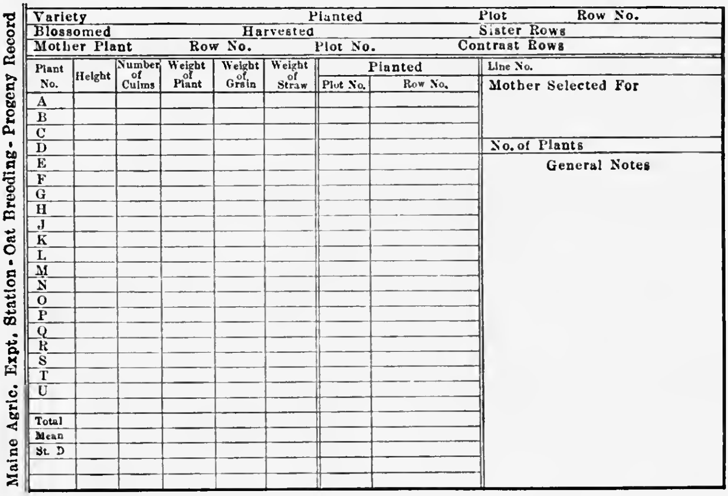
Height of Plant	No. of Ears	Weight			Length of Head	Diameter		No. of Rows	Kernels per Row	Germination %			
		Ears	Cobs	Corn		Mid-Ear	Mid-Cob						

Beans, Variety:

Height of Plant	Runner or Dwarf	Weight					Number		Color Pods	Color Beans	Type Beans	Type Leaf	
		Plant	Filled Pods	Beans	Empty Pods	Stalk	Pods	Beans					

Notes:

FIG. 182.—Plant selection record suitable for oats, corn or beans. (*After Surface and Zinn.*)



Maine Agric. Expt. Station - Oat Breeding - Progeny Record

Variety Planted Plot Row No.
Blossomed Harvested Sister Rows
Mother Plant Row No. Plot No. Contrast Rows

Plant No.	Height	Number of Culms	Weight of Plant	Weight of Grain	Weight of Straw	Planted		Line No.
						Plot No.	Row No.	Mother Selected For
A								
B								
C								
D								No. of Plants
E								General Notes
F								
G								
H								
J								
K								
L								
M								
N								
O								
P								
Q								
R								
S								
T								
U								
Total								
Mean								
St. D								

FIG. 183.—Progeny row record blank. (*After Surface and Zinn.*)

Another biological factor is percentage of soil moisture. Piper also suggests the following standards for variety testing.

Minimum Standards Recommended for Varietal and Similar Tests with Corn.

Duration of trials: Five seasons.

Size of plots in plot-tests: Five rows each of twenty-five hills or each 5 rods long. Outer two rows to be discarded.

Length of rows in row-tests: Twenty-five hills or row 5 rods long.

Number of checks: Every fifth plot or every fifth row.

Number of replications: Five times in rows; at least twice, preferably 3 times, in plots.

In row tests only closely similar varieties should be in contiguous rows.

Minimum Standards Recommended for Varietal and Similar Tests with Small Grains.

Duration of trials: Five seasons.

Plot tests:

Size of plots: $\frac{1}{40}$ to $\frac{1}{10}$ acre.

Number of replications: At least twice, preferably 5 times.

Number of checks: Every third plot.

Margins on outside plots: There should be a border of at least 3 feet to discard. Paths or division strips are preferably avoided when possible.

Blocks: Square, so as to permit changing the direction of the plots from season to season.

Shape of plots: Long and narrow. Each season the series of plots should be laid out at right angles to the previous plots.

Previous crops: The record for 3 years should be given.

Row Tests:

Length of rows: One rod or more.

Distance between rows: Six to 10 inches.

Method of seeding: Drilled at optimum rate of seeding under field conditions.

Rate of seeding: To be indicated.

Checks: Every fifth row.

Replications: Ten times.

In row tests the outside row should always be discarded.

CHAPTER XXVI

GENERAL CONSIDERATIONS AND CONCLUSIONS

In these chapters on plant breeding the primary purpose has been to present the methods by which breeders may make practical application of genetic principles. The introductory historical treatment was intentionally pragmatic in trend. It is only just however that students should recognize the debt which modern agriculture owes to those pioneers in biological science who laid the foundation for the science of genetics through their experimental investigations of plant hybrids. Reference has been made to a number of these men in earlier chapters; we may now briefly consider the general bearing of their work on the development of plant-breeding methods.

The Relation of Science to Plant Breeding.—The influence of scientific discovery on the early history of plant breeding is not marked. The pioneer plant breeders, Van Mons, Thaer, Knight, Cooper, Le Couteur, Shirreff and Hallet, undertook the production of new and improved varieties, while the Linnaean theory of the catastrophic origin of all living things was still accepted by most scientists. Even Hovey, Sutton, Bull and Vilmorin completed most of their work before the publication of Darwin's "Origin of Species." Thus the beginnings of plant breeding were made by florists, horticulturists and agronomists, who observed the defects in commonly grown varieties and sought to improve them or to find better ones. Each attacked the problem in the light of his own knowledge or theories, the later ones sometimes profiting by the experience of their predecessors.

However, while the early plant breeders were working along empirical lines, the first efforts to obtain scientific knowledge of plant hybrids were being made. The conception of sexuality in flowering plants began to be formulated during the last quarter of the 17th century. It was in 1676 that Nehemiah Grew first expressed the idea that the anthers are sexual organs (published in 1682). According to Focke, the knowledge of sexuality in higher plants was really established by Rudolph Jacob Cammerer (Camerarius), whose first experiments were made at Tübingen in 1691. Three years later he published his "Epistola de sexu plantarum." During the first half of the 18th century the famous Swedish botanist, Carl von Linné (Linnaeus), also experimented with hybridization in plants, and his cross between two species of salsify (*Tragopogon pratensis* and

T. porrifolius) which bloomed in 1759, was, according to Focke, the first plant hybrid to be produced for scientific purposes. But Linnaeus' ideas as to the possibility of hybrids between even widely different ancestors were somewhat fantastic.

Meanwhile, another investigator had been laboring on many fruitless experiments. Joseph Gottlieb Koelreuter laid the foundation for the modern study of hybridization in plants. It was not until 1760 that he obtained seeds from a cross between two species of tobacco (*Nicotiana rustica* ♀ × N. *paniculata* ♂). The hybrid plants bloomed in 1761 and the same year appeared his paper on sexuality in plants. He called attention to the rôle of insects in cross-pollination and estimated the number of pollen grains. According to Focke, but little interest was taken in his work by others as he was decades ahead of his time. He accumulated data of the greatest significance on the characters of interspecific hybrids. Besides Nicotiana, he worked with several species of Dianthus, Aquilegia, Matthiola, Melandrium, Linum, Malva, Lavatera, Lobelia, Datura, Lycium, Verbascum and Digitalis.

Toward the close of the 18th and during the first half of the 19th century this work of Koelreuter was extended in some directions by other scientists, notably by Duchesne, Sprengel, Herbert and Gaertner. Duchesne introduced the idea of races into botany and thus helped in breaking down the Linnaean dogma of the constancy of species. Sprengel studied the relations between flowers and insects in great detail. Herbert interested himself in a long series of experiments with species of Erica, Gladiolus, Hippeastrum and Rhododendron, securing many interesting results. He also engaged in a discussion with Knight on fertility in interspecific hybrids. Focke considers this debate in the nature of an introduction to the later more comprehensive controversy between Cuvier and Geoffrey St. Hilaire. Gaertner's experimental work extended over several decades and in number of experiments probably he is surpassed by no other hybridizer, but unfortunately his records and discussions of results are clumsily reported and, according to Focke, their worth is frequently overestimated. His investigation of fertilization was of greater value.

During the last half of the 19th century the scientific knowledge of plant hybrids was extended by a number of other investigators whose contributions have been thoroughly reviewed by Focke. Especially significant for agriculture was the work of Godron, Naudin, Nägeli, Darwin and Mendel. Godron, by hybridization of wheat and spelt, demonstrated the hybrid origin of *Aegilops triticoides* and so destroyed the old tradition that spelt had been transformed into wheat. Naudin opposed the conception, still maintained by Cuvier, that species are hard and fast entities and, based on his experiments in hybridizing different species of the Nightshade Family, he actually discovered, according to Blaringhem, the essential principle of Mendelism, which he expressed as follows: "*La disjonction des deux essences specifiques a lieu dans le pollen et dans les ovules de l'hybride.*" To Nägeli we are indebted for the first scientific treatise on hybridization that was wholly impartial and coherent. His works served as a common source for most of the later discussions of plant hybrids. Meanwhile Darwin had organized a great mass of information bearing on the general subject of adaptation and had discovered one general principle of evolution, viz., the principle of natural selection. The publication of Darwin's discovery was at once stimulating and deterring. It was stimulating to argumentative controversy as well as to certain students of heredity, notably Hoffman, who conducted numerous experiments from 1855 to 1880, and Galton, whose work during the 80's laid the foundation for the biometrical method of treating the data of genetics. Darwin's theory was deterring in its effect on a further widening of the biological horizon, at least so far as the theory of evolution was concerned. Biologists were so well satisfied with his conception that all minute, fluctuating variations are inherited and so may be preserved by natural selection, that but little real progress was made in the study of evolution until the rediscovery of Mendel's discovery in 1900. The work of Mendel, although unappreciated by Nägeli and other contemporaries who knew of it, was destined to revolutionize the study of heredity. By his critical experiments and keen interpretations of the results of those experiments, Mendel laid the cornerstone of the foundation for the future science of genetics. During the 19th century, plant and animal breeding was in progress in various countries and the reported observations of many experimentalists on a multitude of living forms presented an array of diverse and apparently contradictory phenomena, the classification of which under a few natural laws was hardly considered.

With the announcement of the discoveries of Mendel, de Vries and Johannsen during the first three years of the present century, there was a great awakening of interest among biologists in the problems of variation, heredity and evolution. In the enthusiasm of the hour it was thought by some that the application of these laws of heredity and mutation in practical breeding would be comparatively a simple matter. Many plant breeders went zealously to work only to obtain further conflicting and disconcerting results. At the same time research students the world over began new investigations on variation and heredity. The occurrence of mutations and the existence of pure lines in species that reproduce by self-fertilization only have been verified; but to explain the heredity of most plants requires certain modifications or extensions of the three original Mendelian "laws." The investigations which have determined the nature of these modifications and extensions are very recent and they involve considerable technical knowledge of biology, so that at present the progress of research in genetics is far in advance of the practical application of the principles now known. However, some of the fundamental principles of genetics have become available to the practical plant breeder with the result that much unnecessary waste of time and labor has been prevented and that results have become more certain in some cases.

The Future Relation of Genetics and Plant Breeding.—The extent to which factorial analysis has been carried in the cultivated snapdragon and the garden pea is sufficient to indicate what may sometime be accomplished with plants of greater economic value. East has shown the importance of knowing the chromosome number of a species before planning extensive breeding operations, but in many of our important crop plants the chromosome number has not yet been determined. The development of technical plant breeding along definite genetic lines will follow the work of purely scientific discovery, but it must develop more slowly because of the greater length of time required and the expense entailed in the application of genetic principles to crop plant improvement. However, it is not too much to expect that eventually our more important crop plants at least will have been subjected to such thorough germinal analysis, that the establishment of desired strains will become largely a matter of reference to breeding records and the repetition of certain crosses and selections. In other words, it is probable that the improvement of our important seminally reproduced crops will have become so well systematized as to make it possible to predict the outcome of crosses between recognized types, as well as the behavior of new mutants. This factorial analysis must apply to quantitative as well as qualitative characters. Even the discovery that certain characters of economic importance are conditioned by too many factors to make the production of new desired combinations probable except in very extensive cultures, should prove of direct value to agriculture. If the new form is sufficiently desirable the combined resources of several experiment stations or other agencies might be concentrated upon its production. There must be closer coördination of breeding projects for the purpose of avoiding needless duplication and insuring more rapid progress.

The Importance of Planning Breeding Operations in the Light of Scientific Knowledge.—It is maintained by some that two separate and distinct branches of breeding should be recognized, viz., conservative breeding and constructive breeding. The first is supposed to preserve and utilize the desirable characters already in existence; while the second attempts actually to improve the characters of plants and animals. But, as Cook has shown, there is little to support the popular idea that the operations of breeding result in "new creations" in the sense of bringing new characters into existence outside of those already attained in the course of evolution. Moreover, it would be very difficult to maintain a distinction between conservation and construction in modern breeding. A scientifically planned system of breeding improved crop plants must be founded upon suitable methods of testing the species, varieties and biotypes available in order to discover the most promising material for the constructive work of the hybridist.

Uneconomical methods must be eliminated. There are sources of enormous waste in present day plant breeding work. An example is the useless attempt at improving pure lines through continual selection; another is the assumption that a single pure line selection represents all there is in a variety, a serious mistake since most commercial varieties of self-fertilized plants consist of a mixture of pure lines. The frequency of mutations in all economic plants has a direct bearing upon these questions of breeding practice; hence this is a subject which deserves more thorough investigation. The evidence in some species is rather definite, however. In the potato, for example, it is probable that bud mutations are very, very rare. Yet the idea still prevails that disease resistant strains of commercial varieties of potatoes can be obtained by hill selection methods. In a variety susceptible to a given disease such strains would have to originate as bud mutations and, while it is possible of course that such a mutation in a given variety might occur, still in the light of what is now known about the rarity of bud mutations in the potato it is probable that in order to locate such a strain it would be necessary to test millions of plants under conditions favorable for the disease. Severe epidemics occasionally furnish opportunity for such selection on a grand scale. But the scientific plan of procedure is to undertake variety testing on a large scale preparatory to hybridization of the most promising forms.

The matter of adjustment between varieties and local environmental conditions is of considerable importance. This is more widely recognized in cotton perhaps than in any other crop. Cotton growers are generally advised to secure locally grown seed, provided it has been properly selected and handled. Unless recourse is had to the production of F_1 hybrid seed, this consideration of adaptation to local environment is destined to become increasingly important as greater improvement is sought through more intensive selection. For this reason seed production will probably become more localized even though the business of handling and retailing remains in the hands of comparatively few commercial establishments. The recent rapid development and localization of truck crops in the United States as reported by Blair is a case in point. Specialization of this sort is bound to increase along with increase in population and the utilization of superior locally adapted varieties or strains will become correspondingly important.

More comprehensive study of all the factors involved in a plant breeding problem will be demanded of future plant breeders. Not only must the inheritance of the economic characters of each crop plant be determined, but also the important desiderata of correlation between these characters as derived from biometrical studies such as Harris' on the physiology of seed production will need to be considered. Variety and strain tests must become more comprehensive and at the same time more specific as regards standards of selection. The data on disease resistance especially should receive more particular attention. Finally the mathematical adequacy of experimental data derived from breeding investigations is a matter requiring the most serious consideration.

The successful plant breeder will not only approach his problem from a scientific point of view and with a knowledge of genetic principles; he will be conversant with the developing requirements of 20th century agriculture. If he would do his share in the creation of new and more efficient types of crop plants, he must utilize the facts brought to light by botanical, physiological, agronomic and horticultural investigations. Of course there will always be the chance of accidental discovery and the empiricist who operates on a large enough scale will occasionally obtain valuable results. But the scientific plant breeder of the future should combine the qualities of investigator and practical agriculturist. The field is almost unlimited. During the 50 years preceding the war plant breeding had increased the yields of crops in Germany about 25 per cent. There were forty breeders of rye, seventeen breeders of potatoes, sixty of oats, and so on with the important crop plants. When we consider the extent and diversity of agriculture in America and the low average production per acre in most of our important crops, it is evident that the plant breeder has abundant opportunity. Yet it must always be remembered that the full possibilities of applying genetics to breeding problems must await the gradual development of scientific research.

PART III—ANIMAL BREEDING

CHAPTER XXVII

THE GENERAL ASPECTS OF ANIMAL BREEDING

From a scientific standpoint it would be practically useless in this treatment of genetics in relation to animal breeding to develop extensively the historical features of the subject; because they cannot be related effectively and satisfactorily to a growing knowledge and application of the principles of variation and heredity, and because of the peculiar nature of many of the problems of animal breeding. Accordingly this chapter will be devoted for the most part to a discussion of the importance and possibilities of the breeding industry, and of the opportunity for service which genetics has therein.

The History of Animal Breeding.—The domestication of animals occurred very early in the history of man; so early that accurate historical documents do not carry us back within sight of the time when man first began to take wild animals under his care. The history of most of our domesticated animals, in fact, is very incomplete, and in many cases we can only conjecture as to the wild species which were probably subjected to domestication, or from the hybridization of which our tame breeds have had their origin. This difficulty of determining precisely what wild species have been utilized by prehistoric man, or in finding among wild species any which are obviously closely related to those under domestication, is in itself proof conclusive that improvement in herds of livestock, kept at first perhaps in a state of semidomestication only, must have been coincident with the beginnings of domestication. Through long centuries of slow progress the level of excellence in early tribal herds had gradually been raised, partly by the action of factors unknown to and undirected by primitive herdsmen, partly under his conscious direction. As a result man has established numerous races more definitely suited by far to his particular purposes than were their wild ancestors which roamed the plains or inhabited the forests. Consequently even at the dawn of history, domesticated animals had already been developed to a high state of excellence, when measured by their adaptability to particular local conditions of life and their suitability for the purposes for which they had been bred.

During historical times constant improvement has been made in the material thus provided by the early herds and flocks, a century sometimes sufficing for the establishment of a new breed of very superior excellence. Seemingly these have been remarkable achievements, but we must never forget when we consider them that they have been associated almost invariably, particularly those which have been most striking, with changes in the conditions of life of man himself and the purposes for which he has employed his animals. The Arab, nomadic inhabitant of the desert, needed for his purpose a horse of speed and stamina, a single favorite steed sufficing for each individual. Constant association between master and mount developed in the Arab that high pride in the excellence of his steed, a most commendable characteristic of the desert dwellers of Arabia. We find, therefore, that the horses of these peoples are superior in intelligence, stamina, and beauty of form to those of almost any other land; we find them with pedigrees carefully kept and tracing back to the seventeenth century before the Christian era. According to reports of Upton, who lived among the Anezah Bedouins, famed even among the Arabs for the superior excellence of their horses, no animal was recognized as pure bred which did not trace back to the five mares Al Khamseh of Sheik Salaman; and the descendants of these five mares are divided and sub-divided into an intricate system of families and subfamilies. But the modern French farmer with a settled mode of life needed horses for different purposes, primarily for drawing implements of tillage. Accordingly he took horses of the old draft type, large, rawboned, and heavy of weight, but not high in quality or energetic in disposition and crossed them with Arabians, Barbs, and Danish horses; and it was not long before all the neighboring regions of France and Germany were demanding horses from La Perche. No long period of improvement was necessary for the establishment of the Percheron breed; the excellent qualities which it possessed were contained within the old breeds which existed at that time; the improvement was merely a rearrangement and blending of existing qualities in a form to meet the particular demand of modern rural conditions. Such a breed would have been of doubtful value to the barbaric races which swarmed over Europe over a thousand years ago, but for the life that those races lead today, it and other breeds possessing similar utilitarian advantages are performing a tremendous agricultural service. It would be possible to recount similar cases of breed improvement in all kinds of domestic animals. Fundamentally practically all these instances agree in this respect that when breeds have been established within a relatively short period of time, potentialities have been made use of which already existed in the foundation stock. Translated into the more precise terms of genetics this statement would imply that the hereditary material of modern breeds of livestock is made up of elements drawn from that variety of material which constituted the early foundation stock; the hereditary material for the most part represents a recombination of factors already existing rather than discovery and utilization of new factors.

The Animal-breeding Industry.—Any just conception of the extent and magnitude of the animal-breeding industry can only be gained by a consideration of the statistics of animal industry. In crude form these are given for the United States in Table LVII. The total number of the major kinds of livestock on date January 1, 1916, exceeded 200,000,000.

Table LVII.—Estimated Number and Value of Livestock on the Farms of the United States on January 1, 1916

Kind of stock	Number	Average value	Total value
Horses	21,166,000	$101.60	$2,150,468,000
Mules	4,565,000	113.87	519,824,000
Dairy cattle	21,988,000	53.90	1,185,119,000
Beef cattle	39,453,000	34.49	1,321,135,000
Sheep	49,162,000	5.17	254,348,000
Swine	68,047,000	8.40	571,890,000
Totals	204,381,000		6,002,784,000

Their total value which was perhaps slightly augmented by war conditions obtaining at that time was in excess of $6,000,000,000. Animal industry on an average contributes over 35 per cent. of the total income of the agricultural industries. These totals when examined closely show how great is the need and opportunity for improvement. For in this connection it is the average value which is of most importance, and average values as given here do not reflect much credit on the quality of livestock in the United States as a whole.

Particularly is this true when the average value or production is compared with the high-water marks which have been reached within the past few years. Thus to consider a matter upon which we can get fairly specific statistical data of value as a basis of comparison, the average production of the dairy cow in this country is about 3500 pounds of milk, yielding about 150 pounds of butter. The figures are not very accurate, but they are sufficiently so for purposes of comparison. We may compare this figure with the records which have been made by pure-bred cows of dairy breeds. Thus the Holstein-Friesian record is above 30,000 pounds of milk, and is very nearly 1500 pounds of butter. The Jersey record stands at about 1200 pounds of butter, and other breeds are not far behind. The Holstein-Friesian cow Tilly Alcartra produced almost as much milk and butter in 1 month as does the average cow in 1 year.

From an economic standpoint, the importance of high production must be emphasized, because it is closely associated with economy of production. Fig. 184 based upon 443 yearly farm records of dairy cows shows clearly how closely net income is dependent upon high yield.

The comparison of other pure-bred livestock with the general average is not so direct, but is sufficiently striking. The great trotting sire, Peter the Great, with 230 performing offspring to his credit, forty of which had records of 2:10 or better, at 21 years of age sold for $50,000. He was considered so valuable that his service price was placed at $400.

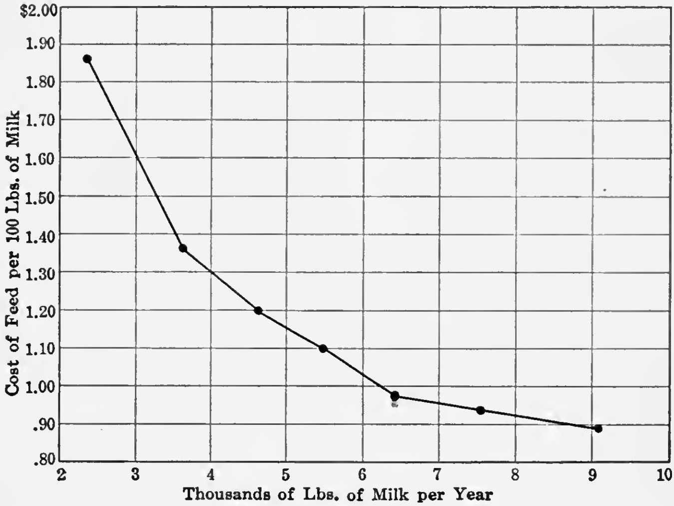


Fig. 184.—Relation of yield of cow to feed cost of milk. (*From* 1915 *Yearbook, U. S. Dept. of Agr.*)

Thirty-two pure-bred Percheron horses sold at auction for an average of $705 per head. A half interest in the Percheron stallion Carnot was sold in recent years for $20,000. Overton Harris sold at public auction 61 head of Hereford cattle at an average price of $1246; and at about the same time the American Hereford Breeders' Association sold 45 head at an average price of $1005. Within the last few years two yearling Holstein-Friesian bull calves have changed hands at public auction at $20,000 each. Forty-six head of pure-bred swine were sold at an average of $214 each. These figures, all of which are of sales which have taken place within recent years, are far above the average of the breeds which they represent, but they are by no means isolated records. The average auction price of pure-bred beef cattle for breeding purposes is at least five times as high as the average farm value of beef cattle, and about the same ratio probably obtains in other breeds of livestock. The figures testify eloquently to the opportunity for improvement which exists in the livestock breeding industry of the country.

The Art of Breeding.—As an inevitable result of the years of careful management to which livestock has been subjected, there has grown up a considerable fund of empirical knowledge having to do not only with the best methods of caring for and feeding animals, but also with the best methods of mating them to ensure the production of the proper type of offspring. Many systems of breeding have been subjected to rigid practical tests; tests which have been duplicated and reduplicated in single breeds and in different breeds. Consequently, although many mystical ideas have often survived over long periods and although some still have their following among practical men, particularly if they happen to have been championed by breeders of outstanding success, nevertheless the tendency has been slowly, but surely, to separate the true from the false. Animal breeding practice in its best form has reached an exceedingly high state of development; the old herdsmen who have grown up among their livestock, although their scientific training may be very limited, are masters of the art of breeding. Like artists in general they do not need to know very much about the composition of the materials with which they work; what they do need to know, and in truth what some of them do know marvellously well, is how to utilize the materials to the best advantage.

The Problems of Animal Breeding.—Here we may be permitted to digress a moment in order to emphasize the fact that the problem facing the animal breeder is different from the one facing the plant breeder. There are many reasons for this fact some of which it may be well to state here in order that no misunderstanding as to the general applicability of the laws of variation and heredity may arise. In the first place in plant breeding we are more particularly concerned with questions of local adaptation and matters of kindred nature. Plants are notoriously susceptible to differences in the environment because of their close relationship to conditions of soil and climate. It is a familiar experience to find that varieties of plants of proven worth in one locality fail miserably to live up to their reputation in some different region. Now to a certain extent this is true also of animals, but it must be patent to anyone that livestock is on the whole relatively independent of environmental influences. Man himself has migrated into new regions from the beginning of time, usually taking his herds with him. Inclemencies in the new surroundings have been met by construction of rude shelters or by seasonal emigrations. In the present time the construction of suitable shelters is, indeed, a universal practice, so that today domesticated animals exhibit an independence from the environment almost as great as that of man himself. As a consequence of the lesser need of considering environmental conditions, therefore, those breeds of livestock which have been improved in older localities have been utilized in the newer agricultural regions such as those of the United States with little if any impairment of their superior excellence. We see this fact expressing itself in the importation of large numbers of animals representing the established breeds of other countries; Shorthorn cattle from England, Jersey cattle from the island of Jersey, Percheron horses from France, and many other notable examples.

In the second place questions of expediency intervene, and this is particularly true when the larger domesticated animals, horses and cattle, are considered. It is usually a simple thing for a plant breeder to grow a thousand individuals in order to try out some idea, but it is out of the question for a practical animal breeder to do so. Ordinarily his system of breeding is dictated by the rigid requirements of the highest total result, he cannot like the plant breeder seek for the one individual among thousands and then satisfied at finding it discard the rest. Too few generations can be obtained in a limited time, too great expense attaches to the raising of progeny which must finally be for the most part rejected, and too great difficulty arises from the universal occurrence of bisexuality among domesticated animals for him to attempt to follow the methods of the plant breeder.

In the third place, and this perhaps is the most important item, animal breeding has progressed to a higher relative state of excellence than plant breeding. With practically all domesticated animals the herdsman has known individually every animal under his care, not only from the standpoint of individual excellence, but with respect to ancestral worth as well. Famous individuals have arisen from time to time the merits of which have attracted the attention of all herdsmen interested in the breeds to which the animals have belonged, and if they proved to transmit their good qualities in any degree, advantage has been taken of the best possible matings to insure the perpetuation of those qualities. This process has gone on to a notable extent in some breeds and with remarkable results; in some breeds it is estimated that not more than 5 per cent., or one individual in twenty, of early animals is represented in the pedigrees of animals living today. The inevitable result of such methods has been to raise the level of the breed to a very high plane, to a position where the only means of improvement lies in a consideration of the finer points of function and conformation, and in methods of maintaining more rigidly the high standards which have been erected. These then in the main are the problems which confront breeders of the best types of livestock; and they are problems, which we may admit frankly, have been handled admirably by the more proficient livestock breeders.

The Service of Genetics.—The geneticist, whether laboratory investigator or philosophical theorist, cannot but admire the excellence of the great body of experience which has grown up from the constant application of the method of trial and error in animal breeding. The art of the breeders' craft is not a thing to ridicule, for measured by the rigid test of results it abundantly justifies itself. The geneticist with all his knowledge of natural law and principle could not successfully compete with the practical breeder in the attainment of a definite standard of excellence, unless he added to his technical training a fund of practical detail. It is moreover too early in the science of genetics rigidly to lay down rules of procedure, particularly if those rules at any point are at variance with the established mode of practical procedure. It is too often the case, as any geneticist will be forced to admit when he reads accounts written not more than half a decade ago on the application of the principles of genetics to livestock breeding, that proper allowance is not often made for the future expansion of our knowledge of genetics itself neither with respect to the extent to which it will go nor the direction which it may take. From time to time in the chapters that follow, we shall have occasion to point out how later developments of the science have given room for beliefs formerly scoffed at.

What then is the service of genetics to practical breeding? Clearly the answer to this question lies in a consideration of the fundamental contrast between the science and the art of breeding. The object of both when applied to practical breeding is to attain and maintain a definite standard of excellence. The standard of excellence is the same, at least there is no good reason why it should not be identical in both cases. With respect to this goal, the art of the breeder merely outlines how it may be reached by the utilization of a system of rules of procedure based on the results of experience. The science of genetics seeks for the natural laws operative in the attainment of standards in general, and in discovering them of necessity includes in its findings the methods by which they may be attained. Obviously the methods of attaining standards are by no means dependent upon a knowledge of the underlying principles; but they may and in this case evidently have run far ahead of scientific knowledge. The service of genetics lies, therefore, in the clarity of thought which it promotes, just as knowledge of principle always reinforces art. This then is the service to the skilled breeder, it tells him why his methods give the success they do, why some things are true and others false, and in case anything is rejected, which is occasionally done because of the stubborn tenacity of some erroneous ideas which by their very construction are difficult at one time both of verification and refutation, it endeavors to describe in terms of the operation of natural laws and principles the actual conditions which obtain, and which are responsible for the erroneous beliefs.

The Service of Genetics in Education.—Up to this point, the discussion of the general aspects of animal breeding has been based upon the practical methods of procedure followed by the most successful animal breeders. The rules of procedure which they follow have been handed down from herdsmen to herdsmen, they are the traditions of the art of animal breeding. They have of course always been modified in directions which the genius of each herdsman may dictate, for indeed much of the success of particular breeders has depended upon the aptitude which they as individuals have shown in dealing with problems of the moment. But these rules of breeding and the methods of employing them to best advantage are not known to any great proportion of the animal breeders of any rural districts. In the United States it is estimated that the number of pure-bred livestock in any state does not greatly exceed 2 per cent. of the total number. Now not even all breeders of pure-bred livestock have attained to the high standard of perfection which we have employed as the basis of discussion in this chapter. To the great body of breeders even the empirical rules of practical breeding, therefore, are either unknown or imperfectly understood.

In considering the service of genetics to this class of animal breeders to whom the best practical methods are merely a mass of confused detail, and to the prospective animal breeder who is just approaching the subject, we must take into account certain pedagogical principles. It is a sound major premise that any established mode of procedure in animal breeding must of necessity owe whatever measure of success it achieves to its conformance with the operation of underlying natural laws. It is also true that a knowledge of these underlying laws, by providing a common explanation for rules of procedure which at first sight appear unrelated and sometimes positively contradictory, tends to simplify the task of learning and applying the proper methods in actual breeding operations. To the novice, therefore, a thorough grounding in the principles of variation and heredity provides the firm foundation to which he may later add the superstructure of a complete practical knowledge. Since it is much easier to remember related things than to hold in mind a confusing mass of technical detail, the novice who has a thorough grounding in principle may, by constantly searching for the reason in every new detail of procedure dictated by experience, so bind every fact to his interrelated body of principle that law and empirical procedure form together an effective, coördinated working equipment.

The Personal Equipment of the Animal Breeder.—Now that we have considered some of the outstanding features of animal breeding as related to genetics, we may well go on to a consideration of the method of attack in seeking to apply the principles of genetics, whether with a view to harmonizing existing procedure with them or in an effort to use them as a guide in the acquirement of that fund of practical knowledge necessary to successful breeding. By this time no doubt many of the facts of heredity which the student has learned must have suggested ideas of practical utility, but at the risk of stating some truths already obvious, a brief consideration may be given to some cardinal features which must be taken into account in considering the relation of genetics to animal breeding. These things must be known in order to make proper use of the principles of genetics in practical animal breeding; they are mentioned here in order that it may be properly understood that this text does not pretend to be a complete manual of animal breeding, but merely endeavors to point out the fundamental relations existing between genetics, as a pure science, and animal breeding, the craft or art of improving animals and maintaining present standards of excellence.

Foremost among the requisites of a successful animal breeder must be the intimate knowledge and experience that comes from actual personal contact with livestock. The success or failure of animal breeding operations often depends on little things, which, if neglected, destroy eventually all the results of the most carefully laid plans. The Bates-Duchess line of Shorthorns were at one time far famed for excellence of conformation, but a neglected tendency to barrenness along with close breeding resulted eventually in the extinction of this superior line of Shorthorn cattle. The method of breeding employed in perfecting this famous family was by no means one which from its very nature from the beginning doomed the line to extinction; on the contrary, it is one which gives the greatest possible degree of success provided it is applied intelligently and with a full appreciation of its consequences for evil as well as for good. The intimate knowledge which a breeder has of his herd should include a knowledge of every individual in it. He should know not only the good and bad points of the individuals but also how these points are related to those of their immediate ancestors. A breeder is on the highway to success when he is so well acquainted with the animals of his herd that he can tell from what immediate ancestor has come for instance a tendency to weakness of pastern, to a sluggish disposition, or ugliness or unwillingness under strain, and similarly for the thousand and one things which must be taken into account consciously or unconsciously in all breeding operations. For minute differences as well as greater ones are heritable, even though as yet they have not been reduced to Mendelian formulation. It would be the height of folly for an animal breeder to call in a geneticist, however well trained, to map out his matings for him. The services of the geneticist can only be in giving the principles involved in breeding; the application must be left to the breeder himself, who must temper his theoretical knowledge with an abundant fund of practical detail.

There is another very important prerequisite for success in animal breeding which comes in part from training, in part from the native ability of the breeder himself, and that is the erection of a true and attainable ideal. It is not necessary here to outline fully the various factors which must be taken into consideration in building up an ideal, but that type when it has become fixed in the breeder's mind, and his breeding can hardly be systematic until his standard has been established, must be within the limits of attainability of the breed with which the herdsmen is working, and it must also be a superior type of that breed designed to fill better than any other some definite economic demand. All these are matters with which genetics properly is not deeply concerned, but they make up, nevertheless, a very definite portion of the subject matter which is included under the term animal breeding. We see therefore that the purpose of an account of the relation of genetics to animal breeding is definitely circumscribed, it is to point out the significance and operation of the laws of genetics in animal breeding, not however to provide a complete compendium on this latter extensive subject.

CHAPTER XXVIII

VARIATION IN DOMESTIC ANIMALS

Half a century ago when Darwin found it necessary to demonstrate the widespread existence of variation, he selected as his most convincing evidence the variability which occurs among domesticated animals and plants. In "The Variation of Animals and Plants under Domestication" he has given us a masterly, and at the same time delightful, account of the extreme variation which is exhibited by domesticated breeds of livestock. Even today although we cannot accept the explanations which Darwin offered to account for these variations, this treatise remains the best general account of variation among farm animals and household pets. But since Darwin's time the point of view has shifted from the question of the occurrence of variation, now universally accepted as an established fact, to the problem of the sources and causes of variation, a problem about which we still have much to learn.

The Sources of Variation.—With regard to their relations to each other and their specific causes, our knowledge of variation in domestic varieties of animals is unfortunately considerably circumscribed. Since, however, it has been demonstrated that variability among all living beings arises from the same general sources, we may with confidence state that among domestic animals, as among other living forms which have been studied in greater detail, variations may be classified with respect to source under three primary heads: somatic modifications, germinal recombinations, and germinal alterations or mutations. Moreover, the behavior within these groups among farm animals is strictly typical for the class in question. Somatic modifications arise from environmental causes, and they are merely transient; they leave no impression, whatever, on the germ-plasm. Variation by germinal recombinations arises from amphimixis, and in domestic animals, we have a growing body of evidence in support of the belief that such recombinations universally follow strictly the Mendelian law of segregation. Definite, authentic cases of mutational changes in higher animals are exceedingly rare, but those which we have leave no doubt that they involve single locus alterations in the germinal material in a manner strictly analogous to that of mutation in the fruit-fly. Of all these kinds of variation, there are good isolated examples among domestic animals, but very often there is a deplorable lack of detail about problems which offhand appear to be very simple and easy of solution. This deficiency will undoubtedly be remedied as the results of definitely planned experiments become known; for the present it is necessary to make the most of the meagre data now at hand.

Selection as a Cause of Variation.—It is unnecessary to reopen here the question of the causal connection between variation and selection, for the arguments which have been presented in various places for the belief that modifying factors, rather than quantitative changes in a given Mendelian factor, are responsible for changes in a given character by selection apply just as well to domestic animals as to any other living beings. It is, however, true that a large number of the characters of farm animals are of a type such that they may be shifted with comparative ease in a given direction by selection. The characteristic white-face pattern of Hereford cattle behaves as a unit in heredity, but unquestionably there is sufficient evidence to show that by continued selection the extent of the white area may be increased or decreased in exactly the same fashion that Castle by selection was able to increase or decrease the amount of the black pigmented area in hooded rats. No experiment, however, has yet been carried out, or is likely to be undertaken, in which over 30,000 Hereford cattle have been bred and raised for the purpose of determining definitely what are the limits of selection for this character. Similarly in such breeds of cattle as the Ayrshire and Holstein-Friesian the proportion of pigmented area to non-pigmented may be shifted at the will of the breeder from a solid pigmented condition to one almost entirely white. With more complex characters such as speed, milk production, and others of utilitarian value the evidence is even more convincing that selection does gradually shift the mean of the race. Whatever may be the true interpretation, there can be no question that the breeder may guide the variation of nearly every character in a definite direction by proper methods of selection.

Variation by Modifiability.—The success of the art of the caretaker and feeder in animal breeding depends upon the existence of a high degree of modifiability in domestic animals. Extreme cases such as the effect of starvation contrasted with the effect of liberal feeding are easily recognized, but in more obscure cases it is difficult to state how much of a given effect is due to inheritance and how much to modifiability. Thus the high standard of present racing records does not depend solely upon more careful attention to the selection of breeding stock, for improvement in methods of feeding, care, and training has been associated with this greater discrimination in the selection of breeding stock. The same fact is true in even greater degree with respect to the marvellous records which have been made by dairy cows during recent years, for elaborate methods of development and feeding have been devised to stimulate production to the highest possible degree. It is necessary, therefore, to exercise unusual judgment in comparing the records of recent years, whether of race track or dairy, with those which have been made a number of decades ago.

With reference to dairy cattle it is possible to make some very interesting comparisons, first of old records as compared with those of the present day, and second of records of cows of uncertain breeding at the present time with those of cows of established dairy breeds. Thus Pearl has unearthed the record of a scrub cow owned by Mr. George A. Scott of Nashville, Tennessee, which in 1863 produced about 12,450 pounds of milk. The record of an Old Sussex cow for the 5 years beginning in 1805 is given in Table LVIII. In recent years a grade Jersey cow produced in 1 year 16,286 pounds of milk, the butter fat content of which, 844.8 pounds, was equivalent to 1056 pounds of 80 per cent. butter. At the time this record was made, it had been exceeded by only four cows within the Jersey breed itself. Scrub cow No. 131 in the government herd at Washington, an old cow between 15 and 20 years of age, was in milk continuously from October 6, 1909 to August 1, 1913, during which time she produced 33,066 pounds of milk. It appears, therefore, clearly to be established that so far as milk yield goes much of the improvement of late decades may have depended upon better methods of care and feeding; for over a century ago cows of very great excellence in this respect were produced occasionally, and at the present time cows of mongrel breeding may sometimes exhibit high performing ability. Undoubtedly, however, there has been an enormous multiplication of the best yielding families during recent years, even if there may not have been any actual increase in dairy potentialities.

Table LVIII.—Production of Milk and Butter by A Cow of the Old Sussex Breed, 1805–1810 (*After Pearl*)

Year	Weeks in milk	Pounds of milk	Pounds of butter
First	48.0	10,580	540
Second	45.5	8,895	450
Third	51.5	12,367	675
Fourth	42.5	9,071	466
Fifth	48.0	11,543	594
Totals	235.5	52,456	2,725
Averages	47.1	10,491	545

Obviously modifiability may act in a variety of ways. An interesting specific instance in dairy cattle is reported by Kildee and McCandlish. At the Iowa Station a comparison was made between seven cows of mongrel breeding, and reared under unfavorable environmental conditions, with seven calves, their offspring, of the same type of breeding reared under favorable conditions since birth. The seven developed scrubs, that is, those which had been reared under favorable conditions since calving, gave 13 per cent. more milk and 12 per cent. more butter than those scrubs which were brought to the station as mature cows. The numbers are not large, but the test as far as each individual was concerned was fair and extensive, covering for the most part four lactation periods. Since the animals while under test were given the same kind of treatment, we may justly conclude that the unfavorable development of those scrubs which were brought to the station as mature cows had permanently lowered their milk producing capacity. This is by no means a surprising conclusion; on the contrary, it is exactly what would have been expected. The same relations obtain in all other characters in domestic animals; modifiability in its effect may be either permanent or transient.

Fig. 185.—A graphic representation of the results of breeding for high winter egg production. The period from 1899 to 1907, that of mass selection: 1908 to 1915 of genotypic selection; the dotted line for low production, the broken line for high production. (*After Pearl.*)

Modifiability and Breeding Value.—Often modifiability is of value to the herdsman in selecting his breeding stock, because it enables him to magnify differences between different individuals, and, therefore, to select his animals more accurately. For if modifiability is proportional to genetic variability, the increased production under forced conditions should be merely a somatic expression of the genetic potentialities of the individual. The trouble, however, is that variability of this kind is very often erratic in character, so much so that forced production, or even performance under more normal conditions, is often a very unsafe guide, except when reinforced by a knowledge of family history.

A most striking case is reported from the Maine Station where breeding investigations in egg production have been carried on for about 20 years. An attempt was made during the period from 1899 to 1907 to increase egg production by a system of mass selection. For breeding stock, pullets were selected which had produced 160 or more eggs during the first year of production, and they were mated to males the mothers of which had produced 200 or more eggs in their first year of production. The results of this rigid system of selection are shown graphically in Fig. 185. The solid line connecting the dots represents the line of actual average winter egg production of the entire flock during the period from 1899 to 1915. The fitted straight line for the period 1899 to 1907 shows clearly that during this period of mass selection there was an actual decrease, rather than an increase, in average winter egg production. Pearl and Surface point out that certain environmental factors may have had something to do with this decrease in production, but even when such factors are accorded a fair maximum effect, the evidence favors the interpretation that this system of mass selection has had absolutely no effect upon the average winter production of eggs.

That this conclusion is a sound one is also supported by correlation studies of egg production of mothers and daughters in these flocks. In Table LIX the winter egg productions of 192 daughters are entered

TABLE LIX.—CORRELATION BETWEEN DAUGHTERS AND MOTHERS WITH RESPECT TO WINTER EGG PRODUCTION, $r = -0.068 \pm 0.048$ (*Data of Pearl and Surface*)

MOTHER'S EGG PRODUCTION

Daughter's egg production	24–27	28–31	32–35	36–39	40–43	44–47	48–51	52–55	56–59	60–63	64–67	68–71	72–75	76–79	80–83	Totals
0–3	1	3	2	.	1	3	7	5	3	5	12	8	.	1	1	52
4–7	.	3	2	.	1	2	2	3	3	3	3	8	.	2	1	33
8–11	1	3	1	.	.	1	1	.	.	2	5	6	.	.	1	21
12–15	.	1	2	.	3	2	.	1	1	1	4	1	.	1	1	18
16–19	1	.	3	.	.	.	3	1	1	1	.	4	.	.	.	14
20–23	.	.	1	.	1	.	1	2	1	1	3	.	.	.	.	10
24–27	.	.	.	.	.	1	1	1	.	2	.	1	.	.	.	6
28–31	1	.	.	.	1	.	2	.	.	1	1	1	.	1	.	8
32–35	2	.	.	.	.	.	.	.	.	.	1	3	.	.	.	6
36–39	.	.	.	.	1	1	.	.	.	.	1	.	.	1	.	4
40–43	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1
44–47	.	.	.	.	.	.	1	1	.	1	1	.	.	1	.	5
48–51	.	.	1	.	1	1	.	.	.	1	.	.	.	.	.	4
52–55	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	2
56–59	.	2	.	.	1	.	1	.	2	.	.	.	.	.	.	6
60–63	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1
64–67	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
68–71	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
72–75	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
76–79	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1
Totals............	6	12	12	0	10	11	20	14	11	19	32	34	0	7	4	192

against the productions of their mothers. The correlation of mothers and daughters with respect to winter egg production, as determined from this table, has the value, – 0.068 ± 0.48. There is, therefore, no demonstrably significant correlation between mother and daughter with respect to winter egg production, and so likewise with spring and total egg production, the correlation coefficients do not differ sensibly from zero.

Fortunately, however, for the efficacy of pure selection in breeding operations, correlation coefficients as low as this one are not usually reported. As an example of the more common condition, we give in Table LX the data of Rietz on correlation between mother and daughter with respect to milk production. The data are taken from the advanced registry records of the Holstein-Friesian cattle. They represent, therefore, selected individuals, for both mothers and daughters have met the requirements for advanced registration. For that reason the values of the constants calculated from these data can only be regarded as approximately representing those which might be given in a population both of individuals which failed and those which succeeded in living up to advanced registry requirements. The value of the correlation coefficient in this case, 0.284 ± 0.025, although low, indicates the existence of a significant degree of correlation.

TABLE LX.—CORRELATION OF HOLSTEIN-FREISIAN MOTHERS AND DAUGHTERS WITH RESPECT TO PRODUCTION OF BUTTER FAT, $r = 0.284 \pm 0.025$. RECORDS FOR 7 DAYS (*Data of Rietz*)

PRODUCTION OF MOTHERS

Production of daughters	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	Totals
11	1	3	1	3	2	1	1	1	..	1	..	.	.	.	.	14
12	1	8	13	12	6	9	5	..	3	1	..	..	1	.	.	59
13	3	18	18	8	13	11	6	3	3	1	..	.	.	.	.	84
14	.	14	18	14	15	11	12	8	2	4	1	.	.	.		99
15	.	12	16	16	11	11	8	3	3	7	3	.	.	.	.	90
16	1	8	13	16	18	11	8	2	2	5	6	2	1	.	.	93
17	.	3	6	11	13	4	8	3	4	6	4	1	.	.	.	63
18	.	3	5	2	8	5	5	2	5	3	2	1	.	.	.	41
19	.	..	2	1	4	3	6	2	2	..	1	2	.	.	1	24
20	1	..	1	7	3	3	3	..	4	..	1	.	.	.	.	23
21	.	..	1	2	..	1	..	..	..	1	..	1	.	.	.	6
22	.	1	..	..	..	..	..	..	1	..	..	.	.	.	.	2
23	.	..	..	1	1	..	..	..	1	..	1	2	.	.	.	6
24	.	..	..	1	..	..	..	1	..	..	..	.	.	.	.	2
25	.	..	..	..	..	..	1	..	..	..	..	.	.	.	.	1
26	.	..	..	..	..	..	..	..	..	..	..	.	.	.	.	0
27	.	..	..	..	..	..	..	..	..	..	..	.	.	.	.	0
28	.	..	..	..	..	..	..	..	..	1	..	.	.	.	.	1
Totals.	7	70	94	94	94	70	63	25	30	30	19	9	2	0	1	608

Modifiability and Correlation.—Low correlation does not necessarily indicate the relative degree and importance of modifiability in a population, for it is possible to have low correlation between parent and offspring as a consequence of genetic variability. This matter may be pointed our very clearly by considering a few abstract cases. Thus a population consisting largely of different, but homozygous, forms would exhibit a high degree of correlation between parent and offspring; whereas one containing more heterozygous individuals would display a lower correlation coefficient, simply because of the segregation which would take place in such a population. This, of course, is simply a development of the general case that an individual of genotype AA would produce only A individuals, provided A were completely dominant, whereas the genotype Aa would produce individuals of its own type and also of type a. On the other hand, modifiability may be the factor determining the value of the coefficient of correlation, even when the degree of conformance to a given standard is very high. Thus if a population be homogeneous genetically, as is the case in pure lines, then the correlation coefficient within the population would be nil, but when a number of different pure lines are mixed together and the correlation coefficient is determined for the mixed population, the value would be very high, although each pure line within itself would exhibit zero correlation.

This matter requires specific attention because some little confusion has grown up from the use of the coefficient of correlation as a measure of the *intensity of inheritance*, a practice of doubtful scientific propriety and one which might well favor misleading conclusions. The lack of correlation, for instance, in egg production of hens and their daughters theoretically does not indicate that attempts to increase egg production will be absolutely futile. It does indicate that some method of breeding must be adopted that will discount at their proper value the influence both of modifiability and genetic variability consequent upon segregation. The theoretical interpretation in this case is borne out strikingly by the practical results of the application of the method of genotypic selection, for as is shown graphically in Fig. 185, there has been a striking increase in egg production from the year in which the method of breeding was changed.

Variation by Recombination.—Unquestionably the greatest possibility for improvement in animal breeding as well as in plant breeding lies in the isolation of recombinations of germinal elements which are better adapted to specific purposes. There is every reason to believe, as we shall point out in the next following chapter, that the architecture of the germ-plasm, if we may use such a term, in domestic animals is similar to that in Drosophila, that is, that the elements of the germ-plasm are contained in definite arrangement in a fixed number of chromosomes. So far as our knowledge goes the chromosome mechanism behaves in a perfectly typical fashion. It is possible, therefore, to state with some degree of confidence that the mechanical details of recombination are the same in the higher animals as in the lower—the conception is a universal one.

But it is perhaps necessary to enquire whence come the germinal elements which are the basis of the great diversity of characters exhibited by domestic animals. All breeds of the northern cattle are interfertile; they appear to belong to a common, related group; and not only that but there are evidences of relationship of this great group with that other great group of humped cattle of the Orient, the zebus. Diversity among horses and sheep is not less striking than among cattle, and even in swine it is very great. So far as present evidence indicates most of this diversity is a consequence of polyphyletic origin; for from the beginning of domestication, man has constantly taken his livestock with him in his wanderings, and has allowed them to mix with whatever other types of the same species they might come into contact.

Although a unanimity of opinion by no means obtains as to the path of descent of modern horses, the evidence of some kind of polyphyletic origin may be regarded as conclusive. Ewart, who has given a good deal of attention to the problem of the origin of domesticated animals, inclines to the belief that the modern horse has sprung from the intermingling of several wild species which may have been connected with the three-toed horse of the Miocene period by different lines of descent. These wild species may be broadly characterized by their adaptability to different habits of life as horses of the forest type, of the plateau type, of the steppe type, and of the Siwalik type. Horses of the forest type were for the most part small, probably of a fawn color, and richly, although not conspicuously, striped. They were adapted to life in the forests and had very definite characteristics which are still seen in some of the modern breeds of horses. Fairly good representatives of this type are met with among the ponies of Scotland and Iceland, and other Eurasian regions. Evidences of forest ancestry are indicated in some modern breeds such as some Arabians and many of the modern breeds of draft horses such as the Suffolk, and in the Shire, Clydesdale, and Percheron to a certain extent. The plateau type of horse comprises many different races, but in general they are all finely built, slender limbed, fleet ponies of which modern representatives are the Celtic ponies of the British Isles and Mexican ponies. Arabs and Barbs and through them the modern Thoroughbred are largely of plateau ancestry; and there is considerable evidence of the same blood in some Shetland ponies. The steppe type of horse, now represented by the Mongolian or Prejvalsky horse, was a fleet, active horse of about 13 hands height, perhaps most distinctively characterized by its large head and Roman nose. The modern Shire and Clydesdale exhibit this type of head, and evidently trace along one line to steppe ancestors, as do other Roman-nosed breeds. The Siwalik horse of India was a tall finely built horse of racing type. Horses of this type may have been over 15 hands high, and they had a peculiar prominence between the eyes which is still met with among some Arabian and Indian horses. Some Thoroughbreds today exhibit characters which connect them with ancestors of the Siwalik type. The evidence, therefore, is very strongly in support of the belief in the polyphyletic origin of modern breeds of horses. In the characters of these ancient ancestors of the horse we may find represented practically all the characters of modern horses.

In historic times there is abundant evidence that mixing of distinct types of horses was a very common practice. In Europe the fleet, finely built horses of the Oriental desert type, particularly the Arab and the Barb, have been used freely in perfecting practically all modern breeds of horses. At about the beginning of the 18th Century, three Oriental stallions, the Godolphin Barb, the Byerly Turk, and the Darley Arabian were used extensively in England, and from this foundation stock sprang the Thoroughbred and Hackney, and later in America the Standard bred. As late as 1820 two gray Arabian horses Godolphin and Gallipoli were used on draft mares in La Perche, and they had a remarkable influence in the direction of superior quality and action in Percheron horses. And this is only one side of the story of diversity in the foundation stock of modern breeds of horses, for without exception they all have a comparatively short history of strict matings confined to the breed standards.

The horse has been chosen merely as an example; other kinds of livestock show just as striking ancestral diversity. Among cattle there is evidence of zebu ancestry in some breeds like the Shorthorn, whereas the Aberdeen-Angus seems to trace to an ancient Syrian race. As in horses so in cattle there has been much mixing of types within historical times. In the case of the domestic fowl, the opinion is usually defended that there is evidence of monophyletic origin, the wild jungle fowl, *Gallus bankiva* being regarded as the common ancestor. But there is evidence that the Malay breeds have descended from another species, and in view of the freedom with which the Malay breeds cross with other breeds of fowl, it may be wise to reserve judgment of the monophyletic origin of barnyard fowls. It is, however, proper to state that many of the breeds of fowls do show differences which are of the value of simple factor differences, or recombinations of a few such original differences;

but some characters seem to be too complex to admit readily of such formulation. We may, therefore, justly draw the general conclusion that the polyphyletic origin of modern breeds of farm animals has been a fruitful source of germinal diversity.

Mutation in Domestic Animals.—The occurrence of mutations in higher animals appears to be extremely rare, at least cases concerning which definite evidence exists are very few. Those, however, which have occurred appear to be strictly analogous in their nature and hereditary behavior to the factor mutations in Drosophila; they involve changes in definite loci in the germinal material.

The Ancon sheep, one of the earliest authentic cases of the occurrence of a mutation, has been discussed at some length by Darwin. This type of sheep first appeared in a small flock kept by a Massachusetts farmer, Seth Wright. The mutant, a ram lamb, was dropped in 1791. It had an unusually long back, and short crooked legs, characters which appealed to Farmer Wright, because sheep which possessed them could not readily leap the fences which were so laboriously constructed at that time. Seth Wright set to work, therefore, to establish a flock of Ancon sheep, and he had no difficulty in doing so. Humphreys, commenting upon the case, emphasizes the trueness with which the Ancon sheep bred to type, there being only one doubtful case of a mating of an Ancon sheep and ram which produced anything but Ancon offspring. In segregation the character was always sharply discontinuous. The evidence that the Ancon sheep arose by mutation is not unimpeachable, it might have arisen by normal segregation of a recessive factor; but since no other case of such segregation of the Ancon factor has been observed, the mutation hypothesis appears best to account for it. The Ancon breed of sheep is now extinct, having been displaced entirely by Merinos.

Darwin discusses another case of a sport in sheep, namely that from which the Mauchamp breed of France is derived. In this case a Merino lamb which was dropped in 1828 had a fleece much superior to that of the general flock; the wool was long and silky, and so desirable as to command a price 25 per cent. greater than that of the best Merino wool. By judicious use of this ram and subsequent rigorous selection M. Graux was able to establish on Mauchamp farm a breed of sheep having all the superior fleece qualities of this animal.

But the case was not clear cut and definite like that of the Ancon sheep. There was no evidence of distinct alternative inheritance, and rigid selection was necessary in order to establish the new characters in a pure race. In fact reëxamination of the records in this case shows clearly that the original ram lamb was not a mutant, but merely an accidental hybrid from a ewe of the Mauchamp flock and a Dishley ram of an adjoining flock. This case, therefore, as Nathusius points out must be struck from the records of observed mutations in domestic animals.

Another case in sheep which has no importance, perhaps, from a practical standpoint is reported from Norway. Wriedt writes that among the old short-tailed sheep of certain districts in Norway, individuals are found occasionally which possess very short ears. The short-ear character is dominant and alternative in expression when contrasted with the normal long-ear type. The records of one rather small flock descended from a single short-eared ewe showed that during 20 years not a single case of the production of short-eared offspring by long-eared parents was observed. The fact of the simple character difference between long and short ears is clearly established by these records, but whether the short-ear type is the result of relatively frequent mutation may be a matter of some doubt. Ritzman in fact has pointed out that the short-ear character of native ewes when contrasted with the normal long-ear type of such breeds as the Rambouillet, Southdown, and Shropshire behaves as a simple character which exhibits alternative inheritance. This confirms Wriedt's observation as to inheritance, but does not add any evidence as to the origin of the short-ear type.

The most frequently cited evidence of mutation in domestic cattle is that of the polled character. Although this character is a simple dominant the evidence of mutation or segregation in particular cases is not always clear. Polled cattle have been known from ancient times and they have not been entirely wanting in the foundation stock of any modern breed. Within recent years the Polled Hereford and Polled Durham breeds have been established by utilization of polled mutants and by grading from horned Hereford and Shorthorn cattle respectively. Within these breeds the so-called double standard animals, *i.e.*, those which are eligible to registry in the corresponding horned breed herdbooks as well as in the polled records, presumably have all sprung from definite mutations. However, of nine polled sports listed by Spillman all except one were known to have near relatives that were polled. The two Hereford bulls Wilson 126,523 and Variation 152,699 both apparently came from horned ancestors. They were used by Boyd in establishing a pure race of polled Herefords. They were both heterozygous, for in matings with horned Herefords approximately half the offspring were polled and half horned. A herd of pure-bred polled Holstein-Friesian cattle has, also, been established in this country, but it appears to have been established by utilization of normal polled animals of which there are some representatives within the breed. Whatever the explanation as to the origin of these rather numerous polled sports, however, there is no question as to the correctness of Bateson's suggestion that the polled condition is dependent upon a single dominant factor difference from the horned condition; so that, given a polled individual, it is the simplest kind of a Mendelian problem to establish a race all the individuals of which are polled.

From the more strictly economic side there is very slight evidence of the occurrence under observation of any definite mutation. Arenander reported some results with milk cows which might indicate mutation. The evidence deals with a cow Örtvart and her progeny. This cow gave milk of an abnormally low fat content, and she transmitted this character to her daughters. But nothing definite is known as to the parentage of Örtvart. Furthermore she was as strikingly distinct in color characters as in low fat content of the milk; she was white with black ears and small spots. Of her seven daughters five are described as of the same color and pattern, the remaining two were of the same pattern but the ears and spots were red. There is no acceptable evidence of mutation in this case, but the evidence of inheritance of the trait of producing milk of low fat content is unmistakable. So also Pearl's case of a mutant in egg production is, probably, as he himself states, merely a case of extreme Mendelian segregation. The data for this case are given in Chapter XXXI. We may conclude, therefore, and rightly, that any system of herd improvement founded on the search for and utilization of mutants is doomed from the beginning to failure, for mutants of a beneficial character appear so rarely as to have almost no practical significance. If by some fortunate chance a breeder should find himself in possession of a favorable mutant individual, however, it is a simple problem in Mendelism to establish its characters in a constant race.

CHAPTER XXIX

MENDELISM IN DOMESTIC ANIMALS

Although there is a lamentable dearth of specific cases of Mendelian inheritance in domestic animals, there is evidence enough to indicate that Mendelian principles are of general validity. The difficulty is merely a practical one consequent upon the long time and great financial expenditure which are necessary for collecting critical data in animals. Thus far we may state confidently, however, that none of the known facts of heredity in farm animals, or in man himself for that matter, is in conflict with Mendelian interpretation. Such an interpretation cannot, however, be *applied* satisfactorily until more detailed knowledge has been collected of the relation of various characters to one another. Thus far practically all Mendelian data in farm animals are from herdbook records, and we have gone about as far as it is possible to go with such material. Henceforth it will be necessary to depend almost entirely upon experimental breeding, if any progress is to be made. This chapter is designed to give a record of about the present status of our knowledge of Mendelian heredity in farm animals.

Mendelism in Horses.—Practically all the Mendelian data for the horse thus far collected deal with coat color. About the only additional data we have is that for the trotting character as opposed to pacing in the Standard bred. However, in addition to the characters just mentioned, Hurst lists the following contrasted characters as allelomorphic: concave and convex faces; straight and curved thighs and hocks; prick-ear, drooping ear, forward droop and outward droop of ears; sprinters and stayers; liability to cataract blindness, breaking blood-vessels and paralytic roaring (contrasted with normal conditions); long-back and short-back. The natural trotting gait appears to be a simple dominant to pacing, although there is still considerable doubt as to these characters. The records in Table LXIV are of interest in this connection for they show that of these ten stallions only one, Electioneer 125, was homozygous for the trotting character. It is true that two pacers are credited to him, but this may possibly be accounted for by training, for it is often possible to change the gait of a horse by proper attention.

Of coat colors, chestnut appears to be the simplest one. Chestnut includes a series of colors varying in depth from dark liver to light sorrel. Chestnut mated to chestnut produces only chestnut. Of 14,131 matings tabulated by Anderson only sixteen of other colors were recorded. Anderson is confident that these were all mistakes, and since herdbook records are in error to the extent of about 2 per cent. this explanation would appear to be acceptable. Suffolk Punch horses are always chestnut, but even in other breeds when chestnuts are produced from matings of horses of other colors, they, when mated *inter se*, produce only chestnut progeny. Of the shades of chestnut, sorrel appears to be recessive to chestnut proper and distinct from it, according to data collected by McCann from studbook records. According to Wentworth, lighter mane and tail, often met with in sorrels, is recessive to the normal darker coloration.

Black is a simple dominant to chestnut, but the data in this case are not so clear cut as for chestnut. For this analysis, we represent the black factor by C. Black varies in shade from a deep, clear black to seal-brown, but very little is known about the relations of the different shades to one another.

Bay is black with a dominant restriction factor B which confines the expression of black to the mane and tail and the extremities in general, the rest of the body being covered with bay hairs. Since the factor B acts only on C it may be present in a latent condition in chestnut horses. This conception, originally suggested by Wentworth, differs from other hypotheses in that it accounts for the fact that black × chestnut matings give a high proportion of bay offspring. Castle suggests that chestnut horses carrying the bay factor be called *sorrel* and those lacking it *chestnut;* but the data presented by McCann indicate that the terms should be reversed, if it be desired to bring the terminology into conformance with common practice.

The position of the so-called brown horses in the Mendelian scheme is a matter over which there has been much speculation. Seal-brown appears to be merely a shade of black; but mahogany-brown, *i.e.*, bay with black patches alternating with bay on the sides of the body, seems to be bay heterozygous for B. The data of Table LXI may be explained by such a formulation, but actual experimental investigations should be carried out, if it be desirable to determine the relations accurately.

Gray is a color in which black and white hairs are intermingled in the coat. Gray foals at birth are very dark, but with age they become progressively lighter until in old horses the color is almost white. As a color gray is not much favored in any except the Percheron breed. The gray factor G is a dominant factor, and its relations to those which have just been mentioned are such that when it is present the coat color is gray irrespective of which of the other factors may also be present. In the Clydesdale gray is tabooed, consequently all gray stallions are castrated, and gray mares are bred to stallions of a different color. According to

Table LXI.—The Transmission of Coat Color in Horses in Various Types of Matings

Mating	Chestnut	Black	Brown	Bay	Gray	Roan
Chestnut × Chestnut	14,115	10	1	5		
Chestnut × Black	111	83	20	124		
Chestnut × Brown	60	32	31	130		
Chestnut × Bay	597	56	49	764		
Black × Black	11	295	15	5		
Black × Brown	14	198	219	115		
Black × Bay	123	295	261	634		
Brown × Brown	13	64	334	157		
Bay × Brown	177	132	817	1,449		
Bay × Bay	474	107	300	2,831		
Roan × Chestnut	9	3	2	9	1	14
Roan × Black	1	11	3	1	0	15
Roan × Brown	1	5	16	18	1	28
Roan × Bay	9	5	13	39	1	50
Roan × Gray	......	...	3	.....	5	7
Roan × Roan	......	...	...	3	2	9
Gray × not Gray		Not gray		528	439	
Gray × Gray		Not gray		18	47	

Wentworth, Cole found in tabulating the offspring of gray mares recorded in the Clydesdale studbook that exactly 50 per cent. were gray and 50 per cent. not gray, which is in strict conformance to expectation.

Roan is a coat color characterized by a slight sprinkling of white hairs in a pigmented coat. The roan color is even less popular in breeds than gray, and it occurs to any great extent only in Belgian draft horses. The roan factor, *R*, is a dominant pattern factor independent of any of the color factors. It is, therefore, possible to have gray roans, red roans, blue roans, and chestnut roans according as the pigmented coat color is gray, bay, black, or chestnut, respectively. Gray roans are not distinguishable from ordinary gray of course, except at birth, so that this class is merely a genetic one not recognized in practical breeding operations. At birth gray foals are black, whereas gray-roans are black with interspersed white hairs. The data of Table LXI indicate plainly enough that roan is a dominant color, but some reports of individual animals are even more interesting. Thus J. Wilson reports that a red-roan Belgian stallion standing for service in Story County, Iowa, was bred to all classes of mares, but all of the 256 foals he sired were red-roan like himself. Another red-roan stallion sired 254 colts of which 230 were red-roan and the remaining 24 blue-roan. These two stallions must have been homozygous for the roan factor, and their breeding records establish clearly the dominance of the roan coat color pattern.

This completes the formulation, so far as our present knowledge goes, for the series of colors, usually met with among horses, but there are a few others more rare and less in favor, the position of which from a genetic standpoint is almost wholly speculative. There appears to be, however, a dominant dilution factor, *I*, which acts upon all the color factors. According to Wentworth black with this factor becomes mouse colored, bay becomes dun of the particular shade known as buckskin, chestnut becomes yellowish dun, and sorrel with lighter mane and tail becomes cream colored with lighter mane and tail. The evidence, however, is by no means extensive enough to be conclusive and should receive experimental verification. There seems, also, to be a white which is distinct from the faded gray of old horses. This white is dominant to any color. Castle considers it an extreme extension toward white of the spotted condition. The types of spotting are mostly dominant over uniform coloration, and often the pattern is very faithfully reproduced. This statement applies to stars, blazes, skewbald markings, calico types of pattern, and other kinds of white spotting of the same general type. Fig. 186 shows a case of accurate reproduction of skewbald markings by the offspring of an Iceland pony when bred to a bay Shetland pony stallion. Tundra had previously produced a dun foal to the service of a stallion of unknown coat color, and subsequently she produced another skewbald foal. Her zebra hybrid foal, however, was of a dun color,

Fig. 186.—The skewbald Iceland pony, Tundra, her skewbald filly, Circus Girl, by a bay Shetland pony, and her hybrid foal, Sir John, by the Burchell zebra, Matopo. (*After Ewart.*)

indistinctly striped. Indistinct striping and other types of marking occasionally occur in horses, but the hereditary relations concerned in their appearance are not well understood.

J. Wilson has advanced a formulation which is fundamentally different from the one which has been outlined above. He assumes that gray, dun, bay, black, and chestnut form a series of polygamous factors as he calls them, multiple allelomorphs according to our terminology, in which each member of the series in the order named is dominant to succeeding members and recessive to the preceding ones. In Fig. 187 we have outlined the possible combinations which could occur within such a series of multiple allelomorphs, and the consequences of such combinations. In addition to this pentuple series of multiple allelomorphs, Wilson assumes that there is an independent dominant roan factor for the roan pattern, and that there are modifying factors which affect the shade and distribution of pigment. Brown he considers a modified bay. Although this formulation is undeniably simpler than the one which was discussed first, it is highly probable that this simplicity is very misleading. The series of colors evidently does not well conform to the general rule of multiple allelomorphism of exhibiting a graded series with a diminishing intensity; but, so far as the stud book records of Table LXI are concerned, about the only place where this formulation fails to meet all the ob-

	g^c	g^h	g^b	g^d	G
G	Gg^c Gray 3 gray : 1 chestnut	Gg^h Gray 3 gray : 1 black	Gg^b Gray 3 gray : 1 bay	Gg^d Gray 3 gray : 1 dun	GG Gray All gray
g^d	g^dg^c Dun 3 dun : 1 chestnut	g^dg^h Dun 3 dun : 1 black	g^dg^b Dun 3 dun : 1 bay	g^dg^d Dun All dun	
g^b	g^bg^c Bay 3 bay : 1 chestnut	g^bg^h Bay 3 bay : 1 black	g^bg^b Bay All bay		
g^h	g^hg^c Black 3 black : 1 chestnut	g^hg^h Black All black			
g^c	g^cg^c Chestnut All chestnut				

FIG. 187.—The genotypes of gray, dun, bay, black, and chestnut coat colors in the horse according to the formulation of Wilson. The way in which animals of a particular genotype behave in a subsequent generation when mated together is shown in each square.

served facts is in the relation of bay, black, and chestnut to one another. Wilson's formulation does not account for the production of bay foals from matings of chestnut and black, although such matings produce a large proportion of bay foals, whereas the first formulation accounts for them very simply. Moreover the first analysis is more nearly in harmony with our knowledge of the inheritance of coat color in rodents, which is so well understood that there is no question of this kind as to factor relations. Wilson's formulation, however, is of this service: it points out clearly how uncertain are analyses based on herd book records, and thereby at the same time indicates the need of actual experimental investigation. It would be a very simple matter to demonstrate experimentally which of these analyses accounts for the actual factor interrelations.

We cannot refrain here from indicating some of the consequences in breeding practice of a formulation such as the one we have favored in this discussion. The really important feature of the analysis, of course, lies in the emphasis it gives to the definiteness of phenomena of coat color inheritance in the horse. In every case there is a definite reason why a horse should be of a certain color, and the reason is comparatively simple. Moreover, since the phenomena are so definitely predetermined, it is possible within certain limits to control them.

To take a definite instance, the government has set itself the task at the Iowa station of creating a gray breed of draft horses. Since gray is dominant to all the common horse colors save roan, it is impossible to get gray from matings of other colors. Moreover, grays when mated together produce gray, bay, brown, black, and chestnut foals, according to the particular gray genotypes which are involved. Grays of the genetic constitution *HhBbGg* mated *inter se* produce the entire series of colors in the ratio

48 gray:9 bay and brown:3 black:4 chestnut.

The bay, brown, black, and chestnut offspring of such matings, or any other for that matter, might be mated together ever so often, yet they would never produce gray foals, although themselves the offspring of gray horses.

Accordingly the method which should be followed in establishing a gray breed of draft horses is not difficult to map out. An effort should be made to get homozygous gray horses for breeding stock. Such horses, of course, will be met with only in breeds in which there is no prejudice against gray, as for example in the Percheron breed; but, if it should be thought desirable to utilize some of the good qualities of other breeds in which gray is not a favored color that may be done at the sacrifice of uniformity of color in the first generations. Matings should, however, always be of gray to gray individuals, and all animals of other colors should be disposed of. As the type becomes well established and there is a wide field of choice among the grays the selection should be further refined by disposing of *both* parents of any foal of a color other than gray. By this method it should be a simple matter to establish a gray breed of draft horses which would not only breed true to color among themselves, but would also give only gray foals when mated to bay, brown, black, or chestnut horses.

Mendelism in cattle. The state of knowledge of the inheritance of coat color in cattle is even less satisfactory than that in horses, but there are some results from experimental investigations which have firmly grounded our knowledge of certain points of it.

White is a natural starting point in the discussion of Mendelian inheritance of coat color in cattle, but it proves to be by no means capable of simple treatment. The difficulty of dealing with white in cattle appears to be due to the variety of whites of different genotypes which are met with. Thus the white of Shorthorn cattle is apparently never a true white, for the eyelashes, face bristles, and particularly the ears always bear some red hairs, although often so few that they are ordinarily overlooked by breeders. This type of pigmentation is not an extreme condition of red and white blotching which is often met with in Shorthorn cattle, but it is entirely independent of spotting. This is indicated by the clean cut segregation which this type of coloration exhibits. Lloyd-Jones and Evvard present data which favors the explanation that white with colored extremities depends on a recessive extension factor, *e*. Another type of white met with in modern breeds appears to be merely an extreme condition of spotting. Such whites are not uncommon among Ayrshire and Holstein-Fresian cattle, but they are undoubtedly genetically different from whites with colored extremities. The wild white Park cattle of Britain and the white feral herds mentioned by Darwin always have colored ears, but it is doubtful whether they are genetically identical with the white Shorthorn. They apparently produce colored calves at times in spite of the fact that such calves are never retained in the breeding herds. It is known that some of these white herds were of mixed origin, and that some of them are creamy white rather than pure white. Accordingly it is not impossible that the colored calves which are produced by wild Park cattle are the result of recombinations of complementary factors rather than of recessive segregation. The problem of white in cattle is far from a complete solution.

Red in cattle varies from a very dark red to light yellowish red. In the early days of the Shorthorn breed all these shades were represented but now the very dark reds and the yellowish reds are looked upon with disfavor. There is a little evidence of sharp segregation between some shades, but on the whole our knowledge of the relations of the different shades to one another is very imperfect. In Shorthorn cattle red appears to breed true, at least records of white calves from red × red matings are so rare as to lead one to suspect they were due to error of registration. Compared with white in this breed red represents a condition of extended pigmentation, dependent upon the dominant factor, *E*. Here a difficulty is introduced by the fact that red × white matings ordinarily produce roan rather than red and white offspring.

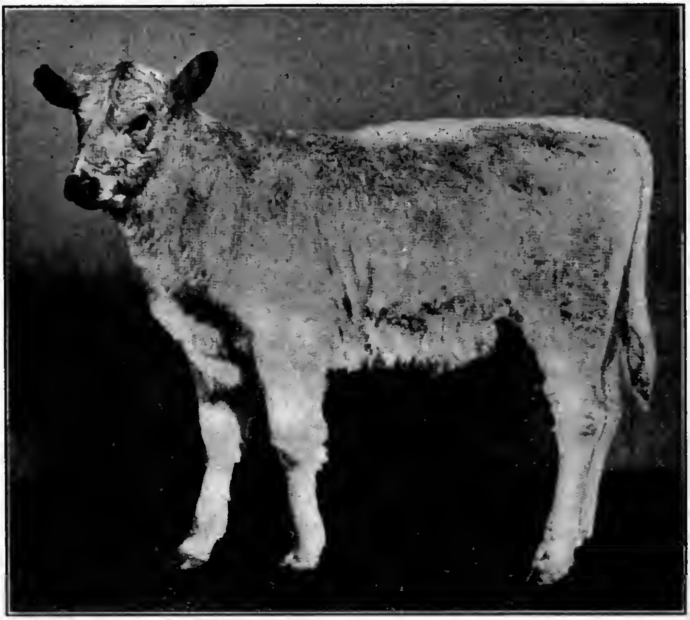


FIG. 188.—A white polled heifer with black ears and muzzle; an F_2 individual from the cross Galloway × white Shorthorn. (*After Lloyd-Jones and Evvard.*)

The roan color in cattle, like roan in horses, appears to depend upon a definite dominant factor, *R*. Strictly of course roan is not a color, but a pattern effect due to admixture of white hairs in a pigmented coat, and it may affect black as well as red. This roan type of coloration is characteristic of Shorthorn cattle. The predominance of roan animals in this breed probably accounts for the fact that white mated to red usually gives roan offspring, for the whites are derived almost wholly from roan matings and they should therefore of necessity often bear the roan factor. There are also some apparently authentic accounts of red and white animals, the progeny of matings of red × white, such as the case of the noted white Shorthorn bull, Whitehall Sultan, which sired fifteen red calves out of various red cows. Were it not for this, J. Wilson's assumption that roan is merely a heterozygous condition of red and white, or in terms of the above factors, the expression of the *Ee* genotype, would be satisfactory.

The black color of Aberdeen-Angus and Galloway cattle is definitely dominant to red. This is shown by the fact that such cattle occasionally produce red calves. Since red was a common color in the early foundation stocks of the two breeds, it follows that the production of occasional red calves is merely a consequence of the handing down of the factor *b* in a heterozygous condition, and of the rare matings of animals both of which are heterozygous for it. In the black-and-white Dutch cattle of various types it is also not uncommon to have red-and-white offspring produced from black-and-white matings, but red-and-white matings never produce black-and-white calves. The factor *B*, as well as *b*, is affected by the extension factor *E*. Lloyd-Jones and Evvard have demonstrated this fact in the F_2 of Galloway × white Shorthorn matings, the white animals of which had black ears and muzzle like the Chillingham Park cattle. An excellent representation of such an animal is given in Fig. 188. Black is, also, affected by the roan factor in the same way as red, giving a blue-roan or blue-gray. The famous blue-gray cattle produced by mating Galloway, or less frequently Aberdeen-Angus, cows to white Shorthorn bulls are evidence of this fact; but the critical test necessary to decide between the two rival hypotheses of blue-gray as a simple heterozygote between black and white or as a consequence of the action of a separate roan factor has not yet been carried out.

Of the relations of other colors to each other, we know very little. J. Wilson states that there are five colors in cattle which breed true, namely black, red, light dun, brown, and white, and that aside from matings of black and red which give blacks, matings of different colors give what may be called, for convenience, intermediates. The exact colors which represent the heterozygotes are given in Fig.189. But there is no satisfactory way of determining the relations of the factors to each other save by the experimental test. Wilson presents some data gleaned from the Highland Cattle Herdbook on the relation between black, red, brindle, yellow, dun and light dun; but they are not of such a nature as to be capable of accurate Mendelian interpretation. The data do, however, indicate that black is the highest member of the series, and that red comes next to it. As to the relation between black and yellow, dun, light dun, and brown, we are still in some doubt in spite of positive statements by Wilson. On the one hand we have evidence that the foundation stock of Aberdeen-Angus cattle contained animals black, red, yellow, dun, light dun, brown-backed and other mixtures of these, only one of which, red, has survived as a simple recessive. This would lend support to Wilson's idea that the relation of blacks to the colors other than red is not that of simple dominance. Black, however, appears to be dominant to the fawn of Jersey, as is shown by the evidence from Jersey-Angus crosses reported by Kuhlman, the F_1 of which is black. A little definite experimental evidence on these problems would be of more service than much speculation.

J. Wilson arranges the entire series of coat colors in a system of multiple allelomorphs much like the one he advocates for the inheritance of coat color in horses. The essential features of this system are shown in Fig. 189. This formulation, however, falls down in one important instance in which we have definite evidence. Lloyd-Jones and Evvard report the production of some red animals in F_2 in matings of F_1 blue-gray animals from a cross between the black Galloway and the white Shorthorn. Such a result is entirely unprovided for in Wilson's scheme, and very probably other portions of it would break down before critical experimental tests.

	b	b^w	b^d	b^r	B
B	Bb Blue-roan 1 black 2 blue-roan 1 white	Bb^w Brindle 1 black 2 brindle 1 brown	Bb^d Dun 1 black 2 dun 1 light dun	Bb^r Black 3 black:1 red	BB Black All black
b^r	b^rb Roan 1 red 2 roan 1 white	b^rb^w Red brindle 1 red 2 red brindle 1 brown	b^rb^d Yellow 1 red 2 yellow 1 light dun	b^rb^r Red All red	
b^d	b^db ?	b^db^w Light brindle 1 light dun 2 light brindle 1 brown	b^db^d Light dun All light dun		
b^w	b^wb ?	b^wb^w Brown All brown			
b	bb White All white				

FIG. 189.—Wilson's interpretation of the inheritance of coat color in cattle. The factors are B, black; b^r, red; b^d, light dun; b^w, brown; and b, white.

Of other characters in cattle, the white-face pattern of Hereford cattle is dominant to colored face. Fig. 190 shows a typical instance of this kind. This dominance of the white-face pattern extends to species hybrids, for hybrids between the Hereford and bison exhibit the typical white-face markings. The F_1 hybrid between the zebu and Hereford, however, has a broken colored face, as shown in Fig. 206. The early history of the Hereford breed indicates that mottled-faced animals were not uncommon in the foundation stock, and today they are met with not infrequently in grade Hereford cattle. The characteristic pattern of Dutch belted cattle appears, also, to be a dominant character as contrasted with self-coloration. Another color character, the black of Ayrshire cattle, exhibits sex-limited relations and will, therefore, be discussed in another chapter. The polled character in cattle, as we have pointed out before, is clearly dominant to the horned condition, but the F_1 may exhibit slight scurs. The breeding of cattle for the polled condition is a simple problem in Mendelism involving a difference in a single pair of factors. The study of other characters in animals, particularly those which are of economic importance from a Mendelian standpoint, has just begun.

Fig. 190.—California Favorite, grand champion steer at 1916 International Livestock Exposition. Out of a red Shorthorn cow by a Hereford bull. The Hereford pattern is completely dominant. (*Photo from G. H. True.*)

Mendelism in Sheep.—As we have already noted the short-eared condition in sheep has been shown to be a simple dominant to the long-eared character. The factor for black wool in sheep is recessive, as shown by the evidence of C. B. Davenport. Black sheep mated together produce only black sheep, and it is probable that the black sheep met with occasionally in white flocks represent the cropping out of homozygous recessives, like the occasional red calves in some herds of black cattle. Wilson reports that black face and white face in sheep represent a simple character contrast, the F_1 heterozygote being gray. There are, however, breeds of sheep which have gray faces, so that it is a matter of question whether Wilson is not here again advocating too simple an explanation. The inheritance of horns in sheep has been subjected to Mendelian analysis, but questions of sex are involved in this case, for which reason treatment is reserved for a succeeding chapter.

Mendelism in Swine.—About all that is known of Mendelian inheritance in swine deals with coat color. White is dominant to colored, but segregation is rarely definite in F_2, apparently because white often carries latent pattern factors which are responsible for the production of belted and variously spotted individuals in segregating populations. The belted pattern of Hampshire swine is dominant to uniformly colored coat, and it is clearly independent of the particular color in the coat. The evidence regarding spotting of the coat is conflicting, but at least one type appears to be dominant. Black coat color is dominant to red, in which respect it is like the corresponding color in horses and cattle. Red in hogs may be of different shades, and like chestnut in horses, there is evidence that the lighter shades are most easily maintained. There are reports in the literature of roan swine, but the genetic constitution of these is imperfectly known. As to other characters, the union of the two toes found in mule-footed hogs is dominant to the normal condition, and according to Spillman represents a single dominant factor difference from the normal condition.

Mendelism in Poultry.—The Mendelian inheritance of comb character in fowls has been discussed in another chapter. The heterozygous constitution of the Blue Andalusian fowl has, also, been discussed in detail. Blue Andalusians mated *inter se* always produce Blue, White Splashed, and Black Andalusian fowls in the ratio of 2 : 1 : 1; but black birds mated with white-splashed ones produce nothing but Blue Andalusians. The breeder, therefore, must maintain pens of black and splashed white birds if he desires to produce progenies made up wholly of Blue Andalusians. The fact that the Blue Andalusian never breeds true, however, should be sufficient justification for refusing to recognize it as a distinct breed. It is of interest to note that the Blue Breda bears the same relation to a black- and a white-splashed form as the Blue Andalusian. It is just, however, to note in passing, as Pearl in fact has pointed out, that there is some doubt of the authenticity of these cases. They require further investigation.

The great variety of diverse characters in fowls, particularly in color and pattern of plumage, has made them unusually excellent subjects for Mendelian investigations. Although extensive observations have been made upon a large number of hybrids, however, the exact factor relations are not well understood for many characters. In the list in Table LXII some data are presented with respect to dominance of certain contrasted characters; but these contrasts should not be taken to in-

TABLE LXII.—RESULTS OF CERTAIN CONTRASTS IN THE DOMESTIC FOWL

Dominant	Recessive	Expression
Barred plumage pattern..	Uniform coloration	Sex-linked.
Beard....................	No beard	Almost completely dominant.
Black....................	Red, buff	Almost completely dominant.
Black iris color..........	Brown, red, pearl iris	Completely dominant.*
Black....................	White (Minorca)	Almost completely dominant.
Buff.....................	White (Minorca)	Almost completely dominant.
Booting..................	No booting	Imperfectly dominant.
Broodiness...............	Non-broodiness	Almost completely dominant.
Brown striped down......	Pale brown down	Completely dominant.
Crest (Silky).............	No crest	Imperfectly dominant.
Dark shank color.........	Light shank color	Completely dominant.
Extra toes...............	Normal foot	Imperfectly dominant.
Feathered shanks.........	Clean shanks	Imperfectly dominant.
Frizzle feathering.........	Normal repent feathering	Completely dominant.
High fecundity...........	Low fecundity	Sex-linked.
High fecundity...........	Low fecundity	Non-sex-linked.
Joining of toes...........	Normal foot	Imperfectly dominant.
Leaf comb (Houdan).....	Single comb	Imperfectly dominant.
Leghorn pattern..........	White (Minorca)	Sex-linked.*
Long tail (Japanese)......	Normal tail	Imperfectly dominant.
Normal head............	Cerebral hernia (Polish)	Imperfectly dominant.
Pea comb...............	Single comb	Completely dominant.*
Plain feathering..........	Silky feathering	Completely dominant.
Plain heel...............	Vulture hock (Silky)	Imperfectly dominant.
Rapid feathering.........	Slow feathering	Almost completely dominant.
Red.....................	White (Minorca)	Almost completely dominant.
Red ear lobe.............	White ear lobe	Imperfectly dominant.
Rose comb..............	Leaf comb	Imperfectly dominant.
Rose comb..............	Single comb	Completely dominant.
Rumplessness............	Normal uropygium	Imperfectly dominant.
Self-color (Minorca)......	Hackle lacing (Brahma)	Imperfectly dominant.
Silky pigmentation.......	Normal mesoderm color	Imperfectly dominant.
Single comb.............	Comblessness (Breda)	Completely dominant.
Walnut comb............	Pea, rose comb	Completely dominant.
White (Leghorn).........	Colored plumage	Almost completely dominant.
Yellow shank color.......	Light shank color	Completely dominant.*
Yellow skin color.........	White skin color	Completely dominant.*

* Disputed by Punnett.

dicate that the character differences depend upon single factor differences. As a matter of fact most instances of imperfect dominance are probably due to complex factor interaction, and they, therefore, require further study. The list as it stands is more interesting than useful, but it gives a rather vivid idea of the variety of character contrasts which may be obtained in the barnyard fowl. Aside from a few additions and changes in wording, this list is essentially the same as that compiled by Hadley for the 1915 "American Poultry Yearbook."

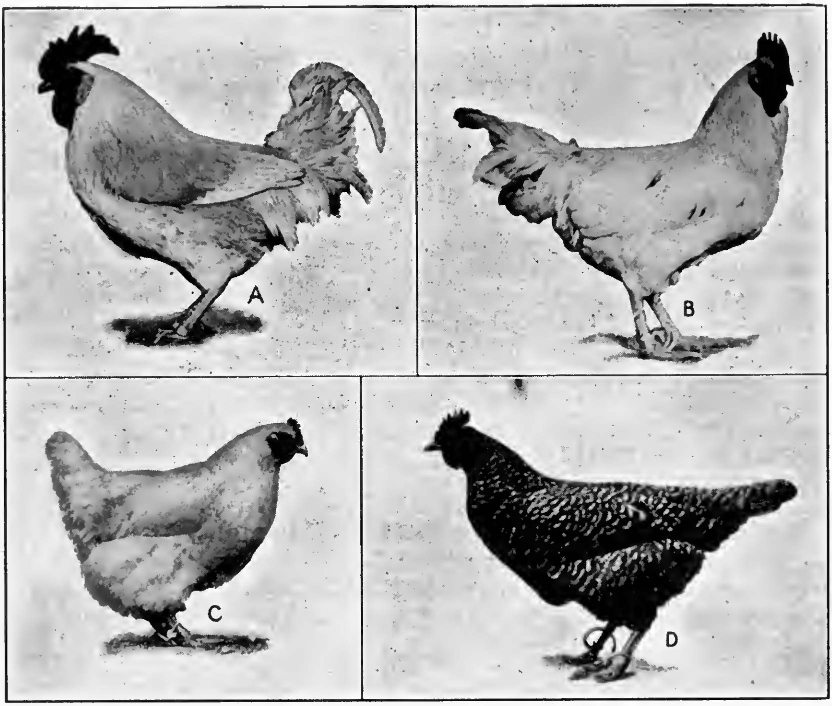


FIG. 191.—Results of crossing White Plymouth Rock and White Leghorn. *A*, P_1♂, White Leghorn; *C*, P_1♀, White Plymouth Rock; *B*, F_1♂, showing a little flecking of black and a barred tail feather; *D*, F_2♀, type of barred birds obtained in F_2. (*After Hadley.*)

The most important kind of Mendelian work is that which leads to some definite analysis of the factor complex characteristic of a given breed. As an illustration of such investigations we have Hadley's analysis of the genetic constitution of the White Leghorn breed. White is often dominant in fowls, so that white breeds may carry latent color and pattern factors in their makeup. Hadley finds the White Leghorn to be of the genetic constitution $CCII(BZ)(BZ)$, if a male, and $CCII$ $(BZ)W$, if a female, the factors having the following effects:

C—a factor for black coloration. The allelomorph, *c*, determines the production of recessive white plumage.

I—a dominant factor for white pigmentation, which supresses the normal production of pigment in the plumage.

B—the sex-linked dominant factor for barring, a pattern factor, which acts on black to produce the familiar plumage effect of the Barred Plymouth Rock. The recessive, *bb*, birds are solid color.

Z—the sex-factor, homozygous in males, and mated to the neutral *W* in females. Hadley found that the White Plymouth Rock was probably of the genetic constitution $ccii(BZ)(BZ)$; male, or $ccii(BZ)W$, female; and obtained results which accorded with this formulation. From matings of White Plymouth Rock females and White Leghorn males, Hadley obtained 63 F_1 birds, all of which were white, although some of them showed a few barred or black-flecked feathers. This is shown in the F_1 bird in Fig. 191. Mating such F_1 birds together should give in F_2 white and barred birds in the ratio of 13 white :3 barred. The actual figures obtained were 134 white :33 barred, a very close agreement with expected results. Facts such as these demonstrate with what care the breeder must proceed in crossing breeds if he wishes to avoid obtaining a heterogeneous mixture of classes in subsequent generations.

CHAPTER XXX

ACQUIRED CHARACTERS IN ANIMAL BREEDING

The problem of the inheritance of acquired characters has been one of the historic battlegrounds of biology. Even yet the question is by no means settled, although a considerable amount of information has been collected about it. Darwin and Spencer both subscribed to the belief that acquired characters might be impressed upon the germinal substance and therefore of necessity that offspring might inherit such characters, for they saw in an intimate relation between soma and germ-plasm a powerful method of evolution. It is not necessary longer to question the fact of evolution, but the method of evolution still awaits a satisfactory solution.

In animal breeding especially the question of the inheritance of acquired characters is of primary importance because much of the functional activity of animals depends for its perfection upon carefully developed training. It is not enough for the race horse to have a good inheritance, it is further necessary that it should be developed and trained in accordance with methods known to be favorable to the bringing out of its inborn qualities, and this is also true in one respect or another of other domestic animals. Now it is only natural for those who have carefully attended to the development of the inherent characters of their livestock to hope and to expect that their efforts have added something of excellence to the hereditary complex of the individual. This in brief is the interest which the inheritance of acquired characters has for the practical animal breeder.

The Scientific Problem.—Before taking up the evidence as to the inheritance of acquired characters, it is necessary to define as clearly as possible what is meant by an acquired character, and to determine what sort of proof is necessary in order to establish the inheritance of such characters. As many writers have pointed out, much futile discussion upon the subject has been due to a lack of rigid definition of terms.

Weismann distinguished between blastogenic and somatogenic characters. The former were such characters as have their origin in the germplasm, and the latter are those which are produced by responses of the soma or body to surrounding conditions or to its own activities. These latter somatogenic variations are the acquired characters of evolutionary literature. Shull's definition of acquired characters is, perhaps, somewhat more precise, namely that acquired characters are modifications of bodily structure or habit which are impressed upon the organism in the course of individual life. This distinction is by no means another instance of the hair-splitting proclivities of modern science; it is on the contrary a real distinction of fundamental importance in shaping conceptions of evolution and heredity. It is unnecessary to give any specific examples of blastogenic characters, since the whole discussion of Mendelian heredity in preceding pages has been confined to them. Of somatogenic characters, however, it is perhaps well to mention a few in order to give a concrete starting point for the following discussion. Acquired characters include a vast number of characters due to environmental effects, for example, small size when a consequence of reduced food supply or other conditions unfavorable to growth, increased size consequent upon unusually favorable environmental conditions, mutilation, the effects of disease, and other modifications of a like character. Those acquired characters which have their origin in response to environmental conditions have often been distinguished from that other class, the motive force in the development of which resides in the organism itself, the effects of use and disuse. Conspicuous examples of "achieved" characters as distinguished from "thrust" characters are increases in the perfection of function dependent upon exercise, such as the increased speed of the trained race horse and the increased sharpness of intellect of the trained mind.

As Thomson has stated it, the precise question at issue is this: Can a structural change in the body, induced by some change in use or disuse, or by a change in surrounding influence, affect the germ cells in such a specific or representative way that the offspring will through its inheritance exhibit, even in a slight degree, the modification which the parent acquired?

Obviously a problem such as this must require very critical treatment, and much, if not all of the evidence brought forward in support of the belief in the inheritance of acquired characters suffers from failure to fulfil the requirements of a rigid proof. Thomson has given an excellent extended treatment of this side of the case, as well as of the subject of acquired characters in general.

To satisfy the rigid requirements of an experimental proof any evidence of the inheritance of acquired characters must fulfil the following conditions:

First, a specific character or modification in the soma must be impressed upon the organism by a known factor in its environment or in its exercise of bodily function.

Second, the character or modification should be new. There must be no question of the reappearance of ancestral traits or characters, or of the specific relation of the determining factor to the character or modification in question.

Finally the induced change in the organism must reappear in succeeding generations in the absence of the original factor which determined its production. Other conditions in the life of the offspring must remain unchanged. The change in question may exhibit a lesser degree in the immediate descendants in the absence of the original stimulus, and in succeeding generations it may become progressively less, but the critical point is the determination of whether such a change is exhibited in any degree whatsoever by offspring produced in the absence of the original stimulus.

The Belief in the Inheritance of Acquired Characters.—Lamarck first stated clearly the belief in the inheritance of acquired characters, and the part which it has been supposed to play in the determination of the characters of living beings as they exist today. From his observations, he formulated two laws, which he stated as follows according to Elliot's translation:

> In every animal which has not passed the limit of its development, a more frequent and continuous use of any organ gradually strengthens, enlarges and develops that organ, and gives it power proportionate to the length of time it has been so used; while the permanent disuse of any organ imperceptibly weakens and deteriorates it, and progressively diminishes its functional capacity until it finally disappears.
>
> All the acquisitions or losses wrought by nature on individuals, through the influence of the environment in which their race has long been placed and hence through the influence of the predominant use or permanent disuse of any organ; all these are preserved by reproduction to the new individuals which arise provided that the acquired modifications are common to both sexes, or at least to the individuals which produce the young.

It is a curious fact which has been pointed out by Lankester that these two laws are mutually contradictory. The first law states that adaptive changes occur when organisms are subjected to new environmental conditions; the second states that such newly acquired characters become a part of the heritage of the individual. In other words according to the first law the old established characters of the organism are unable to maintain themselves under new conditions; according to the second law it is implied that acquired characters having a much less extended history possess a permanence and stability not accorded to the older established characters. It should be noted, however, that this implication was not what Lamarck emphasized. He dwelt rather upon the very gradual, "imperceptible" effects of use or disuse, for example, in permanently changing characters.

The belief in acquired characters is still held by some modern biologists, but in a more refined form. Semon, for example, has proposed the "Mnemetheorie" as founded upon two premises. First, that although the stimulations of the "sensitive substance of the organism" disappear as such, yet after they cease they leave behind in this same sensitive substance changes which he has called Engramme. Second, that these "Engramme in the sensitive substance" persist not only in the soma, but also under favorable circumstances in the germ cells. This form of the "memory theory" of heredity might seem to be a convenient hypothesis for explaining the assumed inheritance of modifications resulting from the use of organs, but it is difficult to imagine how it would favor the assumption of inheritance of modifications resulting from disuse of organs or loss of parts through mutilation. Obviously the inheritance of mutilations, in spite of a few circumstantial cases, cannot be maintained with any degree of conviction. The many generations through which circumcision has been practised in the Jew and the deforming of women's feet by the Chinese are two instances opposed to it. Dehorning of cattle, docking the tails of horses and sheep, clipping the ears of dogs, are instances which come within agricultural practice and have no permanent effect upon the breed. On the whole the neo-Lamarckians have come to believe, therefore, in the inheritance of those acquired characters which depend upon use or disuse of organs, achieved characters as distinguished from thrust characters. A rather crude example of this belief which has of late years obtained some notoriety among livestock breeders is Redfield's theory of dynamic evolution. According to this statement of the belief, the exercise of any organ or function results in a corresponding storage of energy in the germ cells, such that the effects are transmitted to the next generation. The idea receives practical application from the further consequence, that this storage of energy having been granted, developed animals must of necessity possess more of it than those undeveloped, and consequently such animals produce superior offspring. E. Davenport, Marshall, Pearl and others have taken issue with Redfield upon this subject and have demonstrated clearly that the facts which have been cited in support of his theory of dynamic evolution may be interpreted with far greater probability in other ways. In fact, the biological basis for such assumption as the storage of energy in germ cells is very slight. Moreover, the theory is evidently based upon a naive disregard of known biological facts, and a non-critical interpretation of statistical data. The matter deserves mention here, not because of any merit in it, but solely because of the publicity which has been accorded it in various journals devoted to practical breeding interests.

As an example of the kind of agricultural data which those who believe in the inheritance of acquired characters point to for support of their views, nothing is more striking than the rise and improvement of

TABLE LXIII.—REDUCTION OF THE TROTTING RECORD

Name of horse	Place of record	Date	Record
Boston	Philadelphia, Pa.	Aug. 25, 1810	2:48½
Trouble	Jamaica, N. Y.	Oct. 3, 1826	2:43½
Sally Miller	Philadelphia, Pa.	Nov. 21, 1834	2:37
Edwin Forest	Philadelphia, Pa.	Oct. 16, 1838	2:36½
Dutchman	Hoboken, N. J.	July 18, 1839	2:32
Lady Suffolk	Hoboken, N. J.	Oct. 13, 1845	2:29½
Pelham	Jamaica, N. Y.	July 2, 1849	2:28
Highland Maid	Jamaica, N. Y.	July 14, 1853	2:27
Flora Temple	Jamaica, N. Y.	Sept. 2, 1856	2:24½
Flora Temple	Kalamazoo, Mich.	Oct. 15, 1859	2:19¾
Dexter	Buffalo, N. Y.	Aug. 14, 1867	2:17¼
Goldsmith Maid	Milwaukee, Wis.	Sept. 6, 1871	2:17
Goldsmith Maid	Boston, Mass.	Sept. 2, 1874	2:14
Rarus	Buffalo, N. Y.	Aug. 3, 1878	2:13¼
St. Julien	Oakland, Cal.	Oct. 25, 1879	2:12¾
Maud S.	Chicago, Ill.	Sept. 18, 1880	2:10¾
Jay-Eye-See	Providence, R. I.	Aug. 1, 1884	2:10
Maud S.	Cleveland, Ohio.	July 30, 1885	2:08¾
Sunol	Stockton, Cal.	Oct. 20, 1891	2:08¼
Nancy Hanks	Terre Haute, Ind.	Sept. 28, 1892	2:04
Alix	Galesburg, Ill.	Sept. 19, 1894	2:03¾
The Abbot	Terre Haute, Ind.	Sept. 26, 1900	2:03¼
Cresceus	Columbus, Ohio	Aug. 2, 1901	2:02¼
Lou Dillon	Readville, Miss.	Aug. 24, 1903	2:00
Lou Dillon	Memphis, Tenn.	Oct. 24, 1903	1:58½
Uhlan	Lexington, Ky.	Oct. 8, 1913	1:58

the American Standard bred horse during the past century. As some indication of this improvement we reproduce here Table LXIII, which shows how the trotting record has gradually been reduced. Not all of the decrease in the record represents a real advance, for along with improvement in potential ability have gone improvements in methods of training and in the circumstances under which records have been made. Aside from these factors, however, the reduction in the record does indicate very strikingly the improvement which has taken place in the American trotter. It is a grave question, however, whether any of this improvement can be ascribed to the inheritance of acquired characters, for such a position fails to evaluate the effect of rigid selection which has been followed in building up the American Standard bred. This matter will be treated further in the next chapter.

The Argument against the Inheritance of Acquired Characters.—Just as Lamarck was the moving spirit in formulating the belief in acquired characters, so Weismann was the leading protagonist of the contrary opinion. Weismann was forced to this position by his belief in amphimixis as a cause of variation, but he found other and abundant evidence to confirm his scepticism. Even at the present time his reasons for the opposing position are valid and sound. They may be stated briefly as follows:

1. There is no known mechanism by which the soma may influence the germ-plasm in a specific fashion.

2. The evidence which has been presented in support of the belief in the inheritance of acquired characters in not a single case satisfies the rigid requirements of an experimental proof.

3. The theories of the continuity of the germ-plasm and of germinal variation can account for all known facts of heredity without resorting to the inheritance of acquired characters.

These statements represent a formidable indictment of the belief in the transmission of effects of somatic modification. Some of the evidence in support of these statements is given in what follows.

The Soma and Germ-plasm.—That there is no known mechanism by which the soma may influence the germ-plasm in a specific fashion is a fact admitted alike by neo-Lamarckians and Weismannians. But, as the former point out, an admission of this point by no means necessarily includes a denial of the existence of such a mechanism. The present knowledge of biochemical relations within the body is in a lamentably inadequate condition to serve as a basis for either the denial or affirmation of specific relations between body and stirp.

Fortunately, however, some definite experiments have been performed which throw light upon this question. Of experiments on ovarian transplantation those of Castle and Phillips deserve the greatest confidence because they were performed with animals the genetic behavior of which was known. The account of one successful experiment follows:

> On January 6, 1909, the left ovary was removed from an albino guinea-pig, No. 27, then about 5 months old, and the ovary of a pure black guinea-pig about a month old was fastened near the tip of the uterine horn, distant a centimeter or more from the site of the ovary removed. One week later, January 13, a second operation was performed, in which the right ovary of the albino was removed, and as a graft was introduced the ovary of a second young black guinea-pig, of like age with the first but of different ancestry. After the albino had fully recovered from the second operation, she was placed with an albino male, No. 654 with which she remained until her death about a year later.
>
> On the 23rd of July, 198 days after the operation, she gave birth to two female young. One was black but bore a few red hairs. . . . The other young one was likewise black, but had some red upon it, and its right forefoot was white.
>
> On October 15 the grafted albino bore a third young one, a male which, like those previously borne, had a few red hairs interspersed with black. . . .
>
> On January 11, 1910, the grafted albino was observed to be pregnant for the third time, and this time she was very large. Unfortunately, on February 2nd, she died of pneumonia with three full-grown male young *in utero*. The skins of these animals were

> saved. . . . Like the other three young they were black, but with a few red hairs among the black ones. They bore no white hairs. . . .
>
> Female 1970, daughter of the grafted albino, was mated with the albino male, her father, and bore three young, two of which were albinos and one black with some red hairs. If female 1970 had been the daughter of a pure-black mother, instead of a grafted albino, we should have expected her to produce an equality of black and of albino young. The observed result was the nearest possible agreement with this expectation.
>
> A control mating of the albino male, 654, was made with a female of pure-black stock. As a result there were produced two litters of young, including five individuals, all black, with red hairs interspersed. This result shows that the red hairs found on the six young of the grafted albino was due, not to foster-mother influence of the grafted albino, but to influence of the male parent. The young of the grafted mother were exactly such in color as the black guinea-pig which furnished the graft herself might have been expected to bear had she been mated with male 654 instead of being sacrificed to furnish the graft. The white foot borne by one of the young furnished no exception to this statement. Spotting characterized the race of guinea-pigs from which the father came. He was himself born in a litter which contained spotted young whereas neither the pure-bred black race that furnished the graft nor the albino race that received it was characterized by spotting.
>
> Inasmuch as the offspring of albino parents are invariably albinos, it is certain that the six pigmented offspring of the grafted female were all derived from ova furnished by the introduced ovarian tissue taken from a black guinea-pig. This tissue was introduced while the contained ova were still quite immature, and it persisted in its new environment for nearly a year before the eggs were liberated which produced the last litter of three young. These young, like the earlier litters, gave no indication of foster-mother influence in their coloration.

The conclusion is forced upon us that the egg-cell during its growth does not change in germinal constitution. Its growth is like the growth of a parasite or of a wholly independent organism: what it takes up serves as food; this is not incorporated merely in the growing organism, it is *made over* into the same kind of living substance as composes the assimilating organism. Thus a critical experiment designed to test the relation of soma to germ cells with respect to coat coloration failed to demonstrate any direct interrelation whatever, and further experiments by the same investigators indicated that for other factors also the foster-mother exerted no influence whatever on the developing ova. The ovary of the black guinea-pig produced exactly the same kind of ova in the body of the albino as it would have produced had it remained in the body of the black guinea-pig. Figs. 192 and 193 show the nine animals reported in this experiment. The full record of this experiment of Castle and Phillips' shows in detail the character of critical investigation which has been brought to bear on various phases of the question of the inheritance of acquired characters.

In passing, it should be mentioned that a few previous experiments on germinal transplantation appeared to indicate the existence of some influence of the foster-mother. Of these the experiments of Guthrie on fowls are alone entitled to any considerable treatment. Guthrie believed he obtained evidence of foster-mother influence in a number of cases of ovarian transplantation. But, as Castle and Phillips point out in their discussion of these cases, the genetic behavior of the fowls concerned in the experiments was imperfectly known and the results were such as lent themselves to more logical interpretation as cases of ovarian regeneration. C. B. Davenport in fact repeated these experiments in a more critical fashion and found that in every case ovarian regeneration occurred, and

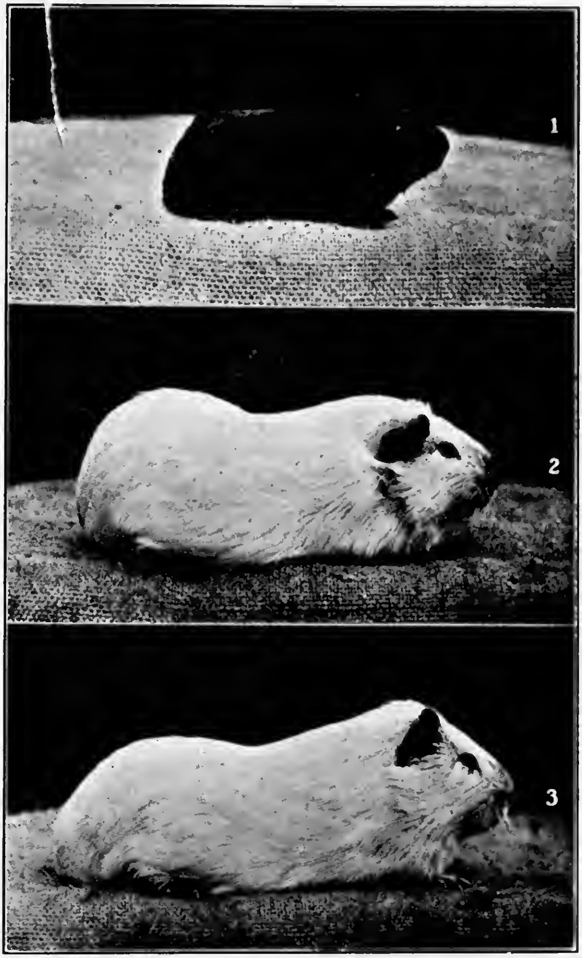


Fig. 192.—Guinea-pigs used in experiments on germinal transplantation. 1, a young black guinea-pig about 3 weeks old, type of the animals from which ovaries were taken; 2, albino female No. 27 into which the ovaries from the black guinea-pigs were transplanted; 3, the albino male No. 654 which was mated to No. 27. (*After Castle and Phillips.*)

the transplanted tissue failed to function. Accordingly as the matter stands at present with regard to the relation of soma and stirp it has not been demonstrated that any mechanism for the direct influence of the germ cells by the body exists; and such critical experimental evidence as has been obtained indicates that probably no such mechanism does exist.

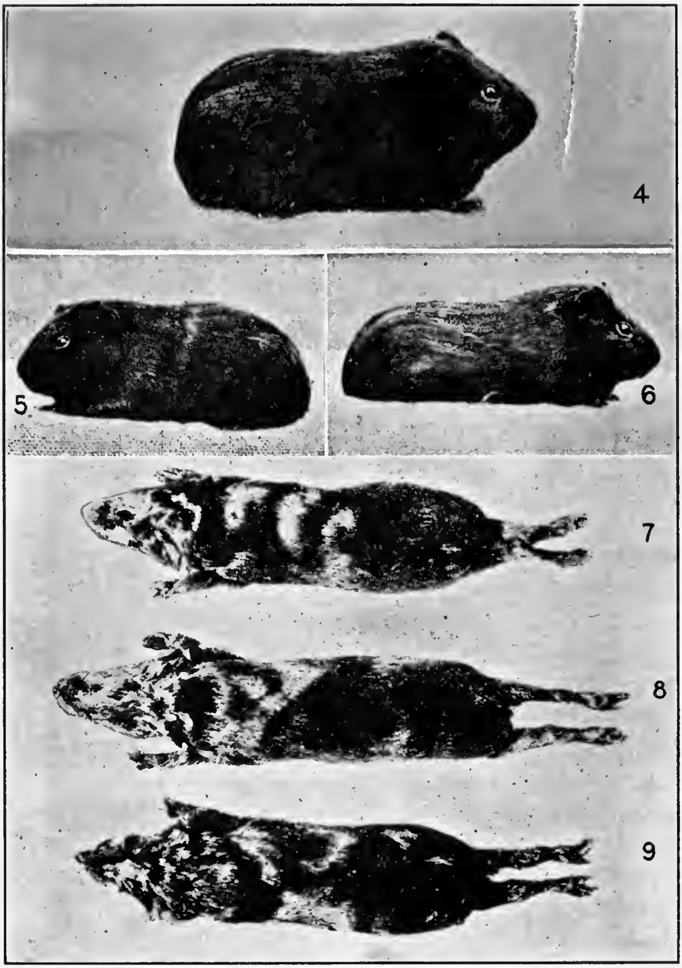


Fig. 193.—The offspring of the pair of albinos shown in Fig. 192. 4 and 5, young black females of the first litter; 6, young black male of the second litter; 7, 8, 9, skins of the black males found in utero after the death of No. 24. (*After Castle and Phillips.*)

The Isolation of the Germ-plasm.—Many biologists see in the continuity of the germ-plasm and in its apparent isolation from the soma an insuperable difficulty to an acceptance of the possibility of any germinal influence by the soma. It is true that Spencer's theory of the unceasing flow of protoplasm through the body, and Darwin's theory of pangenesis by which the body cells were supposed to throw off gemmules which pass to the germ cells were advanced to account for a direct relation between body and soma, but even in more refined form such hypotheses have received not the slightest verification. The present conception of the complex organization of the germinal material, which has been outlined in detail in the first part of this text, adds to the difficulties in the way of a conception of an interrelation between body and stirp. Weismann emphasizes this difficulty in the statement that the belief that a functional modification may be reflected in the corresponding constituents of the germ-plasm "is very like supposing that an English telegram to China is there received in the Chinese language." This, however, is undoubtedly an overstatement of the difficulties involved, for the nuclear constituents of each and every body cell is on the whole the same as that of the germ cells. Accordingly it is not inconceivable that a bodily effect might be impressed upon the germ cells by hormones liberated into the blood stream by the nuclear constituents of affected body cells.

The Inadequacy of Affirmative Evidence.—All the evidence which has been presented in support of the inheritance of acquired characters fail to satisfy some one or other of the conditions necessary for a rigid proof. Attention has already been called to the fact that the transmission of the effects of mutilation definitely can be denied. For twenty-two generations Weismann cut the tails off mice at birth, yet there was no effect upon the length of the tails of new-born mice.

The case for environmental effects appears to be in no better condition. Here in particular we meet with the kind of evidence which practical men consider favorable to the theory of the inheritance of acquired characters. The hardy little Shetland pony has been bred for centuries on the rocky islands of Shetland where climate is unfavorable and provender often scarce. What more natural than to assume that this scantiness of food has had cumulative, stunting effect from generation to generation until now the average height is only from 40 to 42 inches, and many are much smaller? This belief is further strengthened by statements to the effect that under more favorable conditions there is a progressive increase in size. Thus we find in one account of the Shetland pony this statement, "On the prairies of the American corn belt the pony tends to increase in size from *generation to generation.*" The italics are ours, for the fact must be emphasized that an increase in size would not of itself be evidence of inheritance of an acquired character, even though it persisted through any number of generations. An increase in size under more favorable conditions is indeed to be expected, and it should persist as long as the ponies are kept under the more favorable conditions. It would then be merely an instance of the reimpressment of a given environmental effect on each succeeding generation, not a case of the transmission of an acquired character at all. But if the modification increases in degree from generation to generation, as we may be led to believe by the above statement, then we have something very like the inheritance of an acquired character. Unfortunately we have no actual concrete evidence on this point, and we have no instance of the subjection of the case to the third point of proof which has been outlined above. If such increased size should persist when the ponies are transported to their original habitat, rigidly excluding the possibility of any effects of selection, then the evidence of transmission might be accepted.

This, of course, is not an isolated instance of the supposed transmission of acquired characters; on the contrary, the agricultural literature is full of statements which indicate a tacit acceptance on the part of the authors of the inheritance of acquired characters. Large-sized breeds come from regions of correspondingly abundant food supply, small-sized ones from regions of scanty provender. The small size of Alderney cattle has been favored by systematic underfeeding. Sheep transported to a dry climate acquire with succeeding generations a more and more marked harshness of wool. Instances like these may be multiplied indefinitely, but they are all very much alike; they are statements of opinion rather than of fact, and their interpretation is based upon a non-critical treatment of uncertain data. Very often it is exceedingly difficult to separate and to evaluate accurately the particular effects of different factors in a given instance. Moreover, cases which very closely simulate the inheritance of acquired characters may be readily imagined. Thus a Shetland pony dam by systematic underfeeding has been severely stunted in its growth. Now it is hardly conceivable that such a pony could provide for her young while *in utero* or during the suckling period the necessary food for its most favorable development, particularly if the systematic underfeeding of the dam continued during this period. It is conceivable that such an effect might last through several generations when the individuals in question were placed under more favorable conditions, and there would be a simple physiological reason for the fact. But this would not be in any critical sense, a transmission of an acquired character, for the germinal material would remain the same throughout all these changes. The proof of the transmission of acquired characters requires along with it proof that the germinal material has been affected in a fashion corresponding to that of the soma. A case such as the above would be more properly an effect of propagated environment, if we may use such a term, and this might well account for all the increase in size of Shetland ponies from generation to generation in the corn belt. To our knowledge it has not been determined accurately how great such an effect may be, nor how long it may persist. This is a point of some practical interest, but as to its relation to the inheritance of acquired characters, it is well to emphasize the fact that, as Thomson states, "experiments on increased size of parts are more decisive than those which refer only to the size of the whole."

An experiment designed to supply this need of data on change in size of particular body parts was conducted by Sumner, who subjected white mice to extreme temperature differences from the time of birth until 5 days before the females gave birth to their young. It was found that the offspring of warm-room mice, although themselves reared under identical temperature conditions with the offspring of cold-room mice, presented differences of the same sort as had been brought about in their parents through the direct effect of temperature, viz., differences in the mean length of tail, foot and ear. Unfortunately the data, as Sumner points out, give evidence of considerable heterogeneity in the genotypic composition of the population of mice used in the experiment. Furthermore no control lots from the same stock of mice were reared under average temperature conditions for comparison, and the pregnant females were not removed to the common temperature room until after the young had been carried *in utero* for 2 weeks. When, in view of these uncertainties, it is learned that in only three out of twenty-one cases of statistical comparison of the offspring of warm-room and cold-room parents is the actual difference more than 4 times the probable error of that difference, it appears that the evidence hardly warrants any definite conclusions. The investigation is mentioned here in order that the student may realize something of the difficulties involved in attacking this general problem.

The Transmission of Functional Modifications.—There finally remains the question of the transmission of the effects of use and disuse, and this in a sense is the field in which most tenacious adherence to the doctrine of the inheritance of acquired characters is found. Use and disuse was one of the chief factors considered by Lamarck in his attempt to account for change in species; use and disuse with Darwin, in spite of his open hostility to Lamarckism, was an important factor in the evolution of species. Use and disuse was supposed to account for the blindness of cave fauna, for the reduction in size of wings of the ostrich and emu, for the loss of legs by snakes, and for a host of other similar structural changes.

In animal breeding it is in this category perhaps that the inheritance of acquired characters assumes its greatest practical importance. The development of speed in race horses has already been referred to. But although it might seem at first glance a very simple matter to account for the increased speed of the American trotter in successive generations by use inheritance, nevertheless in the light of modern conceptions of germinal constitution, the simplicity of this explanation is a snare and a delusion. Similarly the inheritance of milk- and butter-fat producing capacity in cattle and goats, the inheritance of the propensity to lay on flesh in meat-producing animals, and other characters of domestic animals of great practical importance simulate in the way they have been built up, it cannot be denied, the inheritance of acquired characters. But simulation is far from proof, and any attempt to examine the records from the standpoint of rigid proof cannot fail to impress the student with the unsatisfactory nature of the material involved. Practical breeding operations have been designed to produce results, not to prove or disprove any particular theory of inheritance. Consequently every variable which favors the production of results is made use of, so that it is only very rarely that a single variable occurs in a given set of practical data. As the number of variables increases it becomes more and more difficult to assess to each its particular value. To illustrate the difficulties of interpreting data such as we obtain from practical breeding operations, we need merely call attention to some of the important variables which enter into such results, such as original germinal diversity, mutational changes, effects of selection, effects of functional modification, increasing knowledge of methods of developing animals, and maintenance of more favorable environmental conditions. The effect of all of these variable factors often enters into the end result in practical breeding operations. It is possible to determine statistically by means of rigid experimental analysis just how much is due to each one of them, but unfortunately this has not been done. For the present then we must conclude that it is a non-critical, unscientific attitude of mind which would assign to one of these variable factors, viz., the effects of functional modification, a leading importance in the end result, particularly when it is the most debatable one of all. Certainly we are in need of rigidly controlled experiments along this particular line.

Parallel Induction.—It is a well-known fact that the germ cells are susceptible to injury under unfavorable conditions such as occur at times in the body. Accordingly under adverse conditions there is a possibility that the germ cells may be affected along with the body. The first experimental evidence definitely establishing this fact was obtained by Fischer, who subjected pupæ of the moth, *Arctia caja*, to a low temperature and thereby produced a distinct new form with much darker wings, the males being darker in color than the females. By mating a pair of these 173 offspring were reared of which 17 resembled their parents in being much darker colored than the species type and again the males were darker than the females. There is a real distinction between this and similar cases of parallel induction, where the stimulus acts directly upon the germ cells, and the supposed action of a stimulus through a somatic modification on the germ-plasm. So far as practical breeding operations go this matter perhaps has little importance save in relation to disease and immunity, under which head it will be discussed later. The problem comes up for the most part in connection with the effect of adverse conditions upon the individual. Thus conceivably alcoholism in many cases may result in such a thorough poisoning of the entire system that body and stirp are both injured. In consequence offspring of such parents might display structural peculiarities and defects, similar to or different from those produced in the parent by the same adverse conditions. Certain experiments on the effects of alcohol on the progeny of animals furnish the direct evidence of parallel induction. Stockard's investigation with guinea-pigs led to the conclusion that "mammals treated with injurious substances such as alcohol, ether, lead, etc., suffer from the treatments by having the tissues of their bodies injured. When the reproductive glands and germ cells become injured in this way they give rise to offspring showing weak and degenerate conditions of a general nature and every cell of these offspring having been derived from the injured egg or sperm cell is necessarily similarly injured and can only give rise to other injured cells and thus the next generation of offspring is equally weak and injured, and so on. . . This might be construed to show the transmission of acquired characters, but it cannot be properly interpreted in such a sense. There is in this case no transmission of a new or strange character strictly speaking, merely a weakened or injured cell gives rise to other weak cells." On the other hand Pearl, working with chickens, reaches the conclusions, (1) "that the progeny of alcoholized parentage while fewer in numbers is made up of individuals superior in physiological vigor, and (2) that this result is due to a selective action of the alcohol upon the germ cells." Nice, also, who worked with white mice, fails to observe any injurious effect from alcohol in fertility or vigor of growth and but a small one in viability. Thus the evidence now available would certainly indicate that it is dangerous to draw far-reaching conclusions as to the general effects of poisons on the germ cells from data obtained on a single species.

Modern breeds of livestock without question trace back to extremely diverse foundation stocks. This historical fact has been discussed very inadequately in Chapter XXVII, and it has been shown specifically in some cases that the potentialities for high performance existed early in the breeds. Accordingly the constant practice of breeding from the best has resulted in the elimination from the line of descent of a large proportion of those animals which have failed to measure up to the standard of performance. Selection has indeed been a powerful factor in the improvement of modern breeds of livestock, but it is not necessary to assume that selective improvement is due to anything other than the isolation and multiplication of animals possessing the best combinations of germinal elements. Mutations or germinal changes sometimes occur. They are not necessarily favorable, but when useful they are likely to be preserved. They add to the store of heritage in our breeds of livestock. Favorable conditions of this kind may be maintained, and to the non-critical mind produce results simulating the inheritance of acquired characters.

The Conclusion.—There appears to be no escape from an attitude of extreme scepticism with respect even to the transmission of functional modifications. There is no conclusive experimental demonstration in the true sense of the word of the inheritance of any acquired character, and there is abundant experimental evidence, although it cannot of course be conclusive, for the contrary belief. Accordingly it should be evident to the practical breeder that anything which is so difficult for scientists to demonstrate must have little possibility of practical value. There is enough experimental evidence to demonstrate that it cannot possibly be the rule for the great majority of characters, and that it cannot produce significant effects in short times. The individual breeder works with relatively few generations, and he should shape his operations in accordance with that fact.

But although the inheritance of acquired characters may be denied, particularly from a practical standpoint, that denial does not carry with it any under-estimation of the importance of modifiability in animal breeding operations. Thomson has given this point happy expression in the statement that, "Although what is 'acquired' may not be inherited, what is not inherited may be acquired." And also just as some of the data of practical breeding operations seem to indicate an inheritance of acquired characters, so some methods of breeding the success of which is apparently based upon the inheritance of acquired characters really depend for their success upon harmony with other laws of heredity. A change in theoretical interpretation need not necessarily change breeding methods.

CHAPTER XXXI

THE SELECTION PROBLEM IN ANIMAL BREEDING

There are two general views respecting the effectiveness of selection, namely, that it depends upon the isolation of hereditary material of the most excellent kind, or in metaphor that selection separates the gold from the dross, and secondly that it is due to modification of germinal elements, that by selecting in a specific direction the hereditary material itself is actually molded in a corresponding fashion. The two interpretations are fundamentally at variance each with the other; one interpretation would have it that the hereditary elements are relatively constant, at least that they are not subject to gradual continuous change; the other interpretation favors a belief in factor inconstancy, insignificant fluctuating variability as it were in factors themselves, which provides opportunity by appropriate selection for actual modification of germinal elements. These opposed views have already been discussed at some length in other chapters, it remains to apply the conclusions therein reached to practical animal breeding operations; and to discuss certain other phases of the selection problem which are of particular interest in practical work.

In spite of vigorous statements to the contrary, there seems to be little reason to doubt that the isolation view of selection can account for all results which have been communicated thus far with respect to this question, whether of practical experience or of experimental research. In the preceding chapter we had occasion to consider, in passing, the reduction which had occurred in trotting records during the past one hundred years. Data of this kind are not lacking in the annals of agriculture, and are often offered as evidence in support of the belief in the gradual accumulation of favorable increments in the development of breeds. But although this old Darwinian idea of improvement in animals is very generally subscribed to, at least verbally, by practical men, it is nevertheless true that whenever a critical examination is made of specific instances the support for it largely disappears.

The American Standard Bred Horse.—In Table LXIII are given the data which indicate how the trotting record has been lowered during the history of racing in America. A parallel table might be given to show how the pacing record has been reduced. Now although these records have been used on the one hand in support of belief in the inheritance of acquired characters and on the other hand in advocacy of the doctrine of the creative effect of selection, there appears to be little foundation for either of these views when the evidence is analyzed critically.

The moving spirit in the establishment and improvement of the American Standard bred has been the demand for fast race horses. Throughout the history of the breed performance has been emphasized strictly and consistently; the judgment of merit has been based upon actual track records, or upon the ability to produce animals of superior performing ability. The requirements for registration adopted in 1882 by the National Association of Trotting Horse Breeders are an eloquent testimonial of this. They are given in full below.

> In order to define what constitutes a trotting-bred horse, and to establish a breed of trotters on a more intelligent basis, the following rules are adopted to control admission to the record of pedigrees. When the animal meets with the requirements of admission and is duly registered, it shall be accepted as a standard trotting-bred animal.
>
> *First.*—Any stallion that has, himself, a record of 2:30 or better; provided any of his get has a record of 2:40 or better; or provided his sire or his dam, his grandsire or his grandam, is already a standard animal.
>
> *Second.*—Any mare or gelding that has a record of 2:30 or better.
>
> *Third.*—Any horse that is the sire of two animals with a record of 2:30 or better.
>
> *Fourth.*—Any horse that is the sire of one animal with a record of 2:30 or better; provided he has either of the following additional qualifications: (1) a record himself of 2:40 or better; (2) is the sire of two other animals with a record of 2:40 or better; (3) has a sire or dam, grandsire or grandam, that is already a standard animal.
>
> *Fifth.*—Any mare that has produced an animal with a record of 2:30 or better.
>
> *Sixth.*—The progeny of a standard horse when out of a standard mare.
>
> *Seventh.*—The progeny of a standard horse when out of a mare by a standard horse.
>
> *Eighth.*—The progeny of a standard horse when out of a mare whose dam is a standard mare.
>
> *Ninth.*—Any mare that has a record of 2 :40 or better, and whose sire or dam, grandsire or grandam, is a standard animal.
>
> *Tenth.*—A record to wagon of 2 :35 or better shall be regarded as equal to a 2 :30 record.

These are rules well calculated to sort out and preserve the most excellent lines of descent. That they have operated by discovery and utilization of unusually excellent genotypes is rather strikingly indicated by a study of some of the famous families of standard-bred animals. In Table LXIV E. Davenport has presented data relative to the ten greatest producers of speed in the history of American racing up to and including 1901. Without exception these ten sires belong to the famous Hambletonian family of racing horses. They are all descendants of Hambletonian 10: for Belmont 64 is a grandson of Hambletonian 10, and Geo. Wilkes and Happy Medium were both sons of Hambletonian 10. Within

Table LXIV.—The Ten Greatest Producers of Speed up to and Including 1901
(*After E. Davenport*)

Sires	Sired by	Trotters	Pacers	Total
Nutwood 600	Belmont 64	131	34	165
Electioneer 125	Hambletonian 10	158	2	160
Onward 1411	Geo. Wilkes 519	124	34	158
Red Wilkes 1749	Geo. Wilkes 519	116	41	157
Alcantara 729	Geo. Wilkes 519	102	47	149
Pilot Medium 1579	Happy Medium 400	94	20	114
Simmons 2744	Geo. Wilkes 519	82	23	105
Wilton 5982	Geo. Wilkes 519	89	14	103
Gambetta Wilkes 4651	Geo. Wilkes 519	49	52	101
Baron Wilkes 4758	Geo. Wilkes 519	78	21	99

a few generations, therefore, this famous family of racing horses has produced a remarkable series of performers, horses which have been able to trot or pace a mile within 2:30. There seems to be little question, therefore, that this family of fast horses had its foundation in the careful fostering of the favorable genotypic material of Hambletonian 10; and a transmission of it through a relatively small number of exceptional sires which may have possessed a genotypic arrangement somewhat superior to that of Hambletonian 10, as the record of Geo. Wilkes 519 in particular might indicate. Davenport has made a very careful study of the records in the Register and Yearbook, a study which should be continued and extended. Without considering in any detail the extensive data which have been collected, it appears fairly certain that selection in the improvement of trotting and pacing horses has operated by detecting and multiplying the most favorable genotypes; and that training, in so far as it has had influence, has served as a means of developing inborn potentialities to the full, and, therefore, of detecting most favorable lines of descent.

Fecundity in Fowls.—Pearl's investigations on the inheritance of fecundity in fowls have already been touched upon, but they deserve more extended treatment at this point, for in them the relative effectiveness of phenotypic and genotypic selection is strikingly contrasted. For if performance has anything to do with development of more favorable hereditary material, or if selection has a creative effect in a given direction, then it would appear to be a conclusion unavoidable that mass selection must result in increased average winter egg production. Yet as a matter of fact, as shown graphically in Fig. 185 there was actually a slight decrease in average winter egg production during a 9-year period of such selection.

That this selection was rigid and a fair demonstration of the ineffectiveness of purely phenotypic selection for fecundity in the Barred Plymouth Rock is indicated by the plan which was followed during this portion of the investigations. Only pullets were used for breeding stock which had laid 150 or more eggs during their first laying year, and cockerels were selected from among the progeny of 200 egg hens. The type of selection practised was, however, strictly mass selection, for the selected birds were bred together without respect to genetic relationship, and no tests were made of the laying capacities of progenies from particular matings. This last point is of particular importance, because it definitely distinguishes the method of breeding used as one typically of mass selection.

Obviously the reason for the ineffectiveness of selection during this period of mass selection lies in the fact that modifiability in fecundity is very great. This particular fact has been discussed fully in a preceding chapter, but here it must be considered again as the reason for the fact that this system of selection failed to result in improvement in egg-laying capacity, for were performance and genotypic constitution closely correlated, then this system of mass selection should have been effective. But as a matter of fact the criterion of selection used in this portion of the investigations, namely total yearly egg production, was evidently not a good index of genotypic constitution, for apparently it failed to distiguish between individuals belonging to a number of intergrading genotypes. Consequently, whenever, by chance a female was selected which by phenotypic variation represented the *upper limits* of her genotypic class, the population was thereby thrown back by that much to the level representing the *mean* phenotypic performance of her particular genotypic class. A wide range of modifiability for each genotype, therefore, continually held the average yearly production down to the original value for the population.

But beginning with the year 1908 a radical change was made in the method of selection. During the first portion of the second period, the object was merely to ascertain the actual mode of inheritance of fecundity, a subject which is discussed more fully elsewhere; but during the second portion, from 1912 to the present time, selection was only carried out for high egg production. Essentially, however, the mode of selection during these two portions of the second period was the same so that we may consider this as a single period. The performance index during this period was winter egg production rather than total egg production. But in the selection of high winter producers for breeding purposes, a progeny performance test was employed as well as an actual individual performance test. Every female which was selected during this period came from a high-producing mother, the female progeny of which were all high producers. In case such a female failed to give progeny of high performance in the first year she was not retained for further breeding purposes. Males for breeding purposes were selected on a like rigid basis; they were from high-producing mothers, the daughters of which were all high producers, and any male was rejected immediately if his progeny failed to measure up to high standards. Complete individual pedigrees were kept during this period. For the sake of comparison low and mediocre strains were also selected on a basis equally rigid for their particular characters.

The success of this type of selection is strikingly evidenced by the data set forth in Table LXV, which gives the means from which Fig. 185 was constructed. From an interpretative standpoint, therefore, the direct contrast is brought out sufficiently well in this case, for when selection was placed on a fairly rigid genotypic basis it was immediately successful. It seems hardly possible to explain the facts of this series of investigations by any other than an appeal to the isolation view of selection, particularly when consideration is directed toward the rapidity with which genotypic selection established high-producing strains in a flock which had failed to respond to a rigid system of mass selection.

TABLE LXV.—MEAN WINTER EGG PRODUCTION OF THE MAINE STATION BARRED PLYMOUTH ROCK FLOCKS FROM 1899–1915 (*Data of Pearl*)

Laying year	Mean winter production of all birds	Number of birds making winter records	Mean winter production of all birds selected for high production	Mean winter production of all birds selected for low production
1899–1900	41.03	70		
1900–1901	37.88	85		
1901–1902	45.23	48		
1902–1903	26.01	147		
1903–1904	26.55	254		
1904–1905	35.04	515		
1905–1906	40.65	635		
1906–1907	22.44	653		
1907–1908	19.93	780		
1908–1909	26.69	359	54.16	22.06
1909–1910	31.76	247	45.57	25.06
1910–1911	30.49	264	50.58	17.00
1911–1912	35.93	232	57.42	16.43
1912–1913	43.01	182	52.61	
1913–1914	52.20	192	52.20	
1914–1915	45.89	179	45.89	
Total and means	35.05	4,842	51.49	20.14

Bantam Fowls.—In a previous chapter evidence was presented tending toward the general conclusion that the most potent source of that variation which has been made use of in the establishment of modern breeds of domestic animals has come from amphimixis, the result of polyphyletic origin. But modern breeds have become highly standardized and they are closely guarded by rigid rules of pedigree registration. In consequence improvement within them has been effected purely by methods of selection without hybridization between breeds. In poultry, however, and here again we turn to Pearl for data, new breeds are still being created, and almost entirely by methods of hybridization. Thus for practically every variety of larger domestic fowl there is a corresponding bantam variety. Pearl sent queries to bantam breeders in all parts of the world for the purpose of obtaining information upon the method of creating new varieties of bantams. Here it would seem was an ideal test for the utility of Darwinian selection in the establishment of breeds, for it would appear to be a very direct mode of attack in breeding bantams corresponding to a given larger variety of fowl simply to select for smaller size within the larger breed. Pearl's enquiries brought out the fact, however, that in no case were bantam breeds created in this fashion, but always by crossing the larger breed with some bantam variety and then selecting within the hybrid progeny of subsequent generations. In view of the demonstration of the relatively simple Mendelian heredity of body weight in Seabright × Hamburg crosses which has been demonstrated by Punnett and Bailey, we can readily understand how this method should be quickly and uniformly successful. The creation of bantam varieties of fowls, therefore, strikingly bears out this general thesis, that so far as the results of selection go in actual practice, the isolation interpretation is sufficient to account for all facts. The creative view of selection is an uncertain doctrine to accept for guidance.

Selection and Breeding Methods.—Finally it becomes necessary to again point out that a change in interpretation does not necessarily call for a change in breeding methods. In fact it can be shown that in general those breeding methods have been most successful which are most closely in accord with the isolation view of heredity. This fact is particularly patent when the earlier histories of breeds is taken into account, and the vast amount of inbreeding which has been employed by the best of these old pioneer breeders is given a true valuation. For inbreeding determines the fixing of a given genotypic constitution, because in such a system of breeding family excellence is the basis of judgment, just as in the successful selection for high winter egg production progeny test was the basis of selection for breeding stock. That most famous of all early breeders, Robert Bakewell, when he set about establishing his herds made excursions all over Britain for the purpose of selecting and purchasing the best of all sorts for his foundation stock. However, after he had brought this stock together he used only the progeny of these animals in his herd, no other animals were introduced from outside sources. Of necessity, therefore, his was a method of close inbreeding, and he did not shrink for a moment from using this method to the fullest extent. The same method of breeding characterizes the work of other early breeders. Thus one of the most famous of early Shorthorn bulls, Comet (155) was very closely inbred as shown by the pedigree in Fig. 194. At public auction this great bull was sold in 1810 for 1000 guineas, a very high price at that time. He was considered the crowning achievement of Charles Colling's notable career as a breeder of Shorthorn cattle. The extremely close breeding shown in this sample pedigree from a notable herd of Shorthorn cattle may again be used as an argument in support of the isolation interpretation of selection in successful practical breeding operations.

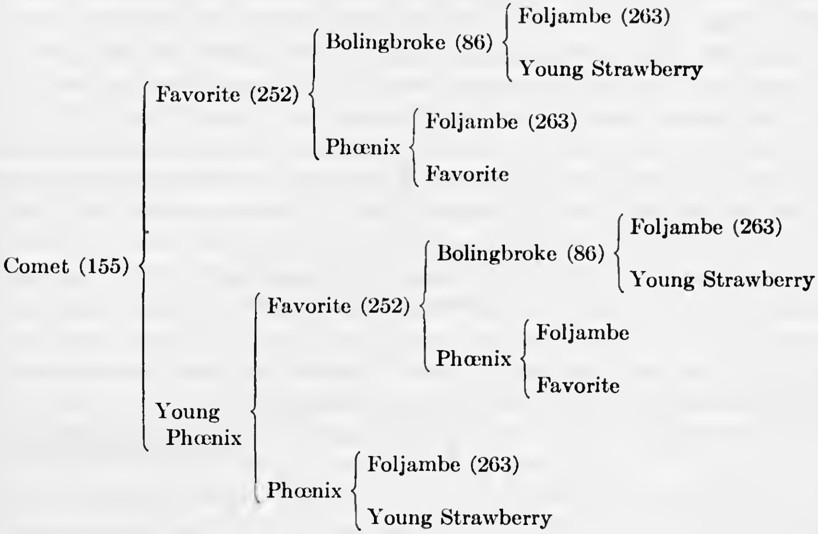


FIG. 194.—The pedigree of Comet (155), an illustration of extreme inbreeding in Shorthorn foundation stock.

In fact throughout the entire history of animal breeding, improvement has been most strikingly referable to the influence of a limited number of families and individuals of superior excellence, a fact which speaks strongly for the isolation view of selection. Every breed has its famous animals and families, and every breeder who has studied pedigrees at all must have been impressed by the small percentage of early animals which are represented in almost every pedigree of present-day individuals of the breed. The "search for the prepotent sire" and full utilization of him when discovered have been the central features of the breeding methods of many a successful animal breeder. But prepotency, if it indicates anything, points to the supreme importance of genotypic constitution as the measure of excellence, and not to augmented excellence from development, performance, or any other factor, for these prepotent animals are often not themselves superior in individual excellence to many other animals of the breed although the latter have failed to impress the breed so strongly with their characteristics.

It is safe to say, therefore, that the isolation view of selection is sufficient to account for any of the results which have been obtained in practical breeding operations. Since practical breeding methods have often been very successful it follows as a matter of of course that the adoption of such an interpretation does not involve of necessity any alteration in livestock-breeding methods. Why then emphasize the importance of this interpretation? The answer to the question should be clear. It follows that, if a method of breeding is not creative with respect to addition of new and better elements to the hereditary material, full utilization must be made of those existing elements of the germinal material which are of most value commercially. It, therefore, follows that no method of breeding, however excellent, can attain a full measure of success unless the very best existing foundation stock is utilized, for in such individuals alone are contained in the very best combinations those hereditary elements upon the utilization of which the breeder must rely for success. The importance of extreme care in the selection of foundation stock cannot, therefore, be overestimated.

Selection Indices.—In all selection work, as indeed in all practical breeding, it is necessary for the stockman to have his ideal thoroughly in mind. In the absence of such a definite ideal, it is difficult to understand how any breeding operations can possibly have an orthogenetic trend. The requirements of efficient selection, therefore, demand first an accurate method of judging the comparative worth of a series of animals with respect to certain definite characters, and second a method of weighting different characters in the same individual according to their comparative value from a breeding standpoint. It is here that science may be expected to give definitely useful contributions to practical breeding methods in the determination of mathematically accurate means of comparing data.

With respect to the first point, the comparative value of a given character in a series of individuals, several factors must be considered. Only one definite case can be considered here, that of milk production in dairy cows. Obviously with cows kept under identical conditions, two factors have a great influence on the amount of milk produced within a given period, namely, the age of the cow and the stage in lactation. Pearl has shown that the amount of milk produced by a cow within a given period is a logarithmic function of her age. His investigations further show that the curve of milk production with respect to age is of the general form

$$Y = a + bX + cX^2 + d \log X.$$

In this equation, Y denotes the amount of milk produced in a given time, X the age of the cow, and a, b, c, and d are constants the value of which must be calculated for different breeds. Stated in general terms, therefore, milk production increases with age until at about 5 years a maximum is reached, after which it decreases with advancing age. With reference to milk production within a given lactation period, it is of course a matter of common experience that milk production decreases gradually during the lactation period. These two factors have been taken into account by Pearl in preparing a table of comparative efficiency percentages for dairy cows. In this table the maximum efficiency is set at 100 per cent. and the comparative excellence at any given age or stage of lactation is given a value in per cent. of this maximum value. Pearl has calculated such a table for 24 months of which 10 months only are given in Table LXVI. This table provides a very satisfactory method of comparing a set of individual records from cows of different ages and in different stages of lactation.

Table LXVI.—Efficiency Percentages for Milk Production in Dairy Cattle
(Data of Pearl)

Age of cow in years and months	Months since freshening									
	1	2	3	4	5	6	7	8	9	10
	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
1 : 6 to 1 : 11	58	54	51	47	44	41	37	34	30	27
2 : 0 to 2 : 5	73	69	64	60	56	52	48	43	39	35
2 : 6 to 2 : 11	82	77	72	67	62	57	52	47	41	36
3 : 0 to 3 : 5	89	83	77	71	66	60	54	48	43	37
3 : 6 to 3 : 11	93	87	81	75	69	62	56	50	44	38
4 : 0 to 4 : 11	97	91	84	78	71	65	58	52	45	39
5 : 0 to 5 : 11	100	93	86	79	72	66	59	53	46	39
6 : 0 to 6 : 11	100	93	86	79	72	65	58	52	45	38
7 : 0 to 7 : 11	99	92	85	78	71	64	57	51	44	37
8 : 00 to 8 : 11	97	90	84	77	70	63	56	50	43	37
9 : 00 to 9 : 11	94	88	82	75	69	62	55	49	43	36
10 : 00 to 10 : 11	91	85	79	73	67	61	54	48	42	36
11 : 00 to 11 : 11	88	82	76	71	65	59	53	47	41	35
12 : 00 to 12 : 11	85	80	74	68	63	57	52	46	40	35
13 : 00 to 13 : 11	82	76	71	66	61	55	50	45	39	34

The second difficulty has to do with determining some method by which selection may be made effective for a number of characters, or in other words a method of comparing different individuals with respect to a number of different characters. The use of selection index numbers provides a way of surmounting this difficulty. Pearl has made use of the following fundamental selection index in the Maine Station poultry work:

$$I_1 = \frac{5(a+b)}{c+d+1}$$

in which formula:

I_1 = selection index number for a particular individual.

a = percentage of eggs which hatched.

b = percentage of eggs actually laid to the total number which might have been laid during the breeding season, February 1 to June 1.

c = percentage of infertile eggs.

d = percentage of chicks which died within 3 weeks after hatching.

The application of this index to different hens in a breeding flock is shown in Table LXVII. The selection index ranges in value from 2.8 to

Table LXVII.—Selection Indices for Barred Plymouth Rock Pullets (*Data of Pearl and Surface*)

Band No.	a	b	c	d	I_1	Band No.	a	b	c	d	I_1
10	21	18.33	36.0	33.33	2.8	29	28	28.33	27.0	0	10.0
160	9	15.83	42.0	0	2.9	23	39	35.83	28.0	8.33	10.0
402	14	33.33	30.0	50.00	2.9	428	46	40.08	20.0	22.22	10.0
352	12	41.67	14.0	60.00	3.6	122	49	34.17	15.0	23.53	10.5
358	50	31.67	32.0	69.23	4.0	375	41	37.50	36.0	0	10.6
438	35	35.00	45.0	37.50	4.2	712	42	50.00	20.0	20.00	11.2
441	38	20.00	33.0	33.33	4.3	408	48	45.86	16.0	22.73	11.8
21	25	35.00	14.0	44.44	5.0	38	61	37.50	9.0	28.00	13.0
393	12	47.50	9.0	50.00	5.0	731	27	35.83	23.0	0	13.1
705	38	26.67	34.0	25.00	5.4	395	29	37.50	24.0	0	13.3
717	24	21.67	19.0	20.00	5.7	443	56	54.17	6.0	35.29	13.3
39	23	29.17	26.0	16.67	6.0	409	37	46.67	4.0	25.00	13.9
377	32	37.50	16.0	33.33	6.9	771	43	60.00	13.0	22.22	14.2
746	59	28.33	15.0	47.06	6.9	19	68	24.17	24.0	6.66	14.5
87	36	39.17	17.0	35.71	7.0	152	26	39.17	11.0	9.09	15.5
359	61	32.50	15.0	50.00	7.1	366	52	25.83	13.0	7.14	18.4
442	41	68.33	38.0	28.57	8.2	768	74	45.00	20.0	9.38	19.6
400	44	47.50	16.0	38.10	8.2	434	72	58.33	17.0	14.28	20.2
27	18	40.00	8.3	25.00	8.5	750	57	52.50	16.0	10.00	20.3
757	23	51.67	10.0	30.77	8.9	770	71	50.83	9.8	12.82	25.8
725	33	29.17	6.0	27.27	9.1	752	48	59.17	6.0	12.50	27.5
112	17	46.67	18.0	25.00	9.3	397	38	40.00	6.0	5.89	30.3
753	61	47.50	46.0	10.53	9.4	168	88	35.83	4.7	13.89	31.6
407	41	41.67	18.0	23.53	9.7	749	57	46.50	4.0	6.45	45.2

45.2, those birds having the highest breeding value which have the highest selection index. By this method it is possible to substitute for a vague personal impression of breeding value, an exact numerical expression which is an accurate measure of the breeding value of any individual. It is possible to devise such selection index numbers for other purposes, and they should prove of utility in practical breeding operations.

Another line in which still further necessity for strictly scientific analysis is exemplified is that of detailed study of curves of production. Thus Pearl and Surface have made a detailed biometrical study of the seasonal distribution of egg production in domestic fowls. From this study they find that the polygon of monthly egg production is of the form shown in Fig. 195. They find that with pullets the normal season of egg production begins in November. The mean rises rapidly during the following 2 months, but in February there is a characteristic slackening up in egg production. In March and April egg production is at a maximum, and after that it decreases fairly regularly until it reaches a minimum in October, with the exception of a slight, but significant, indentation in May. These data taken together with certain other facts which have been determined during the course of the Maine Station investigations of egg production indicate that the laying year may be broken up into four periods which correspond broadly with natural cycles of egg production in the domestic fowl. The first of these periods begins in November and ends at about March 1. The end of this winter-laying period is marked rather definitely in the curve of annual egg production by the distinct slackening of increase in egg production during February. The winter period of laying is in a sense an added period for it is not nor-

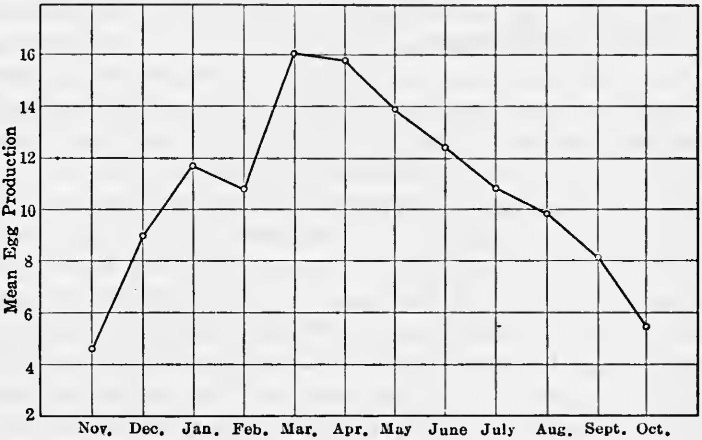


Fig. 195.—Diagram showing the weighted mean monthly egg production for each month of the pullet year. (*After Pearl and Surface.*)

mal to the wild fowl, and some fowls do not show this winter cycle at all. The period of March, April and May on the other hand is the natural reproductive cycle of the fowl. As might be expected it is the period of maximum egg production. It is terminated by the onset of the brooding period, which is indicated in the figure by the slight indentation during May. The third period, June, July and August, is characterized by a falling off in mean monthly egg production. This of course is the period during which chicks are reared, and it represents also a prolongation of the normal spring cycle. Finally, following the summer cycle, there is a period of 2 months, September and October, during which molting normally occurs. It is a period of minimal egg production. Pearl and Surface have made a careful and detailed investigation of each of these periods of laying, only the main results of which are indicated in the above account. However, one practical result of the investigation which has been employed extensively by them in subsequent investigations is the determination of the nature of the winter cycle of egg production, and its value as an index of egg laying capacity. This is a cycle added to those normally found in wild fowls, it is fairly sharply marked off from other cycles, and it represents an invariable characteristic of high laying individuals. It is not participated in by all individuals, and as we shall show later it has been subjected to definite Mendelian formulation. Accordingly there is abundant justification for using winter egg production as an index of egg producing capacity rather than using the longer total yearly production as such an index. The work of record taking in practical breeding operations having in mind the production of strains of superior laying ability has been simplified and made more accurate by these investigations. It is thus plainly to be seen how very important it is that as much detailed knowledge as possible be collected about any character with which the breeder is working.

Correlation and Selection.—Many of the "points to be observed in judging" or "aids to selection" of domestic animals are based upon empirical knowledge of the correlation which exists between conformation and performance. These have been mentioned in earlier chapters and are presented in various texts and manuals on judging, selecting and breeding, and need not be discussed here.

The practical value of a statistical knowledge of correlation between somatic characters and functional variations was mentioned in Chapter III; also the importance of biological soundness in the material used in investigating such correlations. Very few investigations have been conducted in this field of scientific research, but the increasing utilization of statistical methods is an earnest of future progress in this direction. A fine illustration of what the biometrician can do in this line is found in the recent work on the correlation between body pigmentation and egg production in the domestic fowl by Harris, Blakeslee and Warner. This study dealt with the relationship between the concentration of yellow pigment in the ear lobe of White Leghorn hens and their egg records of the preceding months. It was found that there is a very close interdependence between October ear-lobe color and the egg production of the pullet year.

"Expressed in absolute instead of relative terms, the correlations determined indicate that on an average birds differing by 5 per cent. in the amount of yellow in the ear lobe will differ by about 7 eggs in their annual production. Thus the difference is one of real practical significance. For example, birds showing only 10-20 per cent. of yellow in their ear lobes in October will have laid on an average about 185 eggs each, whereas birds exhibiting 55–65 per cent. of yellow will have an average annual production of only about 130 eggs."

These results prove that in the fowls used in this investigation color of the ear lobe (and presumably, of the leg, beak and vent) would have served as a practical index for selection of high layers. The authors point out, however, that the flocks from which their data were obtained represent a selected class of birds (in certain egg laying contests). "Such birds show, because of better breeding, better feeding and care, or both, a far higher annual egg production than the average flock. Unfortunately data of the kind presented here are not as yet available for the unselected class of layers." This correlation has long been known and utilized by poultry breeders (according to Kent it was noted in published form in 1879) and Blakeslee and Warner made earlier statistical studies than the one we have considered. Both Kent and Warner point out that degree of pigmentation is only one of several characters that may be utilized in selecting high laying hens, the other more important ones being time and duration of molting and size of abdomen.

CHAPTER XXXII

HYBRIDIZATION IN ANIMAL BREEDING

Within the past century the tendency in practical breeding operations has been toward the upbuilding of different breeds by a process of rigid selection. Naturally this method of breeding has looked upon any suggestion for the introduction of foreign blood with intolerance, an intolerance which is shown particularly in the rigid requirements of registration laid down by all breeders' associations. But the work in plant breeding in particular has demonstrated that occasionally hybrids have a commercial value in themselves aside from their usefulness as a source for the establishment of new varieties. Accordingly within the past decade there has been a growing tendency to investigate more closely the question of hybridization in animals, both in its scientific and practical aspects.

Grading.—In practical animal breeding grading refers to the method of improving a herd of animals of indifferent blood by the use of pure-bred sires. In the United States this practice has been very common on western ranches where the common scrub stock of the range has been graded up largely by the use of Hereford bulls, and bulls of other beef breeds. The practice is very common in horse breeding throughout the entire nation, for a large proportion of the stallions which stand for public service are pure-bred animals. In horse-breeding, however, it is regretably too often true that the pure-bred sires used in successive generations are not of the same breed, consequently the term grading is to be applied to this sort of breeding with some reservations. Grading is a practice universally commended. Aside from providing a market for a large number of pure-bred sires which would otherwise be sent to the shambles, a desideratum which may account for some of the warm advocacy it has received from breeders of pure-bred livestock, it does actually lead to notable improvement when practised intelligently, for pure-bred livestock which has been selected for many generations for particular utilitarian purposes is on the whole very much superior to scrub stock. Moreover, since the proportion of pure-bred animals is very low, it is a positive fact that any considerable improvement must depend upon some method of raising the general level of the great number of inferior animals.

Perhaps in no line of livestock production are results so readily comparable as in dairy cattle. Here performance is becoming more and

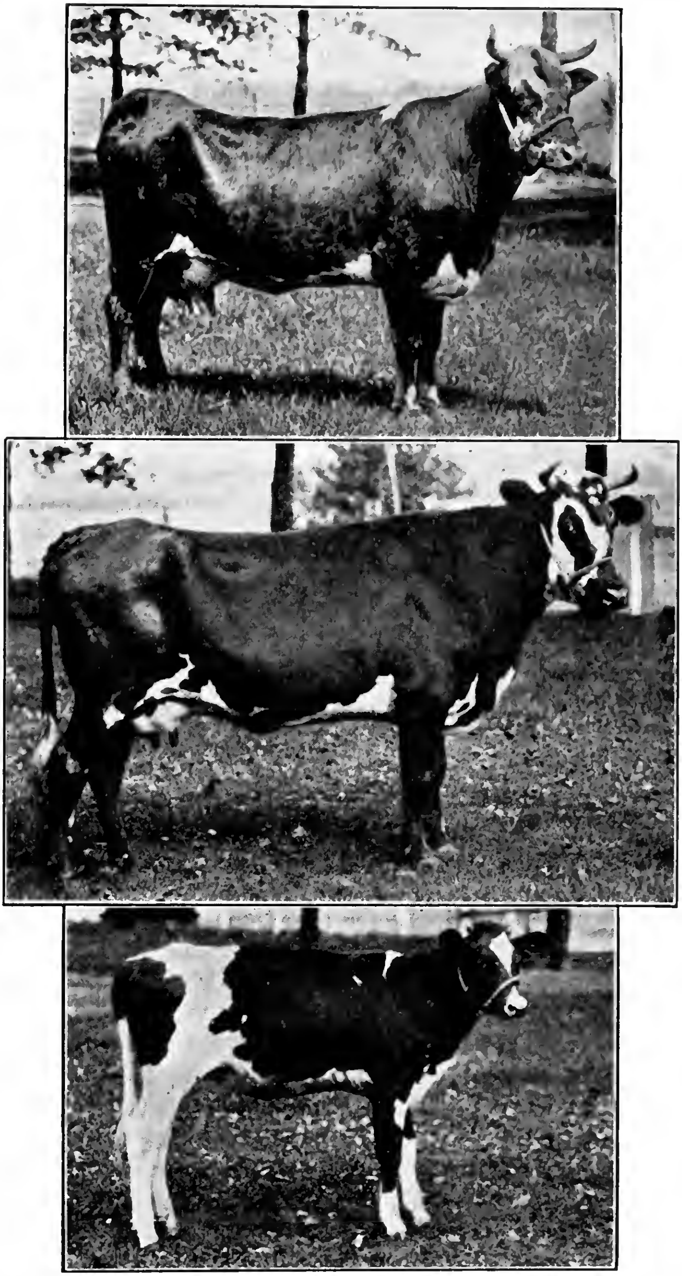


Fig. 196.—The results of grading scrub dairy cattle with pure-bred Holstein-Freisian bulls. (*After Kildee and McCandlish, Iowa A. E. S.*)

more the decisive standard of excellence, a fact which is reflected in the establishment of advanced registry records by pure-bred dairy cattle associations for those animals which prove of superior performing or breeding ability. Many experiment stations have enthusiastically recommended the use of pure-bred sires in building up dairy herds, a few have conducted investigations for the purpose of determining precisely how much improvement may be expected from the use of such sires. An investigation of this kind at the Iowa Station has proceeded far enough to warrant a preliminary report. For this investigation seven cows, six heifers, and one young bull were purchased in an isolated region of Arkansas where it was practically certain that no pure-bred bulls had ever been used. These were developed at the station, and their records are available for comparison with those of their daughters which have been sired by Guernsey, Holstein-Friesian, or Jersey bulls. In Fig. 196 are shown the results of grading two generations to pure bred Holstein-Friesian bulls. The first generation of grading has given a heifer which is intermediate in most characters between its dam and the general type of Holstein-Friesian cow. She, however, lacks the characteristic color markings of the Holstein-Friesian, a fact which obscures somewhat her resemblance to that breed's type. The second generation calf, her daughter, however, possesses characteristic Holstein-Friesian markings and would pass for a very fair specimen of the breed. The important consideration, however, is the comparative excellence of these animals in milk and butter fat production. The data relative to this question are given in Table LXVIII. The most notable feature in these records is the increase of 64 per cent. in average net returns.

TABLE LXVIII.—COMPARISON OF A SCRUB COW, NO. 52, WITH HER DAUGHTER, NO. 69, SIRED BY A HOLSTEIN-FREISIAN BULL (*Data of Kildee and McCandlish*)

No. of cow	No. of lactation periods		Pounds of milk	Pounds of fat	Net returns
52	6	Ave.	3,856.4	174.53	$19.29
		Best	4,588.4	201.67	16.27
69	4	Ave.	5,757.4	242.31	31.57
		Best	6,822.8	283.75	38.65
Per cent. increase of daughter over dam		Ave.	49.3	38.8	63.7
		Best	48.7	40.7	?

Table LXIX has been so compiled from the data of Kildee and McCandlish as to give a general résumé of their investigations. The cows have been divided into three lots according to the kind of sire used in grading. In the first lot scrub cows are compared with their daughters which were sired by a Holstein-Friesian bull; in the second lot the scrubs

TABLE LXIX.—COMPARATIVE RECORDS OF SCRUB DAIRY COWS AND THEIR GRADE DAUGHTERS (*Data of Kildee and McCandlish*)

Lot	No. of cows	No. of lactation periods	Average yearly records			Per cent. increased; grades over scrubs		
			Pounds of milk	Pounds of butter fat	Net returns	Pounds of milk	Pounds of butter fat	Net returns
Scrubs	4	17	3,156.6	158.10	$18.42			
Scrubs × Holstein	4	12	5,428.5	230.10	23.86	71.90	41.50	29.9
Scrubs	4	19	4,056.1	181.85	24.59			
Scrubs × Guernsey	4	8	4,146.7	194.92	19.98	2.21	7.18	−18.7
Scrubs	1	7	3,437.5	166.74	24.39			
Scrubs × Jersey	1	2	3,643.1	199.64	21.01	6.00	20.00	−13.8

which produced heifer calves to Guernsey bulls are compared with their daughters, and in the third lot a Jersey grade cow is compared with her scrub mother.

This table must be interpreted with some care, because it suffers from the same fault which mars a large proportion of agricultural data; things are compared which are not directly comparable. In Table LXIX have been presented the indices which would have made it possible to evaluate these data with respect to milk production and butter-fat content, but the evaluation has not been made in this case. The comparison of scrub cows with their grade Holstein-Friesian daughters shows substantial increases in milk production, butter-fat production, and net returns, and this in spite of the fact that immature cows are compared with mature ones. The increases here are due to several things. The scrub cows of this lot were the most inferior of all, the Holstein-Friesian bull which was used probably came from better producing lines within his breed than did the bulls of the other breeds, and a more representative test has been made of the grade Holsteins than of either of the other two lots of grades. If proper allowance had been made for the immaturity of the Holstein grades, they would compare even more favorably with their dams. In the Guernsey class the average excellence seems to be somewhat lower than that of the dams. The scrub cows of this lot, however, were better producers than those of either of the other two lots. Moreover, the immaturity of the grades in this test has had more effect than in the Holstein class, because two of them are represented by first year records only. Three of them were sired by a Guernsey bull which had been loaned to the station, and he apparently was not a good sire of dairy quality. The fourth member of the lot was sired by a Guernsey bull belonging to the station and she showed an increase of over 100 per cent., in all points of comparison with her dam. She was easily the most exceptional individual reported upon in the investigations; so that there is evidently no lack of excellence in the Guernsey breed for grading up dairy herds. Finally in the third lot, which consists of two individuals, a scrub cow and her grade Jersey daughter, when the immaturity of the latter is taken into account, a substantial improvement is displayed. The numbers in these investigations so far are not large, but they do show that enough improvement results from the use of good pure-bred sires to warrant fully the increased expenditure necessary to obtain them.

In grading, however, as in all other forms of animal breeding, it is necessary to observe all the precautions which have been found necessary for effecting permanent improvement. These may be stated in the following general fashion.

The Sires Used in Successive Generations Must Belong to the Same Breed.—It may be to the best financial interests of the stockman sometimes to breed to a sire of a different breed from the one used in grading, but, if that should be done, the cross-bred stock thus produced should not be retained for breeding purposes. There are several reasons for insisting upon strict adherence to such a plan of operations, and they have to do mainly with uniformity of the finished product, a requirement which can only be met by following a definite, consistent line of procedure. If such be followed, the result is to make the herd in the fourth generation practically pure bred so far as purposes of utility are concerned. In fact, such grade herds, freed as they are from the dictates of fashion which often prevail within breeds, are often superior in actual productive capacity to pure-bred herds.

The Sires should be Selected with Strict Regard for the Improvement which It is Desired to Effect within the Herd.—It is not enough to use any individual of the breed upon which the choice has been set, for paradoxical as it may seem there are some pure-bred mongrels. Within most breeds there are families which are notable for certain definite characteristics. In the interests of uniformity, therefore, the series of sires which is selected should ordinarily belong to the same family: they should at least conform to a single, specific type. Furthermore, the sire should be a superior specimen of his breed. The man who desires to improve a grade herd can afford to neglect fancy points entirely, but conformance to high utility standards should be insisted upon. Among dairy cattle advanced registration records based upon performance are excellent indices for judging the possible value of individuals in grading. In other breeds of livestock an approximation can and should be made to standards of excellence based upon performance.

Dams should be Selected Strictly According to a Definite Utilitarian Standard.—The rate and extent of improvement in a grade herd must necessarily depend to a considerable extent upon the care used in the selection of the female breeding stock. A standard of excellence should be established for them as well as for the sires, and any which fall below that standard when subjected to a fair trial should be promptly eliminated from the breeding herd. The standard should be so high that only the very best females in the herd will be retained, it should consequently be raised gradually as the excellence of the herd increases. The breeder should guard jealously against disposing of his best female stock.

When all this has been done the question naturally arises, through how many successive generations is it necessary or advisable to use pure-bred sires? To this question only a general answer can be given. Improvement in grading is at first rapid and in successive generations becomes less and less rapid as the grade stock approaches more and more closely to the standard of excellence of pure-bred stock. Practically, it appears to be true that four or five generations of grading, particularly if rigid selection of both sires and dams be practised, is sufficient to bring the standard of utilitarian excellence up to that of the pure-bred animal. After that it is a very grave question whether further employment of pure-bred sires is either necessary or desirable, provided it is possible to select a sire from a large number of high-grade animals. To effect improvement in utilitarian excellence in such herds requires sires of very superior excellence, and, if pure-bred, they would usually be too expensive for use in grade herds. On the other hand, it is possible among a large number of grade animals to select a sire from a superior line of grade stock, which would perhaps not be surpassed in utilitarian excellence by any pure-bred animal. Such grade animals do not have an inflated value on account of their breeding. They come within the price standards of sires which may be used in improving grade stock. It is also an open question whether more actual improvement may not be effected in high-grade stock of superior excellence by selection within it, rather than by further top-crossing to pure-bred sires. There is some probability that such stock may be more variable and consequently possess greater potentialities for improvement than the pure-bred stock itself. It is a matter of regret, however, that grading has not progressed far enough in very many cases to make it necessary to consider this problem. As a general rule, therefore, it is best, if possible, to continue breeding to the best pure-bred sires which are available.

In the early days of breed improvement provision was made for admittance to record of animals which were the result of top-crossing several times to pure-bred sires, and the question often arises whether this should be resumed, inasmuch as present day livestock associations with only unimportant exceptions make no provision for entry of any animal that is not the offspring of recorded animals. Fad and fashion play a large part in determining this position, but it must be admitted that it has some other, more secure basis than this, namely in the fact that such grade animals, particularly when crossed together, more often throw animals off-type with reference to breed standards than do pure-bred animals. Such off-type animals may not be at all undesirable from a utilitarian standpoint, they may simply fail to meet fancy points which breed standards insist upon. It is an open question whether livestock associations may not find it conducive to advancement to provide some method for the infusion of new blood, particularly in breeds which are giving increased attention to performance standards.

Crossbreeding.—Crossbreeding is the term applied to crossing of distinct types or breeds for special purposes. For all practical purposes the Blue Andalusian fowl is one of the simplest cases of crossbreeding, for it represents a simple heterozygous condition, the result of crossing Black and Splashed White Andalusians.

Crossbreeding, although often severely condemned by livestock breeders, is by no means a new practice; and the persistency with which it has been followed is in itself some indication of merit. The avowed object of crossbreeding is to combine the excellent qualities of both breeds or types which are used. Whether that object may be accomplished can only be determined by trial, but in general it may be stated that for complex functional characters such as speed in horses, milk or beef production in cattle, wool production in sheep; in short for practically all utilitarian characters a blended condition is to be expected in the crossbred offspring. The degree of excellence with which crossbred stock meets the purposes for which it is bred should be the justification of the practice, for sentimental considerations should have little weight in dictating practical methods.

Perhaps the best known kind of crossbred stock is the blue-gray type of cattle. These cattle are crosses either between Aberdeen-Angus and Shorthorn cattle or more often between Galloway and Shorthorn cattle. In the early part of the 19th century the production of blue-gray calves by mating the black cows of Scotland with white Shorthorn bulls was so common as to arouse grave concern for the future of the Aberdeen-Angus breed. The crossbreds were particularly noted for vigor and rapid growth, along with high quality, uniformity, and superior utilization of food. The high repute in which these cattle were held was apparently based upon superior market excellence, a superiority which has been confirmed by more recent trials at the Iowa station. By crossing two beef breeds, therefore, it is apparently possible to secure an animal superior to either one of them from the feeder's standpoint. There is here exhibited, therefore, a rather mild form of that hybrid vigor which is so often exhibited in crosses between different races within a species.

In certain cases, however, crossbreeding has been used for the avowed purpose of employing a given breed for a double purpose. An example of this is the practice in some herds of grade Holstein-Freisian cattle of using Aberdeen-Angus bulls in order to obtain calves which may be fattened for the baby-beef market. In this case the Holstein-Freisian calves are themselves not unsuited to the purpose, and the Aberdeen-Angus cross simply gives them increased excellence in quality and early maturity. The use of the Dorset ram on Merino ewes for the production of grade ewes for hot-house lamb production is another instance of crossbreeding for a definite purpose. There is room for purposeful crossbreeding such as this, but for unsystematic crossbreeding without definite purpose, condemnation cannot be too severe.

The reasons for the condemnation of crossbreeding as a systematic breeding program are not far to seek. The threatened extinction of the Aberdeen-Angus breed in Scotland in the early 19th century is only one phase of the problem. The first and primary reason for such disfavor, however, is the neglect of pure-bred stock which follows such a practice. The success of crossbreeding depends largely upon the excellence of the breeding stock which is utilized, but it is probably true that minor defects in the foundation stock are often totally obliterated by increased vigor and excellence in the cross-bred progeny. The temptation to lower the high standards of excellence in the pure-bred stock which is being used in crossing and to retain all animals which give any promise whatever of producing good cross-bred offspring is, therefore, very strong. Moreover, for continuation of the practice it is necessary to maintain two lines of breeding, one to supply the pure-bred foundation stock for crossing and the other to supply the cross-bred animals themselves. When only a small part of the herd is set aside for continuing the pure-bred lines, the number of individuals from which selection may be made is so much smaller that the chances of producing superior individuals is considerably less. It is also extremely difficult to enforce the rule that the cross-bred stock must not be used for breeding purposes. The tendency to breed from particularly excellent individuals which are sometimes obtained by crossbreeding is very great; but, if yielded to it will surely result in loss of the uniformity of type and excellence which characterized the original cross-bred animals, a natural consequence of the operation of the Mendelian law of segregation and recombination. These are facts the full gravity of which must be realized before embarking on crossbreeding operations.

Species Hybridization Among Domestic Animals.—Species hybrids among domestic animals are by no means uncommon, although in large part they have been regarded as curiosities rather than as foundation sources of breed improvement, or as themselves of practical value.

In this account species hybrids will be treated according to whether they themselves are of some value or are possible sources of breed foundation stock.

The hybrids which are themselves of some practical value, so far as utilization in this country goes, are confined to the genus Equus and its allied genera, and the typical example of this class of hybrids is the mule. The mule has proved a very satisfactory draft animal, and at the present time it is largely used, particularly in warmer climates, for that purpose (Fig. 197).

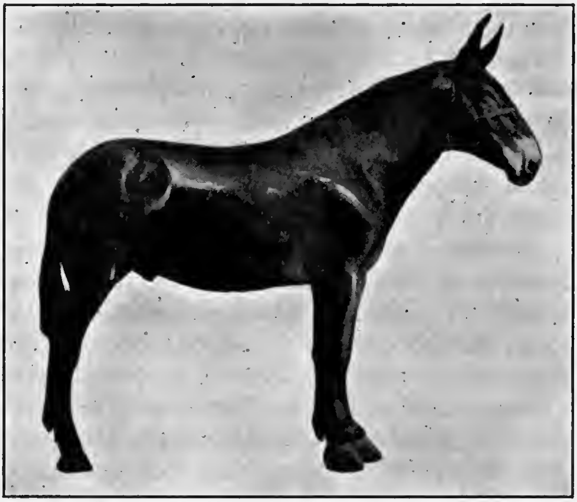


Fig. 197.—A choice draft mule. Height 18-2 hands, weight 1900 pounds. An unusually heavy mule of excellent type. (*After Obrecht.*)

The mule is a hybrid between the mare and the jack; the reciprocal cross of the jennet and stallion is called a hinny (Fig. 198). The cross is an instance of strict species hybridization and both sexes of the hybrid are sterile. The importance of the mule breeding industry in the United States may be judged from the fact that according to statistics of 1915 the estimated number of mules was about 4,500,000 with a farm value exceeding $500,000,000. The average value of mules per head according to U. S. Department of Agriculture estimates was $112.36, while that of horses was placed at $103.33. These latter figures may be taken roughly as an indication of the relative esteem in which horses and mules are held for draft purposes, which is practically the only purpose for which mules are employed.

Although the mule breeding industry is of such great magnitude, the relative merits of the horse and mule even for draft purposes are still in dispute. It is not the purpose of this account to enter into the debate, nevertheless a brief mention of a few considerations which tend to cloud the issue cannot be held out of place. The mule at its best, when compared with the beauty of form of a well-bred horse, suffers greatly. It partakes too much of the characters of the ass, ancient symbol of all that is silly and ugly, to excite greatly the admiration of those who have sentimental regard for the horse, the close companion of man in battle, foray, and chase. A second consideration is the fact, also true in crossbreeding, that the breeding of mules withdraws permanently from the racial stream much of the very best of horse blood. While inferior mares may produce mule colts that are better for draft purposes than any horse colts they might produce, nevertheless for the production of the best class of mules, it is absolutely necessary to select with care the very best type of brood mares. For these reasons, and others of less importance, strong partisans of the horse are prone to permit their prejudice against the mule and their high regard for the horse to influence strongly their judgment of the point at issue, namely this, whether a given lot of mares when bred to a good jack will produce mules which are better suited for draft purposes than would be the horse colts produced by these mares when bred to an equally good stallion.

FIG. 198.—A hinny, obtained by mating a jennet to a stallion. (*After Mumford.*)

By common consent the mule is considered more vigorous, hardier, and freer from disease than either parent. Part of these qualities may be ascribed to the ass's influence, but certainly these are characters common to a large number of species hybrids. The reciprocal cross, jennet × stallion, the hinny, is commonly reported to be different from the mule. According to Darwin, the male is prepotent in both crosses so that the hinny resembles the horse more than does the mule. There appears, however, to be some question about the explanation of this case, and it is a significant fact that Goldschmidt, who mentions common report in connection with this case, has seen fit to question the accuracy of it. Apparently many of the differences are due to individual differences in the animals which have been used, and are, therefore, of no significance for determining differences in reciprocal crosses.

The fertility of the mule is an everlasting question of dispute, for from time to time reports are made of fertile mare mules. Unquestionably such cases are very rare, and in most cases some doubt may be thrown either upon the question as to whether the mare "mule" was a mule at all, or whether, if a mule, she was not suckling the colt of some other dam, for there are abundant authentic instances of mare mules which have given milk. Among instances of fertile mules are those reported by von Wahl, who discovered two cases in Brazil of mules which had produced foals when bred to an ass. The foals were somewhat larger than their dams, and were throughout mule-like in appearance. Von Wahl reports, also, a case of a foal from a mare mule out of a stallion, but did not himself examine it. It is only fair to state that in these cases the chain of evidence is not complete. Lloyd-Jones has given a résumé of the evidence with respect to fertile mules, and has noted some new cases, all of which are, however, questionable. Mares apparently occasionally exhibit mule-like characters, and many of the cases reported appear to depend upon a mistake of such a mare for a mule. Figs. 199, 200 and 201 seem to represent an instance of this kind.

Fig. 199.—The mare mule on the left. On the right, her foal by a jack. Note the resemblance in markings of the leg. (*After von Wahl.*)

The male mule apparently never produces functional spermatozoa. Wodsedalek has found that the horse and ass have different numbers of chromosomes, so that the mule comes from the union of an egg-cell containing nineteen chromosomes with sperm cells containing either thirty-two or thirty-three. In consequence reduction divisions in the mule are prevailingly abnormal as to chromatin distribution, and no functional spermatozoa appear to be produced. If we judge by analogy with plants,

Fig. 200.—A mare mule (?) with a foal by a Percheron stallion. (*After Lloyd-Jones.*)

Fig. 201.—The foal of Fig. 200. It is said to exhibit mule-like characters in its feet and actions, although otherwise its characters are all horse-like. (*After Lloyd-Jones.*)

however, there appears to be no reason for questioning the possibility of the occasional production of functional sperm and egg-cells, although unquestionably they would be very rare. In that case it is difficult to see why mare mules when bred to stallions may not occasionally produce foals which would either be very horse-like or very mule-like in appearance. On this basis, however, we are justified in regarding with grave doubt those cases of mare mules which have produced several foals, for cases of fertility should be isolated phenomena which should rarely be repeated in the same animal. The matter of fertile mules possesses some theoretical interest, but little practical importance.

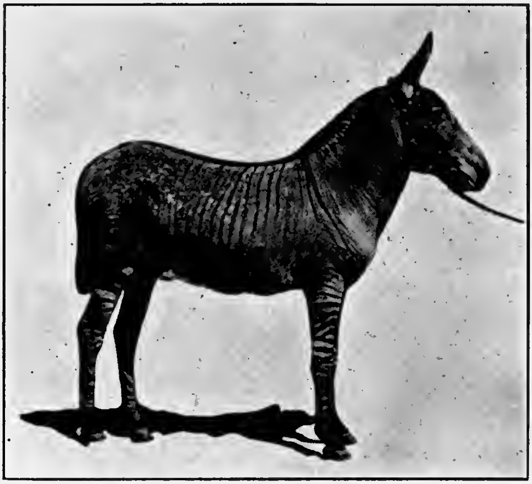


Fig. 202.—A zebroid, produced by mating a burro to the Grevy zebra. (*After Rommel.*)

Hybrids between other species of Equus have been obtained from time to time, and some attempts have been made, as yet unsuccessful, to find a place for them in practical agriculture. The zebra crosses with the horse and the ass, producing in both cases vigorous, growthy hybrids. In Fig. 202 is shown a zebra-ass hybrid, in Fig. 222, a Grevy zebra, and in Fig. 224, a zebra-horse hybrid. Other hybrids have also been produced but they are all simply zoölogical curiosities. They all appear to be infertile, like the mule, although here again reports are not agreed. Darwin mentions a zebra-ass hybrid which when bred to a mare got a foal, very horse-like in appearance. Rommel reports the zebra-ass hybrid to be infertile, although giving greater promise of a limited fertility than the mule.

In the genus Bos a number of species hybrids are known. Detlefsen has given a list of them taken from Nathusius. Thus the domestic cow, *Bos taurus*, has been mated with the yak, *Bibos grunniens;* with the gayal, *Bibos frontalis;* with the gaur, *Bibos gaurus;* with the zebu, *Bos indicus*, and with the American bison, *Bison americanus.* Apparently all these hybrids are fertile in the female sex, and sterile in the male. They are commonly more vigorous than the parents, and in some cases they provide a source for breed improvement for specific purposes. These features are discussed in the next following chapter, in which illustrations also will be found.

Many other species hybrids have been reported among domestic animals. Thus there are persistent reports of hybrids between the sheep and goat. In fowls a great variety of strange hybrids have been produced. Brentana lists thirteen remarkable hybrids in the Phasianidæ among them peacock-guinea fowl, pheasant-fowl, guinea fowl-fowl, and various pheasant species crosses. Although of technical interest these hybrids do not promise to yield anything of commercial value.

CHAPTER XXXIII

DISEASE AND RELATED PHENOMENA IN ANIMAL BREEDING

In the present chapter not only the subject of disease, but the related subjects of defects and immunity will be dealt with from the genetic standpoint. According to the strict definition of the term, disease is an abnormal process exhibited in some part of the body and dependent for its initial impetus upon an external cause. Obviously if a definition such as this be applied, there could be no such thing as the inheritance of disease, but genetic research has demonstrated beyond the shadow of a doubt that conditions in the body which more or less directly predispose it to disease are inherited. The subject, therefore, deserves treatment adequate to the need of outlining clearly the relation of problems of disease to inheritance.

The Inheritance of Disease.—The problem of the inheritance of disease is one very much like the problem of the inheritance of acquired characters, for it is hedged around with confusion of every day thought and the same type of misconception that characterizes this latter problem. Thomson has recognized these elements of difficulty and has given the subject, particularly as it relates to human inheritance, an adequate, extended treatment.

Many of the misunderstandings which have arisen have been derived not only from common folk lore, but from loose thinking on the part of those who practice the medical profession as well. It is not always an easy matter to distinguish between inheritance of disease and inheritance of predisposition to disease, although the distinction is one readily conceivable from a theoretical standpoint, and necessary for clarity of thought. It is necessary, moreover, to emphasize the fact that reappearance of disease in successive generations does not constitute inheritance. It is particularly true in the human race that successive generations are often subjected to the same conditions of life. If these be unfavorable, any predisposition to disease of a specific kind may result in the reappearance of the disease. Illustrations of this sort occur in every day observation; they include such things as the tendency to tuberculosis in certain families, the persistent reappearance of gout in successive generations, nervous disorders which are expressed in various forms in a given line of descent. Finally it is not common in every day thought to draw distinctions as finely as is necessary in scientific treatment. It is possible, for instance, for the fetus to be infected with disease at any time from the moment of conception to that of birth, and ante-natal infections are as truly acquired as are post-natal infections. It is possible for the fetus to be infected directly and independently of the mother, as occurs at times in cases of venereal disease; it is also possible for the fetus to become infected from the mother through the placenta, a much less common phenomenon. In either case, however, it is confusion of thought to speak of such instances as examples of the inheritance of disease. The many ramifications of the subject cannot be dealt with fully here; suffice it to say that as with acquired characters so with disease transmission the affirmative case has not been proven.

The Inheritance of Predisposition to Disease.—Predisposition to disease may be either specific or general. In specific predisposition the individual is liable, should prejudicial conditions occur, to contract a particular disease, as for example gout, whereas general predisposition gives room for infection with a series of similar diseases. This latter type of predisposition is very commonly expressed in general constitutional debility rather than in any specific fashion. It is particularly shown in nervous diseases in man, where a predisposition to nervous derangement is expressed in a variety of ways in a given line of descent, but even here the predisposition is often specific to a remarkable degree.

That predispositions are inherited cannot well be questioned, but in tracing their transmission it is necessary to guard against factors which confuse cases. Thus it does not necessarily follow that an individual predisposed to a disease should invariably become a victim to that disease. Transportation in early life to a new environment or particular attention throughout life to matters making for health with respect to a known inborn tendency may entirely overcome the predisposition. The degree of predisposition also varies; in some cases it is so strong as to amount practically to transmission of disease; in other cases it is relatively weak, and requires either that the inciting cause be impressed frequently upon the individual before resistance is broken down and the individual yields to attack or that some other violently unfavorable condition should enter into the life of the individual.

It is worth while remarking that predisposition to disease like many defects of structure often skips generations in inheritance. In general it appears that the normal state of health is the dominant condition and that predispositions are for the most part dependent upon the action of recessive factors or sets of factors. Accordingly predisposition to disease is more likely to crop out as a result of consanguineous matings, because related individuals are more likely to bear the same recessive factors in their germinal material. In this fashion it is not difficult to account for the persistent atavistic appearance of disease in some lines of descent.

The Inheritance of Defects.—By defects we refer specifically to abnormal structures or processes which are the almost invariable expressions of particular genetic constitutions. Of these a vast number are known, particularly in man where in recent years a considerable amount of attention has been devoted to them. A very familiar example is hæmophilia, a bodily condition such that the blood does not possess the ability to clot when blood-vessels are ruptured. The defect in man is determined by a sex-linked recessive factor and exhibits the same type of inheritance as sex-linked factors do in the fruit fly. A family history showing the inheritance of hæmophilia is outlined in Fig. 203. There is an analogous defect in the horse. In man a number of other defects have been traced some of which display a Mendelian type of behavior, and a surprisingly large number of them are sex-linked.

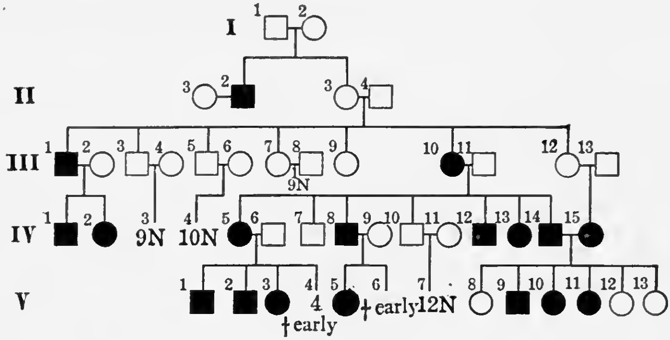


FIG. 203.—Pedigree of a family of "bleeders"—the K. family, located in and about Carroll Co., Maryland. The son, II, 2, was a bleeder but died without issue. The eldest son, III, 1, of the daughter, II, 3, was a bleeder from 18 up to 45 years, "often bled till he fainted." He had 2 unaffected brothers and 3 normal sisters but 1 sister, III, 10, was a "bleeder until 40." He had a son, IV, 1, who was a very bad bleeder from 18 until toward middle life and a daughter, IV, 2, who often "bled until she fainted" and eventually died of dysentery. All 19 children of the 2 normal brothers were normal and 9 children of the normal sister, III, 7. The affected sister, III, 10, had 3 sons and 2 daughters who were affected. IV, 5, is stated to be "a bleeder" and had by an unaffected husband 2 bleeding sons and 1 bleeding daughter besides 4 others who died of scarlatina. Her brother, IV, 8, had a daughter, V, 5, who was a bleeder until 15, and then died of a hemorrhage of the lungs consequent upon tuberculosis. There were other children all of whom died young of scarlatina. The normal brother, IV, 10, had 12 normal children. The next 2 had no offspring. The youngest son, IV, 14, began to bleed while an infant, grew worse until he was 25 and has since improved. He married a cousin who is also a bleeder and they have 6 children. Three of the daughters have not bled as yet. V, 9, has been a bleeder since he was 8 months old and bleeds until he faints; V, 10, has been a bleeder since she was 8 months old and V, 11, bleeds occasionally but not very severely. (*After C. B. Davenport.*)

Thus among dominant defects in man Guyer lists *achondroplasy*, abnormally short limbs along with normal head and body; *keratosis*, thickening of the epidermis; *epidermolysis*, excessive formation of blisters; *hypotrichosis*, a hairless and toothless condition; *diabetes* *insipidus; diabetes mellitus; muscular atrophy* of the ordinary type; *glaucoma,* internal swelling and pressure on the eyeball; displaced lens; *colomba,* an open suture in the iris; *piebaldness,* spotting of the dermal coat; *corneal opacity; Huntington's chorea,* a disease similar to St. Vitus' dance, a dangerous malady which first exhibits itself in middle life; *retinosa pigmentosa,* pigmentary degeneration of the retina; *polydactylism,* extra fingers and toes; *syndactylism,* fusion of digits; *congenital cataract; hemeralopia,* hereditary night-blindness; and *brachydactylism,* shortening of the digits. A corresponding list of recessive defects includes susceptibility to cancer; *chorea,* St. Vitus' dance; true dwarfism in which all parts are proportionally reduced; *alkaptonuria,* urine darkens after passage; alcoholism and criminality when based on mental deficiency, hereditary hysteria; *multiple sclerosis,* diffuse degeneration of nervous tissue; *Friedreich's disease,* degeneration of the upper part of the spinal cord; *Ménière's disease,* dizziness and roaring in the ears; *Thomson's disease,* lack of muscular tone; hereditary *ataxia;* possibly the tendency to become hard of hearing in advanced age; possibly non-resistance to tuberculosis; feeble-mindedness of various types. In man the sex-linked defects include *Daltonism,* color-blindness characterized by inability to distinguish between reds and greens; *hæmophilia,* excessive bleeding from wounds; *myopia,* near-sightedness; *multiple sclerosis; neuritis optica,* progressive atrophy of the optic nerve; *Gower's muscular atrophy; night-blindness,* some forms; *ichthyosis,* a peculiar scaly condition of the skin; *syndactyly,* some forms.

When the short time in which true systematic attention has been given to the inheritance of human defects is recalled, it can be seen that this even now incomplete list is truly a formidable array of infirmities. Commonly of course prejudice against those individuals which display noticeable defects is so great that they have less opportunity for reproduction than the more fit members of society. This is particularly true of the more serious, dominant defects, and there is a consequent tendency for these to run out. Some very serious dominant defects, however, such as Huntington's chorea are commonly not exhibited until late in life after the common reproductive period is passed. It is difficult, therefore, to state in such cases which individuals should and which should not be permitted to bring forth offspring. In the case of recessive defects, the factor may be carried by normal individuals, and may therefore continually crop out among the progeny of normal parents. To breed out defects in general, therefore, it is necessary to reject all defectives for breeding purposes, and to mate all individuals from defective stock, if at all, to stocks known not to be defective with respect to the infirmity in question. A word of warning is necessary here on account of the nature of our knowledge of human heredity. The data which have been collected are of the observational type, the conclusions which have been drawn are inferential, and many of them are still in dispute among skilled investigators, nevertheless the results which have been reached have a high degree of probable validity. Whether it is desirable from a sociological standpoint to reject all defective individuals from reproduction, and to exclude in addition those individuals which while themselves normal may transmit some defect, is a grave question which should be considered very carefully. It is not, however, a question of genetics, the geneticist can only point out the remedy. It is a matter of grave concern to any nation that 30 per cent. of its population should carry hereditary taints, and yet that is about the proportion which Rosanoff estimates on the basis of data from certain localities in the United States.

An example nearer home might be taken, but that of the cretins of Aosta described by Whymper is perhaps one of the most striking cases of the baneful effects which may follow an improper social treatment of defectives. These horrible examples of human deformity, often goitrous and almost devoid of intelligence and common decency, had been the objects of such pity and charity on the part of society that the condition had actually been favored and preserved rather than weeded out. Under the old regime the cretins were given the best of care and attention, intermarriage between them was sanctioned by the church, and such a premium paid upon the deformity that it was multiplied from generation to generation. The disease was known to reappear in successive generations, yet no attempt was made to stamp it out in the perfectly obvious way by preventing reproduction by cretins. Later, however, when this method of dealing with the problem was applied, the prevalence of cretinism was soon strikingly decreased.

Whether or not the rate of reproduction in cretins is greater or less than that in normal stocks is a question. It is, however, known that many families which carry the taint of feeblemindedness are astonishingly prolific. None but a positive method, therefore, can deal with cases of this kind under modern conditions; for there is no assurance whatever that such families under present day conditions will tend to run out on account of differential survival when compared with normal stocks. The student who wishes to carry this subject further will find abundant confirmation of these statements in the records of the Juke family, the Nam family, the Hill folk, and the Kallikak family.

Defects in Domestic Animals.—Curiously enough, if it be desired to trace the inheritance of defects in animals, man himself provides some of the most interesting and best investigated cases. The reason for this is very obvious; the animal breeder does not propagate his defectives, he rigidly culls them out of the herd. As a consequence although a few defectives occur from generation to generation in domestic animals, they are immediately condemned so far as breeding purposes are concerned. Little, therefore, is known concerning the inheritance of defects in animals except in rare cases where the defect may be of some use to man. We refer particularly to such characters as the polled condition in cattle, hornlessness in sheep, mule-foot in hogs, taillessness in cats, and like characters. Among them we might also include the famous Ancon sheep, now extinct. A case of an extremely malformed, defective condition is that reported by J. Wilson in Dexter-Kerry cattle. These cattle occasionally produce calves which are monstrous and live only a few hours, but they all conform to a definite type. Wilson describes them thus. "The body is short and stout; the upper jaw is short, giving the head a bulldog appearance; the legs are extremely short, being little more than a finger-length; the tail arises from well up the back; and the ventral skin is unclosed so that the intestines protrude." Apparently in this monstrosity we have a simple factor difference from the normal form of such a nature as to lead to total incapacity for independent existence. This condition is almost certainly the outcome of matings of normal individuals heterozygous for a defective recessive factor. The only moral that need be pointed out here is that a surprisingly large proportion of defective conditions are heritable. The animal breeder is, therefore, fully justified in avoiding so far as lies within his power breeding from defectives or even from normal individuals belonging to defective stocks.

Immunity to Disease.—Animals may exhibit different sorts of immunity to disease. Thus there is a certain kind of racial immunity which is just as characteristic of a given race as its morphological characters are. Fowl cholera and foot-and-mouth disease do not affect men. Apparently the degree of relationship may be even much closer. Thus according to Tyzzer susceptibility to transplantable tumors varies in different strains of mice. Two strains of common mice, one from Buffalo, N. Y., and the other from Providence, R. I., and a strain of Japanese waltzing mice were used in the experiments. Although the investigations were not carried on extensively enough to be conclusive, they do indicate very definitely different degrees of susceptibility to various kinds of tumors. It was found that the Ehrlich tumor developed in 30 per cent. of the Providence mice and in 60 per cent. of the Buffalo mice. It became established in the Japanese mice, but practically failed to develop. The Jensen tumor developed in 40 per cent. of the Providence mice, but failed to develop at all in the Buffalo and Japanese mice. A Japanese type of tumor developed in all but three out of 145 Japanese individuals which were inoculated, but failed to develop at all in common mice. In the zebu we appear to have an analagous condition, for according to Pucci a male and female Gujarat zebu among seventy brown Alpine cows were the only individuals spared by the foot-and-mouth disease.

There is another type of immunity which is characteristic of certain individuals within a race. It is a matter of common observation that individuals occasionally appear which are completely immune to a given disease. It is difficult to state precisely upon what this immunity depends, but it is none the less definite, and it is apparently often heritable. When heritable it may under appropriate conditions become a racial character. It has been thought that upon this depends the comparative immunity which certain races bear against given diseases. The negro of the West Indies is comparatively immune to the ravages of yellow fever, presumably because for centuries the more susceptible individuals have succumbed to the disease, so that the race has been propagated for the most part by less susceptible individuals or those which survived the disease. The white man on the other hand is more susceptible to yellow fever because no process of selection has weeded out susceptible strains. Measles, also, is considered a very mild disease among Caucasian peoples, but among the North American Indians it is very severe, spreading through tribes like a veritable plague and proving fatal in many cases.

There is another type of immunity which is acquired by the individual during life. Persons who have had smallpox have had conferred upon them an immunity which lasts for several years, and the same is true of other diseases in man and in other animals. This type of immunity may be induced artificially in the individual by appropriate treatment such as is done in vaccination, the administration of anitoxins and other forms of immunization. In animals the practice is seen in the distribution by experiment stations of blackleg vaccine for calves and hog cholera serum for swine plague.

A type of indirect immunity is that of resistance to attack by agents carrying a particular disease. Thus yellow fever is carried by a certain kind of mosquito, *Aedes calopus*, and malaria by certain species of the genus Anopheles. It would be possible, therefore, for individuals to enjoy freedom from the attacks of either of these two diseases if they happened to be resistant or repellent to the attacks of the particular mosquitos which carry the disease. Sometimes active immunity is associated with such resistance to attack. This matter does not look so strange when it is recalled that often a very specific relation exists between parasite and host among animals, and that very often diseases are transmitted by insects and other animal pests. In animals immunity of this kind is exhibited by the zebu against the Texas fever tick. According to Mohler the immunity which the zebu enjoys to tick infestation depends upon three factors; the sebum secreted by the glands of the skin, which has a repellent odor repugnant to insect life; the toughness of the skin, which, although as thin as that of domestic cattle, is more difficult to pierce; and finally the short coat, which does not provide shelter for the ticks. The bison also appears to be immune to the attacks of the same pest.

Breeding for Immunity.—The matter of breeding for immunity to disease is one which may have tremendous practical importance in animal breeding. Success in such breeding depends upon the existence of strains or races of immune animals, and upon the transmission of these characters to the offspring. Thus in Tyzzer's experiments with mice it was found that the Ehrlich tumor, which made only a very insignificant growth in Japanese mice, also failed to develop in the F_1 hybrids between common and Japanese mice. In the same fashion F_1 mice of the cross common × Japanese proved to be resistant to inoculation with the Jensen tumor, in this respect resembling the Japanese parent. On the other hand F_1 mice of the cross common × Japanese were very susceptible to inoculation with the Japanese tumor, even more so than the Japanese mice themselves. Here the immunity of common mice to inoculation does not appear to have been carried over to the hybrids. The F_2 of this cross, however, behaved very peculiarly. Of fifty-four F_2 individuals not one proved susceptible to the tumor, and sixteen F_3 individuals gave like negative results. The transmission of immunity to disease is established by these experiments, but the exact factor relations cannot be stated.

In domestic animals the possibility of breeding for disease resistance has long been held in mind, and in some cases steps have actually been taken in that direction. In the Southern States, particularly in Texas, Texas fever has annually levied its millions of dollars' tribute upon the cattle industry. The trouble has apparently been intensified since the attempt to grade up range cattle by the use of pure-bred Hereford and Shorthorn bulls, for these improved types of Northern cattle are more susceptible to tick infestation and splenetic fever than their hardier, but otherwise less desirable, range relatives. Apparently there are some grounds for the belief that range cattle have received infusions of zebu blood from early Spanish importations into Mexico and from zebu cattle brought to South Carolina in 1849. Accordingly it is not impossible that the comparative freedom from tick and insect infestation which is characteristic of unimproved range cattle, has come originally from the zebu.

As in our own domestic cattle so in the zebu there are many different breeds, and they present differences no less striking than those of the Northern cattle. They have been bred for centuries under the tropical conditions of India and Africa. They are disease resistant; they are able to withstand tick and insect pests to which the Northern breeds of cattle succumb; and they can endure great heat; but they suffer from low temperatures (Figs. 204 and 205).

Fig. 204.—A Gujarat zebu bull, a splendid specimen of the breed. Imported from India and used as a herd bull in Brazil. (*From the Journal of Heredity.*)

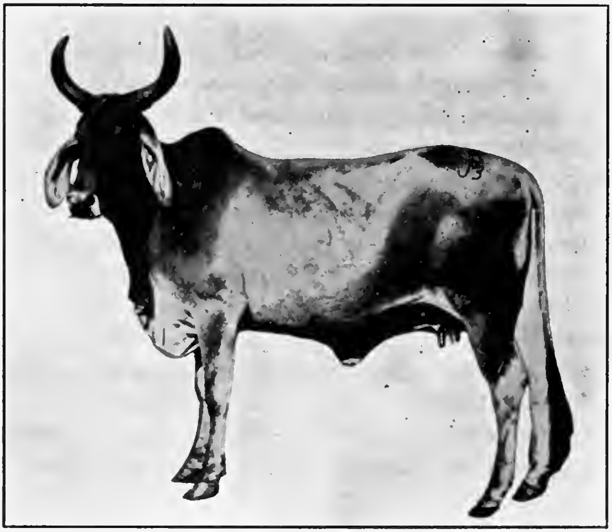


Fig. 205.—A Gujarat zebu cow. Imported from India and considered an unusually superior specimen of the breed. (*From the Journal of Heredity.*)

The zebu may be used in two different ways in animal breeding; either in obtaining direct hybrids with native cattle, or in establishing new breeds. The former manner of utilization is relatively simple—it requires merely that herds of both pure-bred cattle and zebus be maintained; the latter mode of employment necessitates long continued selection before stability of characters will have been reached.

If zebu cattle are to be used for obtaining cross-bred commercial stock, it is necessary that the immediate hybrids possess superior characters for such purposes. This matter appears to be in some doubt, but discounting the opinion of those who are blind partisans of the Northern breeds, it appears that zebu-Northern crosses unite many of the favorable characters of both breeds. The cross is very easily made. Thus Pucci reports upon the results of using a Gujarat bull on cows of the Maremma, Romagnola, and Perugia breeds in experiments conducted at the Perugia Institute of Animal Husbandry in Italy. Of 113 cows used only nine failed to give calves, and these nine were also barren when mated with bulls of their own breeds.

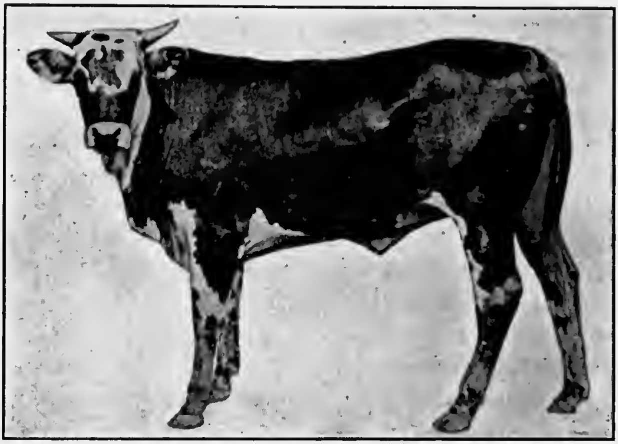


Fig. 206.—An F_1 zebu-Hereford heifer. The Hereford characters appear to be predominant. (*From the Journal of Heredity.*)

With respect to the characters of the F_1 offspring there seems to be a considerable difference of opinion. Pucci who has apparently studied the matter most thoroughly states that zebu characters are dominant with respect to fineness of skeleton, abundance of dewlap, development of ear, slope of rump, and general muscular development. It appears to be generally agreed that the crosses are more vigorous and growthy than the parents; according to early reports, they exceeded either parent by 50 per cent. in this respect. According to Nabours the predominant appearance of zebu characters in the F_1 offspring occurs only when range cattle are used. He ascribes this fact to the presence in range cattle of a strong infusion of zebu blood. He found that when crossed with

Shorthorn or Hereford cattle, the hybrids partook most of the characters of the Northern breed, save for the slight hump and greater development of dewlap and sheath, which are characteristic of the zebu. This observation is borne out by the zebu-Hereford hybrid shown in Fig. 206. With respect to market features, the hybrids appear to be held in high regard in regions where the cross has been made in great numbers. In Tunisia and Brazil at least butchers prefer them and are willing to pay a premium to get them.

With regard to resistance to disease the zebu appears to transmit most of its qualities, at least in some degree, to the F_1 offspring. They are resistant to foot-and-mouth disease, anthrax, and splenetic fever. They withstand the heat of tropical climates, and the insect pests which thrive in such places. According to several notes they are not infested by ticks, but this lack of infestation does not appear to be associated with any definite immunity to Texas fever itself. On the contrary one note states explicitly that both the pure-bred zebu and the F_1 hybrids are susceptible to infection with the Texas fever protozoon, but their high resistance to the disease keeps it from becoming as serious with them as with Northern cattle.

Apparently both male and female hybrids are fertile, in which respect they appear to differ from most other species hybrids among the Bovidæ, the females of which are commonly fertile while the males are sterile. There is evidence of Mendelian inheritance when specific characters are considered, but coupling and physiological relations appear to exert a considerable influence on the segregation and expression of characters. Evidence of this comes from the fact that so many of the F_2 hybrids so closely approach to an expression of the sum total of characters of either the zebu or the Northern breed as to be indistinguishable from them. In Brazil free interbreeding in hybrid herds apparently leads to a predominance of zebu characters in a very few generations, perhaps on account of the greater prolificacy of the zebu. The increased size and vigor of the F_1 is not maintained, and constancy of blended characters has apparently not been attained in any case. Tick resistance at least appears to be carried over to subsequent generations, although unforfortunately the records are not satisfactory.

From a practical standpoint, therefore, it appears that the zebu might be used as a means of combating tick fever in the Southern cattle district. Whether the method would prove desirable in view of the perfection attained by other methods of ridding pastures of ticks is, however, questionable. If utilized, however, it appears that the method should be that of continually mating zebu bulls with range cows. In this fashion it is possible to secure animals free from disease and at the same time of very superior market qualities. This would necessitate a practice like that in crossbreeding, namely of keeping pure-bred herds of both zebu and Northern cattle and continually crossing them. Central herds of zebus could easily be established to supply the demand for zebu bulls. Zebu bulls appear to be more prolific than Northern bulls, for it is possible with them to count upon an average of about sixty calves per year from each bull. The utilization of the hybrids for the establishment of a new breed is another matter, and one requiring long time and careful attention. It should, however, be carried on under competent guidance such as might be afforded by experiment station supervision.

FIG. 207.—Bison bull, *Bison americanus.* *(Courtesy National Zoological Park, Washington, D. C.)*

The other hybrid which gives some promise of use in American agriculture is that obtained by crossing the bison and domestic cattle. Reciprocal hybrids may be obtained, but apparently it is easier to get hybrids by using a bison bull on domestic cows. This hybrid represents a more violent cross than the zebu hybrid, inasmuch as considerable difficulty attends the production of hybrid progeny. Cows very often die while calving, apparently on account of the physical difficulties involved in giving birth to the hybrids, which possess a considerable hump like that on the bison. The hybrids are intermediate between the parents in respect to most characters. In vigor and size they are superior to either parent; from the market standpoint both with respect to flesh and coat they are very desirable animals. Practically all the animals which have been born have been females, and these are fertile. A few males have been born and these have always proved sterile. The hybrids are apparently very uniform. The female hybrids appear to have no difficulty in parturition when bred to domestic bulls or bison bulls.

FIG. 208.—An F_1 hybrid between a bison bull and an Aberdeen-Angus cow. Note polled character. (*From Journal of Heredity.*)

FIG. 209.—Quinto Porto, five-eighths buffalo, three-eighths polled Hereford. A fertile bull which displays the characters of both species. (*From the Journal of Heredity.*)

When bred to bison bulls, the three-fourths hybrids which are produced are intermediate between the bison and the hybrid, and one-fourth hybrids produced by breeding an F_1 female to a domestic bull are intermediate between the hybrid and domestic cattle. Bulls of these two grades are sometimes fertile. The bull Quinto Porto which is shown in Fig. 209 has proven fertile with Hereford cows. His pedigree is as follows:

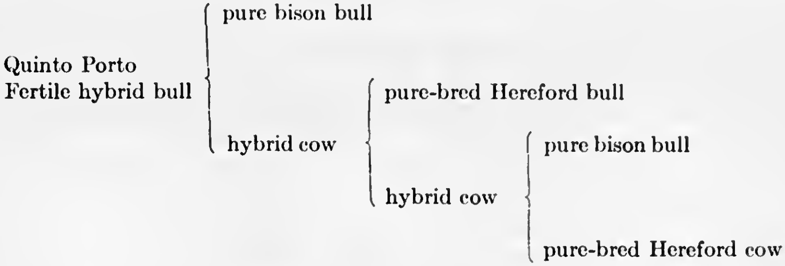


FIG. 210.—Ancestry of a fertile hybrid cattalo bull.

By long-continued selection it would be possible apparently to transfer many of the excellent qualities of the bison such as superior coat, greater hardiness, resistance to tick and insect infestation, and superior beef qualities to domestic cattle. There is no possibility of utilizing it like the zebu for securing cross-bred animals of superior qualities, not because of lack of such superior qualities, but because of the difficulties of securing F_1 hybrids. For range conditions it might be possible to establish a breed of cattalo which would have many advantages. Here again the need of continuous attention and encouragement such as might be given by experiment station supervision would be a valuable aid toward such a goal.

CHAPTER XXXIV

SEX IN ANIMALS

Sex-determination with its attendant problems has always been a subject of great interest to practical animal breeders; and the art of breeding has not lacked rules by which the sex ratio might be shifted in various ways to the advantage of the breeder. But most of these rules, like many beliefs current at one time or another in animal breeding have been founded upon inadequate evidence or unsound reasoning. Sex remains a matter beyond the control of the breeder: its ultimate control is entirely problematical.

The Determination of Sex.—The thesis that sex is determined at the time of fertilization has been elaborated fully in Chapter XI. It was pointed out there that sex, like other characters of the individual, has a definite factorial basis, that the factorial constitution of the individual with respect to sex as well as to other characters is fixed by the constitution of the two gametes which unite to form the zygote. There is every reason to believe that sex is determined in this same fashion in domestic animals, at the time of fertilization; and that any treatment subsequent to that time cannot affect the sex of the individual. At least this much may be said, that any theory of sex-determination in the higher animals which is based upon other factors than chromosome constitution, must be brought into harmony with the known facts of the chromosome relations in sex-determination.

Sex-determination in Mammals.—It appears to be fairly well established that the inheritance of sex in mammals always is of the XY type, that is the females are homozygous for a determiner of femaleness whereas the males are heterozygous. Since this group includes practically all domestic animals, except the feathered ones, it follows that in horses, cattle, sheep, goats, swine, etc., the mode of inheritance of sex is of this type. The direct evidence for this conclusion in domestic animals is exceedingly meager, but the main outlines are sufficiently clear to provide fairly satisfactory confirmation of this general conclusion.

For direct cytological evidence of the mode of determination of sex in these domestic animals we are indebted particularly to the extensive investigations of Wodsedalek. These investigations do not provide a complete body of evidence, but they indicate very strongly that unequal distribution of chromosomes takes place in the male in the horse and swine. Wodsedalek finds that in the horse the somatic number of chromosomes in the female is thirty-eight, in the male thirty-six. In Fig. 211 are shown stages of the heterotypic division from which these conclusions are drawn. There are apparently two accessory chromosomes, and these both go to the same pole. Consequently half the spermatozoa contain nineteen and half seventeen chromosomes. No direct cytological evidence of gametogenesis in the female has been obtained, it is merely assumed that those gametes containing nineteen chromosomes are normally female producing and that those which contain seventeen are male producing. In the pig very much the same state of affairs exists.

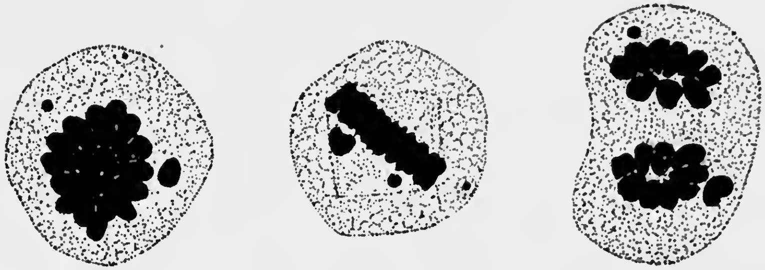


Fig. 211.—Three figures illustrating heterotypic division in the horse. The sex-chromosomes are seen slightly separated from the autosomes in each figure. (*After Wodsedalek.*)

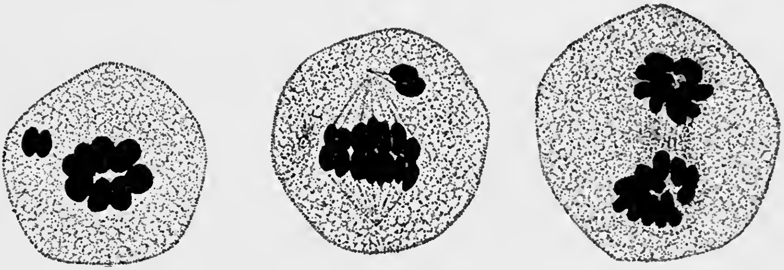


Fig. 212.—Three figures illustrating stages in the heterotypic division in the male pig. The sex chromosomes are seen passing to one pole ahead of the autosomes in the middle figure. (*After Wodsedalek.*)

The somatic number of chromosomes in the female is twenty, in the male eighteen. In the heterotypic division in the male, stages of which are shown in Fig. 212, the two accessory chromosomes pass to the same pole. In consequence in the male half the gametes contain ten and half eight chromosomes. From this the conclusion is drawn without further evidence that the male is heterozygous and the female homozygous for the sex-factors. In man cytological investigations have been made by Guyer, Montgomery, von Winiwarter, Wiemen and Evans.[1] The evidence is very conflicting as regards total chromosome number, but it is not at all in conflict with the hypothesis of an XY type of sex inheritance in man. Von Winiwarter finds that there are forty-seven chromosomes in the male. In the formation of spermatozoa he observed that half received twenty-three and half twenty-four chromosomes. In the female his evidence pointed to forty-eight as the somatic number, consequently it may be assumed that all egg-cells normally contain twenty-four chromosomes. The observations of Guyer and Montgomery which were made with material from the negro, seem to indicate that the chromosome number in this race is one-half that in the white race. This evidence also indicated that a pair of accessory chromosomes exist in the male, but the evidence is not conclusive. The existence of an X and a Y chromosome in the male has been claimed by Wieman. The cytological evidence, therefore, so far as it goes, indicates that there is nothing in the internal mechanism of mammals in conflict with the belief that the female is homozygous for a sex-factor, and the male heterozygous.

The evidence from hereditary phenomena is not very extensive for domestic mammals. In man, however, as has been pointed out in other places, a number of sex-linked characters are known, and these follow the XY type of sex-determination. Here the evidence is strong enough to be conclusive, but in no domsetic animal with the exception of the cat is any sex-linked character known. In the cat the characters in question are black, orange, and tortoise-shell coat colors. According to Ibsen's analysis of the case, which appears to be most satisfactory, there are two factors giving the following color classes and formulæ:

Females	Males	Classes
$(BTX)(BTX)$	$(BTX)Y$	Tortoise shell
$(BtX)(BtX)$	$(BtX)Y$	Black
$(bTX)(bTX)$	$(bTX)Y$	Orange
$(btX)(btX)$	$(btX)Y$	Orange

The experimental evidence as to the relation of the colors has been discussed by Doncaster, Little, Whiting, and Ibsen, but the analysis is still in debate. Such as it is, however, there is no room for doubt that sex-linked characters occur in the cat and are distributed in accordance with the accepted conclusion that the male is heterozygous for sex and the female homozygous.

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[1] Dr. Herbert M. Evans of the University of California. Data not published, but in the case of a white man hundreds of counts give constantly 48 chromosomes in the spermatogonia. If the number in the white male is 48, instead of 47 as von Winiwarter concluded, it would indicate the existence of a Y element as well as one X element in the male.

Sex-determination in Birds.—Contrary to the condition in mammals, in birds the determination of sex appears to depend upon the *WZ* type of sex-inheritance, for in them the female is heterozygous for the sex factor, and the male homozygous. The cytological evidence for this conclusion, while limited to investigations on the domestic fowl, has through the persistent and painstaking efforts of Guyer, been very definitely if not quite completely worked out. In this species there are 18 chromosomes in the somatic and primary germ cells of the male and 17 in the female; in the former there are two sex-chromosomes and in the latter, one. The eggs, therefore, are of two classes, those possessing a sex-chromosome and hence male-producing, and those lacking it and hence female-producing. In the male both the sex-chromosomes pass together during the reduction division into one daughter cell, so that half of the sperm are provided with a sex-chromosome and half are not. The fate of the sperm lacking a sex-chromosome is still somewhat in doubt, but there is considerable cytological evidence indicating that part of the developing sperm degenerate. Moreover, the fact that statistical examination of head length of the spermatozoa reveals only one class of sperm certainly strengthens this inference. Thus the cytological evidence is in complete harmony with the extensive evidence from sex-linked characters in this species.

The mode of inheritance of the barring factor in the domestic fowl has already been described in detail. Other factors in the domestic fowl which have been found to exhibit sex-linked inheritance are those for inhibition of pigmentation in the silky fowl, and of red in the plumage of the Columbian Wyandotte and gray in the White Wyandotte, also a factor for high fecundity. In pigeons, also, it has been found that the factor for dilute pigmentation is sex-linked, and follows the same type of distribution as that described for the domestic fowl.

The Sex-ratio.—The Mendelian theory of the inheritance of sex stipulates that in the heterozygous sex male and female producing gametes are formed in equal numbers; for in every reduction division one pole of necessity must contain the accessory chromosome or sex-determining factor whereas the other must either lack it or contain its unequal homologous chromosome or sex-determining factor. As a consequence of this fact we should expect the sex-ratio to show an approximate

TABLE LXX. Sex Ratios in Animals.

Animal	Males	Females	Authority
Horse.....	98.3	100	Düsing
Cattle....	107.3	100	Wilckens
Sheep.....	97.7	100	Darwin
Swine.....	111.8	100	Wilckens
Rat.......	105.0	100	Cuénot
Dove.....	105.0	100	Cuénot
Fowl......	94.7	100	Darwin

equality of males and females in every generation. Extensive statistical investigations of the sex-ratio in a number of animals demonstrate, however, that there are usually small but significant deviations from the numerical equality of the sexes. The data in Table LXX collected by Morgan illustrate this point.

In man the sex-ratio varies among different peoples, but almost invariably the proportion of males is slightly in excess of that of females.

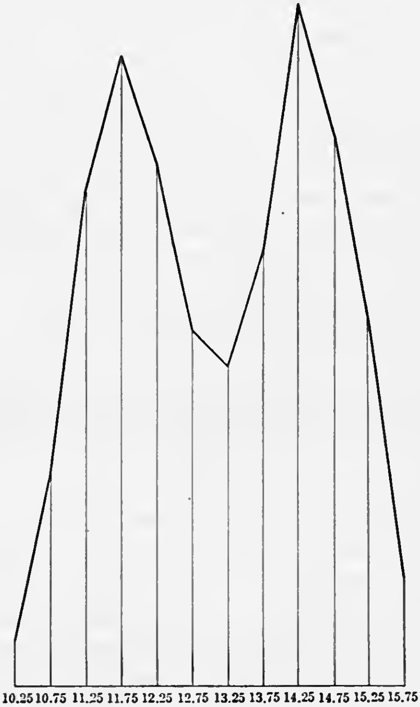


Fig. 213.—Frequency polygon of head lengths of spermatozoa in the pig. (*Data from Wodsedalek.*)

In dealing with sex-ratios it must be emphasized that a study of the deviations which are obtained may point to conditions which alter the sex-ratio without disturbing the mode of determination of sex. The mechanism of sex-determination is not such a one as would lead invariably to numerical equality of the sexes. This may easily be seen by a consideration of several disturbing factors which may enter into it.

The first of these has to do with the relative sizes of male and female producing gametes, particularly in those animals in which the male is the heterozygous sex. Thus Wodsedalek has shown for the pig and the horse that there are two intergrading classes of spermatozoa as respects size (Figs. 213 and 214). Unquestionably in both cases the larger class are those which contain the accessory chromosome or chromosomes. The larger class, therefore, includes the female-producing spermatozoa, the smaller class the male-producing spermatozoa. If this difference in size should be correlated with a slight difference in activity, it is conceivable that chance would favor fertilization with the more active spermatozoa, and would produce a consequent disturbance in the sex-ratio.

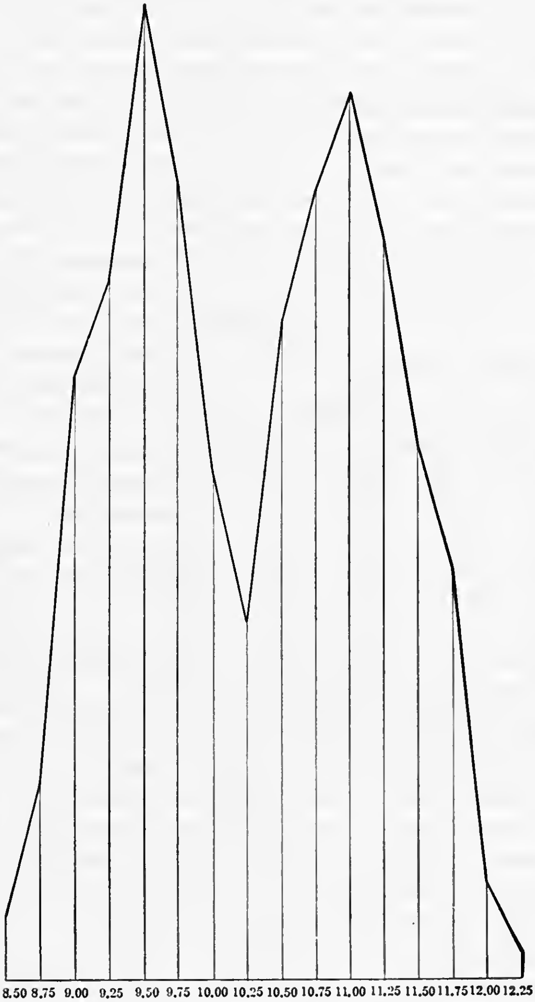


Fig. 214.—Frequency polygon of head lengths of spermatozoa in the horse. (*Data from Wodsedalek.*)

Moreover, the gametes of the heterozygous sex, since they are made up of two classes having different chromatin contents might display differential mortality under the stress of slightly unfavorable conditions. It may easily be seen, therefore, that slight or conceivably wide variations in the sex-ratio may be due to the operation of factors other than those which actually determine sex.

Causes of Unusual Sex-ratios.—In this discussion we desire to treat only of causes of sex-ratio disturbance which may operate in the higher domestic animals. The curious and interesting conditions which are found in some insects and other lower animal forms will not be mentioned save in so far as they may throw light upon the problem of sex-ratio disturbance in higher animals.

In some cases hybridity appears to favor a disproportionate production of one sex or the other. Thus in the bison-cattle crosses, the production of males is relatively rare. This, however, appears to be due to the fact that physical difficulties make it practically impossible for a cow to bear to maturity a bison-cattle fetus and to give birth to it. There are two reasons for this, the increased size of the hybrid fetus, and the development of a large hump which cannot be accommodated by the normal pelvic conformation in the cow. Consequently the fact that practically all the animals born of this species cross are females, may simply be due to abortion and death of male fetuses. The amount of trouble is sufficient in this case to give room for a potential equality of sexes in such crosses. Detlefsen reports similar results from a cavy species cross, which gave a disproportionately low ratio of males. The data are given in Table LXXI. The earlier generations show a considerable deviation from the normal equality of the sexes. With successive back-crosses, however, the ratio soon becomes one of practical equality.

TABLE LXXI.—RATIO OF SEXES IN HYBRID GUINEA-PIGS (*After Detlefsen*)

Generation	Males	Females	Total	Number of males to 100 females
F_1, $\frac{1}{2}$ wild	14	23	37	60.9
F_2, $\frac{1}{4}$ wild	31	52	83	59.6
F_3, $\frac{1}{8}$ wild	101	116	217	87.1
F_4, $\frac{1}{16}$ wild	159	153	312	103.9
F_5, $\frac{1}{32}$ wild	173	171	344	101.2
F_6, $\frac{1}{64}$ wild	58	64	122	90.6
F_7, $\frac{1}{128}$ wild	16	21	37	76.2
Totals	552	600	1152	92.0

When races are more closely related a different result is produced. Thus Miss King found in crosses between wild and albino rats a sex-ratio of 119.1 males to 100 females among 425 hybrids representing the first three hybrid generations of such a cross. Among guinea-pigs crossed *inter se*, Minot found among 410 individuals a sex-ratio almost exactly the same as that among Miss King's rats, 119.2 males to 100 females.

Among wide crosses of hybrid birds the percentage of males also appears to be abnormally high, but this can hardly be taken as in conformity with the data of King and Minot, because in birds the mode of sex-inheritance is exactly the reverse of that in mammals. Accordingly these data should be regarded as confirmatory of the data from bison-cattle crosses, and those of Detlefsen with cavy species crosses.

As another possible source of variation in the sex-ratio, mention must be made of the time of service with respect to the inception of the period of heat. Various theories of sex have from time to time been founded on heat relations, some maintaining that the products of conception in early heat were more often males, others that they were more often females. Pearl and Parshley have made an experimental-statistical study of this question, the data of which are given in Table LXXII. These data were collected from farmers in the state of Maine, and represent all breeds and ages of cattle. Pearl and Parshley draw attention to the fact that they show a steady increase in the proportion of male births with later coitus. The question as to the general significance of this fact, they discuss at some length. In Table LXXIII is given the statistical treatment of these data. Only in one case, that

TABLE LXXII.—THE EFFECT OF SERVICE AT DIFFERENT PERIODS OF HEAT ON THE SEX-RATIO IN CATTLE (*Data of Pearl and Parshley*)

Time of coitus	Total offspring	Sex of offspring		Percentages		Males to 100 females
		Males	Females	Male births	Female births	
Early in heat........	248	123	125	49.60 ± 2.14	50.40	98.4
Middle of heat.....	125	67	58	53.60 ± 3.01	46.40	115.5
Late in heat........	107	65	42	60.75 ± 3.19	39.25	154.8
Totals, all periods...	480	255	225	53.13 ± 1.54	46.87	113.3

TABLE LXXIII.—STATISTICAL TREATMENT OF THE SEX-RATIOS OF TABLE LXXII (*Data of Pearl and Parshley*)

Groups compared	Difference	Odds against chance occurrence
Percentage of male births		
Late in heat and early in heat...............	11.15 ± 3.84	18.80 to 1
Late in heat and middle of heat..............	7.15 ± 4.39	2.69 to 1
Middle of heat and early in heat............	4.00 ± 3.69	1.15 to 1

difference between the sex-ratio late in heat and early in heat can we place any confidence in the significance of the observed differences. In this case the odds are practically 19 to 1 against the chance occurrence of the deviation: the question thus presents itself for consideration, shall we regard this difference merely as a chance occurrence or as possessing real significance? We are informed that more recent data (unpublished) according to Pearl make the relation of time of service to sex extremely doubtful. Moreover, Pearl and Salaman have shown that this relation does not hold for man.

Metabolic Theories of Sex-determination.—Among other theories of sex-determination which have been advanced that of Geddes and Thomson still provokes a considerable amount of speculation and discussion. According to this theory there is no sex-determinant or factor at all, in the strictly Mendelian sense of the word, but rather differences in metabolic relations lead to the production of different sexes. The theory is based on the conception that deep constitutional differences in metabolism-rythms exist between the two sexes; the male being characterized by a preponderance of katabolic or disruptive processes, whereas the female is distinguished by the emphasis placed upon constructive or anabolic processes.

It should be pointed out, and indeed Geddes and Thomson fully appreciate this fact, that this theory is a physiological theory of sex-determination, whereas the Mendelian theory is essentially morphological. The two are not necessarily in conflict with each other, so that an acceptance of the conclusion that differences in metabolic balance exist in the two sexes, does not necessarily imply rejection of the Mendelian theory of sex. It is only when supporters of this physiological doctrine argue for the possibility of sex-determination occurring after fertilization, or in other words, for reversal of sex as fixed at fertilization by the influence of external factors operating subsequently to fertilization that difficulties between the two views arise. Thus to take a particular case, Pearl and Parshley on the basis of their statistical study of sex-determination mention the possibility of changes occurring in the metabolic conditions in ova corresponding roughly to different periods in the time of heat, and that by virtue of these changes alterations of the sex-ratio might occur. But this suggestion carries with it reversal of potential sex as determined by chromosome relations at the time of fertilization. We may ask, therefore, with justice what sort of males are these which arise from such alteration of metabolic balance? Presumably staleness should not lead to extrusion from the egg of an entire chromosome, or should not in the light of present day conceptions of factor stability lead to changes in the factors of the sex determining chromosome. If, therefore, staleness leads to a change in the relations between nucleoplasm and cytoplasm, such males so far as nuclear material goes are potentially female, that is they possess the same nuclear material as do females. We do not argue that this is absolutely impossible, but what sort of germ cells do such males produce? From the morphological standpoint, it would appear that they would be all of one kind, instead of being of two kinds as is normally the case. Such males, therefore, when mated to females should give sex-ratios entirely dependent upon those changed metabolic relations which had been induced by early or late fertilization or some other cause—the entire morphological basis would be destroyed.

Nevertheless, Riddle claims to have absolutely controlled sex-determination in the pigeon by experimental means. Having learned to identify the male and female producing ova, he was able, he says, to force either kind into the production of the opposite sex and he noted that the level of its metabolism was then shifted to the level characteristic of the germs of the opposite sex. Thus chromosomal correlation is here forced to failure but the metabolic correlation persists. Riddle infers, therefore, that the chromosomal constitution is not an efficient cause of sex; that it is but a sign or index and possibly an assistance in the *normal* maintenance of that which is essential—namely two different metabolic levels.

Another case of sex reversal is the free-martin, the female of two-sexed twins in cattle, which has long been known to be perfectly sterile although rarely such females are perfectly normal. Lillie has found by a study of embryonic development that the phenomenon of sterility is due to fusion of the embryonic membranes of the twins and anastomosis of the blood-vessels, especially the arteries, so that there is literal community of blood during fetal life. If the anastomosis of the blood-vessels does not take place, the female is perfectly normal as is usual with the twins or multiple births of all other mammals. This fact, according to Lillie, can be explained only on the assumption that the fetal blood carries specific sex-hormones, because the only system of the female that is affected is the reproductive system. The male, on the other hand, is normal in all its parts, and this finds explanation in the fact that sexual differentiation of the male antedates by a little that of the female, and the development of female sex-hormones is probably inhibited from the start. From the study of extensive data on free-martins Lillie concludes that the female zygote must contain factors for both sexes, and that the primary determination of the female sex must therefore be due to dominance of the female factors over the male. "If we think of this as a simple quantitative relation as Goldschmidt has done, we can explain the intersexual condition of the free-martin as due to an acceleration or intensification of the male factors of the female zygote by the male hormones. The degree of the effect which is quite variable, as we have seen, would of course be subject to all quantitative variations of the hormone. Thus the case of the free-martin could come under the same general point of view as that of the intersexes of Lymantria according to Goldschmidt with the one exception that the quantitative differences between the male and female factors of the female zygote necessary for the differentiation of female characters, are reduced in the free-martin by internal secretions instead of by variations of potency of the male factors in different varieties as in the intersexual hybrids of Lymantria." In attributing the free-martin condition to the male hormones Lillie means only to assert that they are the primary causes, and not that they are the decisive factors in each member of the series of events which result in the intersexual condition. He can, however, state confidently on the basis of present results that sex-determination in mammals is not irreversible predestination, and that with known methods and principles of physiology we can investigate the possible range of reversibility.

It will be observed that neither of these cases invalidates the fundamental hypothesis that the sex-chromosomes are the normal differentiators in sex-determination. Moreover, the sex-chromosome hypothesis has this virtue, that it is based upon observed and firmly established differences between the sexes. It is disappointing in that it provides so little hope for control of the process, but our dissatisfaction with it from this standpoint should not close our minds to its superiority in definiteness and experimental evidence to all other theories of sex-determination.

Inheritance of Unusual Sex-ratios.—From time to time reports are made of families both in man and other animals which appear to exhibit consistently abnormal sex-ratios. Families are reported in which male children only have been born for a number of generations, or in which only females have been born. Now according to the laws of chance such instances may occur occasionally without necessitating in any way the adoption of hypotheses subsidiary to that of the existence of a mechanism which potentially is calculated to give an approximate equality of the two sexes. But sometimes other factors do appear to be at work, and these may be mentioned briefly here.

The existence of sex-linked lethal factors in Drosophila has already been pointed out. Presumably these are factors which affect adversely the development or operation of some vital organ as a consequence of which individuals possessing the factor are doomed from the moment of conception to death at some stage in their life history. In some cases this occurs relatively late in the life history. Thus Bridges reports the discovery of a strain of flies with such a factor in which the morescent larvæ are distinguished by the production of black specks within the body cavity. These larvæ die when they reach maturity, but in other cases death must occur soon after fertilization. Moreover, in some cases the doomed individuals may occasionally overcome the defect and develop into normal adults.

The presence of one such factor leads to the appearance of a sex-ratio of 50 males to 100 females; if two sex-linked lethal factors occur in the same strain the ratio is less than 50 males to 100 females, the exact ratio depending upon linkage values of the two factors. Thus to take a particular case, Lethal I is situated at locus 0.7 and Lethal III at locus 26.5 in the sex chromosome. About 25 per cent. of crossing-over, therefore, occurs between these two factors. A female of the genetic constitution, (l_1L_3X) (L_1l_3X), therefore produces gametes in the following proportions:

$$3\ (l_1L_3X) : 3\ (L_1l_3X) : 1\ (L_1L_3X) : 1\ (l_1l_3X).$$

When such a female is mated to a normal male, $(L_1L_3X)Y$, presumably all the females survive because of the normal allelomorphs received from the sperm cell, but of the males only those which are of the genetic constitution $(L_1L_3X)Y$, therefore, only one in eight survive. This leads to a ratio of 12.5 males to 100 females in such a population.

While this is a hypothetical case it may, however, be mentioned that Morgan and his associates have discovered at different times actual instances of two sex-linked lethal factors occurring in the same strain. Furthermore, the occurrence of sex-linked lethal factors, by virtue of their linkage relations with other factors is as well established as the existence of any other Mendelian factors. They provide one means of explaining definitely unusual sex-ratios without assuming any changes in the mechanistic relations.

The inheritance of unusual sex-ratios in mammals and the reasons for such inheritance are in considerable doubt. About the only results which have been reported upon at all which give definite positive evidence are those of Miss King. These results have not been published in detail but a very preliminary note states that more than 22,000 albino rats have been reared in the course of the investigation. The experiments started with two pairs of rats from the same litter, and two lines of selection were made one for high proportion of males, the other for high proportion of females. The method of experimentation was rather unique. Thus the progeny of pair *A*, one of the original pairs were bred brother to sister without selection for six generations in order to establish a homogeneous race. After the sixth generation the brother to sister matings were continued but selection was invariably made from litters which had a high proportion of males. In Line *B*, the progeny of the other pair, the same procedure was followed except that selection after the sixth generation was made from litters having a high proportion of females. Fifteen generations of selection in Strain *A* give a sex-ratio of about 125 males to 100 females; in Strain *B* a sex-ratio of 83 males to 100 females. This series of experiments seems, therefore, to indicate that unusual sex-ratios may be inherited. Judgment, however, must be reserved until the complete data are published, but we may again emphasize the fact that nothing in a disturbed sex-ratio need necessarily be taken to mean that the mode of sex-determination is anything other than that which we have stated in preceding portions of this chapter.

Secondary Sexual Characters.—By a secondary sexual character is meant a character not immediately concerned with reproduction, but found only in one sex. In the more highly organized animals the differences between the secondary sexual characters of male and female are so great that by means of them alone it is possible to recognize instantly the sex of the individual. The secondary sexual characters include a wide variety of characters some of which are very definite and others are indefinite. Thus in most animals there are differences in size and general conformation, for example the stallion is larger and more rugged in build than the mare. The neck and forequarters are more fully developed than in the mare. These are differences of degree rather than kind. In certain breeds of sheep, however, horns are present in the males and absent in the females. In birds the differences between the sexes are often very striking, extreme instances of which are found among domesticated birds in such breeds as the Brown Leghorn fowl and the Rouen duck, and breeds of similar plumage coloration.

The Nature of Secondary Sexual Characters.—Although secondary sexual characters are intimately related in expression to sex, yet careful distinction must be drawn between the factor basis of secondary sexual characters and that of sex-determination and sex-linkage. Sex-linked characters, of course, are those which are determined by factors borne by the sex-chromosomes. Such characters display peculiarities in heredity which are dependent upon the chromosome relations, but the characters themselves may appear in either sex. Sex-determining factors are those which determine sex. Their presence results in profound effects upon the total developmental processes of the body. The different internal physiological conditions, therefore, which exist in the two sexes profoundly affect the reactions which the normal hereditary system exhibits in consequence of which many characters in the two sexes are different. These are the secondary sexual characters. In their development no difference need be postulated in the factorial basis save in the sex-factor itself. But the incentive to their development is found in the different internal conditions in the two sexes; the factors may be the same in both cases but these differences in internal condition lead to differences in the reaction products of those factors. Evidence of this view has been obtained largely from castration experiments.

The Effects of Castration.—The effects of castration differ so much in different groups of animals that no general statement can be made which describes all these results. Among mammals the effects of castration may be illustrated by a few typical cases. In sheep there are breeds which are hornless in both sexes, hornless in the female and horned in the male, and horned in both sexes. When both sexes are horned there are usually rather striking differences in the horns, those of the male being the better developed. Fig. 215 shows this for Dorset sheep which have been used in such experiments. The effect of castration in such breeds has been studied by Marshall. He finds that as a result of castration of males in those breeds in which males only are horned, the horns fail to develop. In breeds in which both sexes are horned castrated males develop horns like the females.

The above effects are of interest when taken in connection with studies of inheritance of horns in sheep. Thus Wood has studied crosses between Dorset and Suffolk sheep. The latter are hornless in both sexes. The F_1 of this cross consists of horned rams and hornless ewes. The F_2 consists of horn and hornless individuals in both sexes in the approximate ratio:

FIG. 215.—Dorset sheep showing the differences in development of horns in the two sexes. (*After Shaw and Heller.*)

3 horned ♂ : 1 hornless ♂ : 1 horned ♀ : 3 hornless ♀.

Bateson and Punnet assume that the horned breeds are of the constitution $HHXX$, female, and $HHXY$, male; and the hornless, $hhXX$, female, and $hhXY$, male. The F_1 then consists of $HhXX$, hornless females, and $HhXY$, horned males. Here they make the assumption that one dose of the factor H results in the production of horns in the male on account of the sex relations, but in the female two doses are necessary for the development of horns. This hypothesis does not account for those breeds which are horned in the male and hornless in the female, but it is not absolutely necessary that it should. We see here, however, a basis for the modifications of horns following castration for evidently the factor complex for the horned condition reacts differently in male and female.

In birds some striking results of castration have been obtained. Goodale especially has made extensive investigations with ducks and fowls. The results of ovariotomy in Rouen ducks are shown in Plate IV. Early removal of the ovary results in almost complete assumption by the female of the strikingly different plumage patterns of the male, and along with them of other secondary sexual characters peculiar to males. If removal be later or incomplete, the assumption of male secondary characters is correspondingly less complete. Castration of the drake on the other hand has very little effect on the secondary sexual characters. Here if any change in characters occurs, it is toward the infantile condition rather than toward that of the opposite sex. Observations on Brown Leghorn fowls confirm these conclusions. Thus an early ovariotomized female developed almost a complete set of male secondary characters. Capons, on the other hand, exhibited almost the entire set of male secondary characters. The characters of such birds, which are responsible for the current belief that capons are feminized cocks, were shown to be infantile characters rather than characters of the female sex.

Finally, mention must be made of Steinach's experiments on guinea-pigs and rats. Steinach first castrated male guinea-pigs and rats and then transplanted ovaries into them. The animals thus operated upon became strongly feminized. Feminized rats took on the texture of hair, the size of skeleton, and sexual behavior of females. In both cases the mammary glands became greatly enlarged. Throughout the total changes wrought by the establishment of ovaries in the castrated male rats and guinea-pigs were such as to throw the whole set of developmental processes toward the female side. We await with interest further experiments of this kind.

We can only conclude from these experiments that the sex glands actually furnish something, in the way of internal secretions perhaps, which affect the internal conditions under which the cells react. The presence of these hormones is the exciting condition for development of secondary sexual characters, not any fundamental factor difference in the two sexes, save that of the sex-determining factor itself. This, as Lillie has shown, is the most reasonable explanation of barrenness in free-martins. In mammals the effect of castration on the male is to throw the secondary sexual characters toward the female side, but not very strongly. The effect is only complete when ovaries are present. The female, however, is little affected. In birds the relations are reversed, castration of the female leads to the development of the secondary sexual characters of the male; castration of the male to little change.

Plate IV.—**A Normal Rouen Duck** (*Left*). **A Completely Ovariotomized Rouen Duck** (*Right*).

Brief history of the treated specimen: operated on at the age of six weeks, it showed first male characters twelve weeks thereafter. "Later in the year, when the juvenile to adult molt was completed, the bird had essentially the same appearance as that given in the plate. Since that time there has been no change in the character of the bird though she has molted several times."—(Goodale.)

CHAPTER XXXV

FERTILITY IN ANIMALS

Among domestic animals fertility is of direct economic importance. Problems associated with it have been investigated from many different angles, even from the standpoint of inheritance. Unfortunately, however, with respect to this latter feature of the question, not many investigations have been carried out with higher animals. It is necessary, therefore, to seek for the principles disclosed by investigations with the lower forms of life, and to determine to what extent they may be applied to higher animals.

Factors Influencing Fertility.—The factors which affect fertility are extremely numerous and varied. In considering the problems of inheritance connected with it, it is, therefore, necessary to make the inevitable scientific distinctions as to kinds of influences which may affect it and as to the different meanings which the term itself may have. In common parlance the term fertility signifies ability to produce active, living young. In higher animals in general fertility is measured by the reproductive capacity of pairs of individuals. Fecundity is the term used to designate the potential reproductive capacity of individuals. It is measured by the ability of the individual to form mature ova or spermatozoa. Fecundity can be measured accurately and directly only in special cases such as in birds; in mammals only fertility can be determined.

Several physiological factors must be considered in a treatment of fertility in animals. Of these only a few can be mentioned here. For a more extended treatment, the student should consult treatises on the physiology of reproduction, of which that of Marshall is especially valuable.

Among influences which lead to sterility or decrease in fertility are those of domestication. Here the effect depends largely upon the idiosyncracies of the particular wild species which has been domesticated. It has been suggested that food might in some cases be the determining factor, the supposition being that the animal under captivity may not obtain the variety and character of food necessary to maintain a healthy condition of the reproductive tracts. By no means, however, is the sterility of wild animals in captivity visibly correlated with changes in their mode of life, for often the most surprising variations occur in closely related species. Although it is impossible, therefore, to generalize as to what particular factor of the environment is responsible for the condition of lowered fertility among wild animals in captivity, there can be no question as to the strikingly adverse effect of confinement in certain cases.

Unfavorable conditions of the accessory reproductive organs occasionally cause sterility. Thus in cattle barrenness is sometimes the result of an acid condition of the secretions of the vagina. Simply injecting a weakly alkaline solution into the vagina has been found effectively to overcome this difficulty. The practice of artificial insemination has, also, been used in cases where the mucous secretions are unfavorable for conception, and in cases where structural bars to conception exist in the accessory reproductive organs. Among cattle especially contagious abortion is a serious cause of barrenness. This disease is bacterial in etiology, transmissible from animal to animal, perhaps usually by the agency of the herd bull, although possibly at times through food, and experimentally by intravenous injection. Not only does the disease cause abortion in animals in which it has not developed until after conception, but in animals previously infected it leads to barrenness. The disease is characteristic in its lesions and effects and may be controlled by the adoption of proper antiseptic measures.

In general domestic animals are much more prolific than their wild progenitors. Several reasons for this fact may be pointed out. Those species which can adapt themselves to conditions of domestication usually find such surroundings more favorable to development and to the production of offspring. Moreover, there is a natural tendency for selection to favor the survival of those strains or races which reproduce most rapidly, and man has augmented this tendency by choosing the more prolific members of the race for breeding stock.

But even the long-continued selective processes of domestication have not sufficed to attain to the maximum of fertility for the species. Few realize how great is the field for improvement in this respect. In England horse breeding, according to Marshall, suffers an enormous loss each year because of the failure of no less than 40 per cent. of mares selected for breeding purposes to produce offspring. Cattle, sheep, and swine appear to suffer somewhat less in this respect but the loss is far from inconsiderable. Heape estimates the average loss among cattle to amount to over 15 per cent. Among sheep the loss from actual sterility alone amounts to nearly 5 per cent. In view of such statistics the increase of fertility in domestic animals becomes a problem of prime economic importance.

The Darwinian Theory of Fertility.—The results of Darwin's extensive investigations of problems of vigor and fertility in plants and animals may be summed up in the trite statement, Nature abhors inbreeding. From his extensive investigations Darwin concluded that all organic beings benefit from an occasional cross and that the inevitable effect of continued inbreeding is loss of size and decreased constitutional vigor and fertility, and at times unusual tendency toward the production of malformations. Since Darwin's evidence was drawn largely from domesticated animals, and since other serious detrimental features of inbreeding are pointed out in addition to loss of fertility, it is important that enquiry be made into the reasons why inbreeding should result in decreased fertility. It is, also, important to note that we are attempting to harmonize in this treatment Darwin's conclusions with a theory of heredity unknown to him.

Inbreeding not in Itself Harmful.—Although supposed evidence of harmful effects of inbreeding has been presented by a number of investigators, there is nothing in this evidence which necessarily throws the blame upon inbreeding in itself. A single contrary case is all that is necessary for establishing the negative interpretation, and there are a number of such cases. Thus investigations on the effects of inbreeding in the fruitfly have been carried out on a much more extensive scale than would ever be possible with any of the higher domestic animals. For example, Castle and his associates inbred the fruit fly for fifty-nine generations, mating brother with sister throughout the investigations. They reached the general conclusion that inbreeding unaccompanied by selection generally results in decreased productiveness, but that proper selection for high productiveness results in maintaining the original fertility of the race. They found further that low productiveness is sometimes inherited like a Mendelian recessive, as shown by its appearance in alternate generations, and that in crosses between strains of high and low productiveness there was evidence of segregation in F_2.

Castle further comments upon a polydactylous race of guinea-pigs which was descended from a single individual. They have been inbred for over 10 years, yet despite this fact they show no signs of diminished fertility; on the contrary, they are superior in size and in constitutional vigor to most races. Moenkhaus' results with Drosophila also seem to indicate that a high degree of fertility may be maintained in successive generations of inbreeding if sufficient care be taken to select from the most fertile individuals. Hyde, on the other hand, found a decrease in fertility consequent on continued inbreeding. The experimental results, therefore, show that sometimes inbreeding does not result in diminished fertility. The fact, however, that there are so few cases in which inbreeding has not been followed by measurably harmful results calls for some explanation. In the rest of this chapter some reasons for this fact will be pointed out.

Fertility as Related to Mendelian Factors.—There is a considerable body of evidence to show that some Mendelian factors exhibit residual effects upon the fertility of individuals which bear them. This is perhaps most clearly established for certain factors in Drosophila. Thus among sex-linked factors Morgan has shown that those for the rudimentary and the fused wing conditions are practically always associated with sterility. In rudimentary flies the males are fully fertile, but the females are usually completely sterile. Examinations of the ovaries of rudimentary females demonstrate that the eggs do not develop normally, but for the most part remain in a low stage of development. Similarly the mutant fused is absolutely sterile in the female sex, but fertile in the male. Stock must, therefore, be maintained by mating heterozygous females to fused males. Here again examination of the ovaries has shown reduction in the number of mature eggs normal for the wild type.

Between this relatively complete sterility and the normal fertility of the wild type there exist all possible gradations. In fact even in wild type flies as Castle and his associates and others have abundantly shown strains possessing different degrees of fertility exist. But mutant strains often exhibit lessened vigor and fertility specifically attributable to the residual effects of the mutant factors themselves. This effect appears to be cumulative, for the presence of several mutant factors often greatly accentuates it. The difficulty has often proven a very great obstacle in carrying out some Drosophila experiments, but it serves to demonstrate that sterility may be a consequence of certain combinations of factors.

Specifically a number of definite cases may be given. Muller attempted to unite the factors for yellow body color, white eyes, abnormal abdomen, bifid wings, vermilion eyes, miniature wings, sable body color, rudimentary wings, and forked spines in one strain of flies. Here, of course, the factor for rudimentary wings in itself might be expected to have a profound effect upon the fertility of the strain, but aside from this effect it was found that the strain was so deficient in viability and general vigor that it was necessary to propagate it by specially devised breeding methods in the heterozygous condition. The heterozygous flies showed only an insignificant reduction in viability and fertility, whereas their full brothers and sisters which were homozygous for the recessive factors were so weak as to be of no value in the experiments. The same difficulties were met with in dealing with combinations of recessive factors belonging to other groups. It is safe to say that almost any combination of several recessive factors in Drosophila results in diminished vigor and consequent decrease in fertility. The effect is, however, specific, for the degree of diminution depends not only upon the number of recessive factors which are combined, but also upon the specific effects of the factors themselves. The specific residual effects of certain Mendelian factors upon fertility cannot, therefore, well be denied. (See Fig. 216.)

The Chromosomes and Fertility.—Bridges has demonstrated for Drosophila that males of the chromosome constitution *XO*, instead of the normal *XY*, are totally sterile. Here a specific chromosome difference, the absence of the *Y*-chromosome from the hereditary mechanism, leads definitely to complete sterility. Not many other cases are known among animals of sterility dependent upon abnormal chromosome constitution, but Bridges reports several known cases of aberrant hereditary behavior which may be dependent upon irregular chromosome distribution and content.

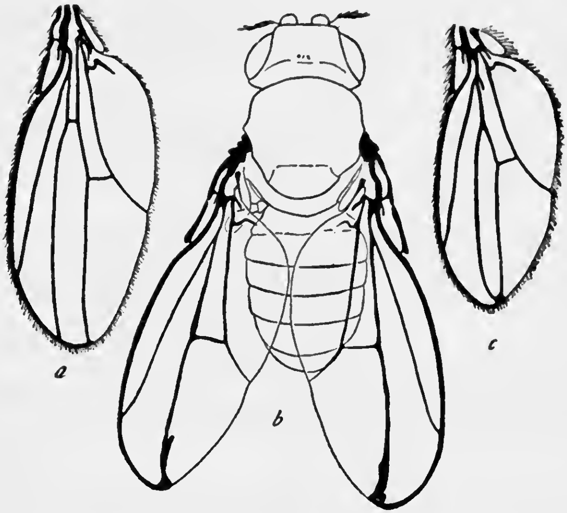


Fig. 216.—Drosophila mutation which exhibits a high degree of sterility. *a*, Normal wing; *b* and *c*, fused wings. (*After Morgan and Bridges.*)

Sterility in Other Animals.—In some other animals there are cases of sterility which suggest strongly the effect of definite Mendelian factors. Thus several writers have commented upon the sterility of tortoise-shell male cats, and apparently orange males are also, sometimes at least, sterile. The reason for this particular case has not yet been established definitely by breeding tests, and there is apparently some possibility that irregular chromosome distribution may account for it.

An instance from practical breeding history which appears to belong to this category is that of barrenness in Bates's famous Duchess family of Shorthorns. This family was noted for superior individual excellence, consequently breeders, naturally desirous of maintaining this excellence, followed a practice of close breeding within the family, an example of which is given in Fig. 217. But the family was tainted from the beginning with the curse of barrenness, which such a system of breeding must inevitably preserve. Shortsighted breeders at the time considered it a fortunate circumstance that Duchess cows were so often barren, for it kept down the number of individuals of this favorite strain and resulted in prices correspondingly high. But as a result of barrenness, the strain eventually ran out completely. In Fig. 218, an attempt has been made to show diagrammatically how barrenness was inherited in this family. The diagram is not complete, for it includes only the females in the family. Nevertheless it brings out very forcibly how barrenness occurred very early in the family history, and how it reappeared in about the same proportion of the total population throughout its history. Far from showing an intensification of the defect as a result of inbreeding, this diagram merely illustrates the heredity of a defective family trait.

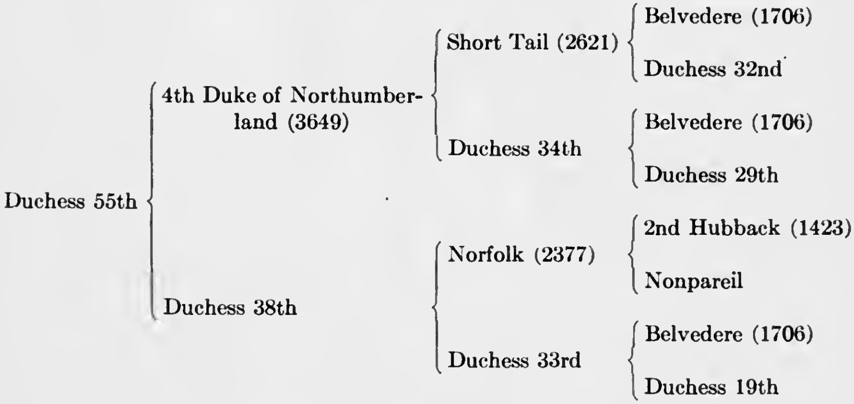


FIG. 217.—Pedigree of one of the latest Duchess cows, illustrating system of close-breeding followed in maintaining the family. Duchess 55th produced two calves.

Sterility of Hybrids.—There is a definite type of sterility which is referable to the effects of species hybridity. We have already had occasion to comment upon this type of sterility in connection with other matters, here we shall however refer to it again with particular emphasis upon certain of its aspects.

For the higher animals we do not possess much in the way of definite data respective to hybrid sterility. The mule, a familiar and oft-cited example, appears from all accounts to be very nearly completely sterile. The accounts of fertility in mare mules are for the most part shadowed in doubt, but the possibility of a slight fertility should not be denied. The hinny, the homolog of the mule, exhibits as high a degree of sterility as the mule. Of other hybrids within the genus Equus the evidence is even less satisfactory. Apparently the cross between the horse and zebra is sterile, like the mule. But the zebra and ass appear to be more closely related, and the possibilities of securing offspring from such

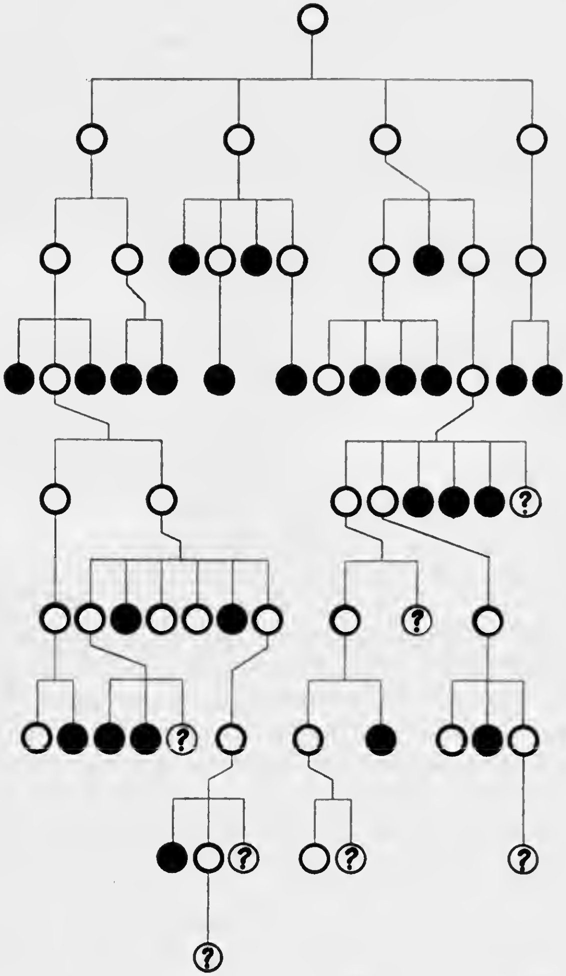


FIG. 218.—Illustrating inheritance of barrenness through the female line of the Duchess family of shorthorns; barren cows represented by solid black circles.

hybrids appears to be somewhat greater. There is in fact one reference in the literature to a fertile male hybrid between the zebra and the ass.

In the genus Bos, taken in the wider sense to include the subgenera Bison and Bibos, there are various degrees of sterility consequent upon hybridization. The domestic cow, *Bos taurus*, gives fertile male and female hybrids with the zebu, *Bos indicus*. With the yak, *Bibos grunniens;* the gayal, *Bibos frontalis*, the gaur, *Bibos gaurus*, and the bison, *Bison americanus*, the female hybrids with the domestic cow are fertile, but the males are sterile. The banteng, *Bibos sondaicus*, and the zebu behave like this latter series in giving fertile female and sterile male offspring. In this respect they resemble Detlefsen's and Castle and Wright's results with species crosses among guinea-pigs, the female hybrids of which were fertile, the males sterile.

Among domesticated birds in particular the reproductive powers are strongly disturbed by hybridization. Not only are such hybrids often sterile, but very frequently the sexual organs develop in an abnormal fashion strongly suggestive of intersexualism of the kind exhibited by Goldschmidt's Lymantria hybrids. Smith and Thomas have examined sterile hybrids between species of pheasants. They found that very often ovarian degeneration or imperfect development occurs in the females, as a consequence of which a marked tendency exists to assume plumage patterns and characters peculiar to the male.

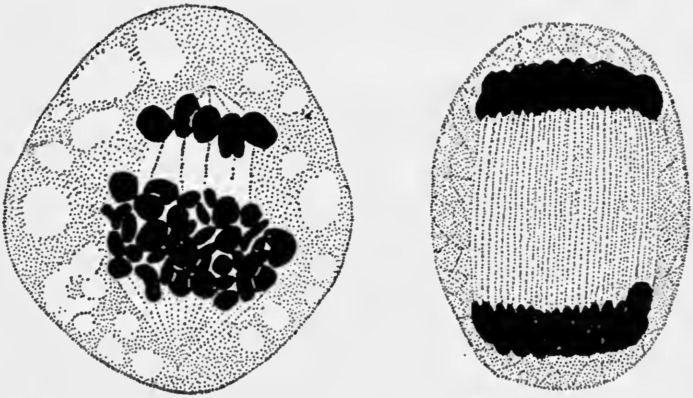


Fig. 219.—Abnormal reduction divisions in spermatogenesis of the mule. (*After Wodsedalek.*)

Here we are dealing rather definitely with a type of sterility different from that which characterizes different families within a species or breed or different mutant types of Drosophila, the sterility here appears to be more deep-seated and strangely enough, far from being associated with a general diminution in vigor, the vigor and size of the hybrids are often very augmented. We are not surprised, therefore, to find that profound disturbances in the hereditary mechanism occur in such hybrids. Wodsedalek has shown that irregular reduction divisions occur in the mule (Fig. 219). Smith and Thomas have shown specifically that in sterile hybrid pheasants of both sexes the abnormal behavior and degeneration of germ cells begins in synapsis. They conclude, therefore, that sterility in pheasant hybrids depends upon the inability of homologous chromosomes derived from different species to conjugate normally. In the mule, which apparently receives a different number of chromosomes from each parent, a morphological cause for such a difficulty obviously exists, but fundamentally the difficulty must be physiological, for it exists as strikingly in hybrids between species having the same numbers of chromosomes as in the rarer cases where the species have different chromosome numbers. We have already discussed this problem at length.

Fertility as Related to Heterozygosis—In another place we have discussed the hypothesis that heterozygosis in and of itself has a favorable effect upon vigor and fertility. This hypothesis is difficult to prove or to disprove. With the facts, however, there can be no question. Crossbreeding definitely does in specific cases lead to an increase in vigor and fertility, a fact which has long been known. But it appears more probable, as Jones has shown, that this increase is due to the establishment of a more excellent factor-complex than to any mysterious stimulation effect of the heterozygous condition. At the same time the possibility of an enlarged expression of the heterozygous condition of a given pair of allelomorphs must not be denied, but like other effects of heterozygosis, it is probably a condition depending upon the specific nature of the factors concerned. As a generalization, however, it must be taken as not proven; certainly the work with Drosophila, which is based upon more definite knowledge of the Mendelian factors than any other investigations to which we can refer, does not provide evidence in support of it. The solution of the problem has in it much of practical importance, for upon the hypothesis of heterozygosis it should be impossible to build up a breed which would reproduce in full the complete set of excellent characters of the cross-bred. If, however, a more favorable combination of factors is responsible for the excellence of cross-bred animals, then it should be possible by careful breeding to fix them in a new breed.

Fecundity in Fowls.—It is a genuine pleasure in a mass of contradictory and illy digested data to meet with something which gives hope for the same definiteness with regard to the problem of the inheritance of fecundity that has been attained in the analysis of the inheritance of other more clearly defined characters. We cannot, therefore, but commend the patient investigation and brilliant analysis to which Pearl has subjected the problem of the inheritance of fecundity in the domestic fowl. Many criticisms have been launched against his conclusions, it is true, but it is highly probable that these criticisms involve a fundamental misconception of the nature and results of scientific knowledge.

Pearl's results deal particularly with winter egg production in the domestic fowl. The conclusions are based upon an analysis of data obtained by trapnesting strains of pure-bred Barred Plymouth Rocks and Cornish Indian Games, and F_1 individuals and F_2 individuals obtained by mating F_1 individuals *inter se* and by mating them back to their parents in all possible combinations. Over a thousand birds were subjected to this definite experimental test.

With respect to winter egg production hens naturally appear to fall into three well-defined classes; (*a*) those birds which lay no eggs during the winter period; (*b*) those which lay something less than about thirty eggs; and finally (*c*) those which lay more than thirty eggs. Since egg laying is a character strongly influenced by environmental conditions and somatic fluctuations, these classes are not absolute, nor on the other hand are they by any means purely arbitrary as has been determined by statistical studies of flock production during the winter period. The differences which exist between the two breeds under investigation are shown graphically in Fig. 220. Taking a production of thirty eggs or more as the standard of comparison between the two breeds, it may be seen from this graph that only about 6 per cent. of the total flock of Cornish Indian Games produced as many eggs as this during the winter period, whereas 54 per cent. of Plymouth Rock pullets measured up to this standard of excellence.

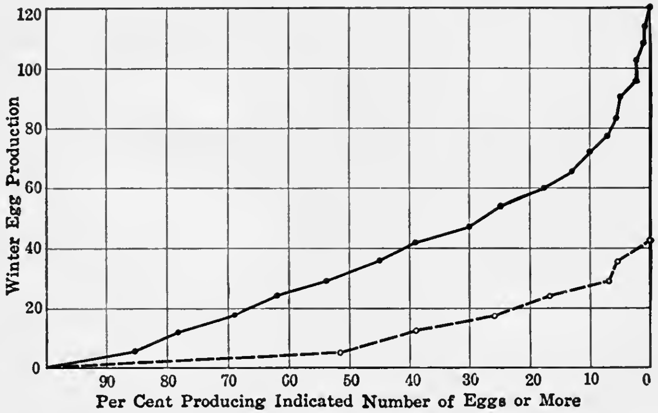


FIG. 220.—Contrasted flock curves of winter egg production of Barred Plymouth Rock (solid line) and Cornish Indian Game (broken line) pullets. (*After Pearl.*)

From a consideration of the data obtained from a wide series of crosses, Pearl proposes the following analysis of the inheritance of fecundity in fowls as measured by winter egg production. For the sake of clearness and conformity to treatment in the remainder of the text, we have used symbols different from those used by Pearl without, however, in any way modifying the essential features of his analysis.

(*a*) *The Sex Factors.*—In the fowl the type of sex-inheritance is that designated *WZ* in Morgan's terminology. Females are heterozygous for the sex-factor; *i.e.*, they are *WZ* in constitution, whereas males are homozygous, *ZZ*. *W* like *Y* in the *XY* type is neutral and carries no demonstrable factors.

(*b*) *A fecundity factor, L,* which determines a winter egg production of something less than thirty eggs. It is dominant over the allelomorph *l*, which is present in fowls which produce no eggs during the winter season, but the homozygous condition *LL* does not condition a higher winter egg production than does the heterozygous condition *Ll*.

(*c*) *A Sex-linked Fecundity Factor, M.*—Like *L* it determines alone a winter egg production of something less than thirty eggs. With *L*, however, it gives a winter egg production of over thirty.

Table LXXIV.—Genetic Constitutions of Barred Plymouth Rock Males for Fecundity Factors

Class	Genetic constitutions	Gametes produced
1	*(ZM)(ZM)LL*	*(ZM)L*
2	*(ZM)(Zm)LL*	*(ZM)L*, *(Zm)L*
3	*(ZM)(ZM)Ll*	*(ZM)L*, *(ZM)l*
4	*(ZM)(Zm)Ll*	*(ZM)L*, *(ZM)l*, *(Zm)L*, *(Zm)l*
5	*(ZM)(ZM)ll*	*(ZM)l*
6	*(ZM)(Zm)ll*	*(ZM)l*, *(Zm)l*
7	*(Zm)(Zm)LL*	*(Zm)L*
8	*(Zm)(Zm)Ll*	*(Zm)L*, *(Zm)l*
9	*(Zm)(Zm)ll*	*(Zm)l*

Pearl was able to classify the individuals which he used in his experiments into classes according to their zygotic constitutions. For the sake of clearness these classes are given in Tables LXXIV, LXXV, LXXVI, and LXXVII. These tables represent genetic constitutions which were realized and recognized during the course of the experiments. It will be observed that among the Barred Plymouth Rocks every possible genetic constitution was represented, but among the Cornish Indian Games the factor *M* was not contained in any individual.

Table LXXV —Genetic Constitution of Barred Plymouth Rock Females for Fecundity Factors

Class	Genetic constitutions	*Z* gametes	*W* gametes	Winter egg production
1	*(ZM)WLl*	*(ZM)L*, *(ZM)l*	*WL*, *Wl*	Over 30 eggs
2	*(ZM)WLL*	*(ZM)L*	*WL*	Over 30 eggs
3	*(Zm)WLl*	*(Zm)L*, *(Zm)l*	*WL*, *Wl*	Under 30 eggs
4	*(Zm)WLL*	*(Zm)L*	*WL*	Under 30 eggs
5	*(Zm)Wll*	*(Zm)l*	*Wl*	No eggs
6	*(ZM)Wll*	*(Zm)l*	*Wl*	Under 30 eggs

It is difficult to present briefly all the evidence which has led Pearl to advance the foregoing analysis for the data on fecundity in fowls, reference must be made to the complete published results dealing with these experiments. In Table LXXVIII the data are summarized and compared with expectations, but not in a satisfactory manner, because different types of matings have been lumped together. It does, however, show as well as can be shown in so short a summary, how closely fecundity conforms to the requirements of a Mendelian analysis. There can be little doubt that Pearl has laid the broad foundations for a more definite knowledge of the behavior in heredity of a complex character of great economic importance. The practical implications of this analysis are discussed in Chapter XXXVIII.

TABLE LXXVI.—GENETIC CONSTITUTIONS OF CORNISH INDIAN GAME MALES FOR FECUNDITY FACTORS

Class	Genetic constitutions	Gametes produced
1	$(Zm)(Zm)LL$	$(Zm)L$
2	$(Zm)(Zm)Ll$	$(Zm)L$, $(Zm)l$
3	$(Zm)(Zm)ll$	$(Zm)l$

TABLE LXXVII.—GENETIC CONSTITUTIONS OF CORNISH INDIAN GAME FEMALES FOR FECUNDITY FACTORS

Class	Genetic constitutions	Z gametes	W gametes	Winter egg production
1	$(Zm)WLL$	$(Zm)L$	WL	Under 30 eggs
2	$(Zm)WLl$	$(Zm)L$, $(Zm)l$	WL, Wl	Under 30 eggs
3	$(Zm)Wll$	$(Zm)l$	Wl	No eggs

TABLE LXXVIII.—OBSERVED AND EXPECTED DISTRIBUTIONS OF WINTER EGG PRODUCTION FOR ALL MATINGS IN PEARL'S EXPERIMENTS

Mating	Class	Winter production of daughters		
		Over 30	Under 30	None
Barred Plymouth Rock	Observed	365.5	259.5	31.0
	Expected	381.45	257.25	17.3
Cornish Indian Game	Observed	2.0	23.0	15.0
	Expected	0.0	25.0	15.0
All F_1	Observed	36.0	79.0	8.0
	Expected	26.5	88.75	9.75
All F_2 and back-crosses	Observed	57.5	98.5	23.0
	Expected	68.6	95.0	15.4

Conclusion.—We may conclude, therefore, fairly, that fertility in animals is a complex character highly modifiable under different conditions of environment, but nevertheless possessing a definite, although intricate and obscure, factorial basis. The character bears the same relation to systems of breeding as do any other characters, that is, the system of breeding in itself has no effect upon it, it is merely a mode of achieving certain results. This is clearly established by Pearl's experiments on fecundity in fowls, for they demonstrate that factors for high fecundity exist, and that these factors behave like other Mendelian factors.

CHAPTER XXXVI

SOME BELIEFS OF PRACTICAL BREEDERS

It is proposed in this chapter to discuss not only some matters which belong to the discarded remnants of scientific thought, but also some beliefs of animal breeders which have not yet been subjected to the rigid scrutiny of scientific investigation necessary for analyzing them completely.

Telegony.—By telegony is designated the supposed influence which a sire exerts upon the females with which he is mated such that the products of subsequent matings with other sires show some influence of the previous ones. The same phenomenon is known in popular speech as infection of the germ, the influence of previous impregnation, etc.

One does not need to go far to find support for the hold which the belief in telegony has upon the popular mind. In certain cases the belief has been so strong as to affect rules of registration of pure-bred animals. Riley has collected from flock book records a few typical rules of registration which are founded upon a belief in telegony. They are given below:

Vermont Merino Sheep Breeders' Association.

Rule 24.—The record of registered ewes will be forfeited if bred to rams other than pure descendants of importations direct from Spain, and it shall be the duty of members to report to the Secretary the label marks and numbers within the year in which they are so bred, who shall enter them on the records of the flocks in which they are recorded. Any member who shall fail to report according to this rule or offer lambs from such ewes for record shall be suspended or expelled.

New York State American Merino Sheep Breeders' Association.

Rule 17.—That this association exclude from its records all breeding ewes that have been previously bred to coarse wooled rams.

American Rambouillet Sheep Breeders' Association.

Rule 4.—No product of a Rambouillet ewe shall be eligible for registry after such ewe shall have been bred to any other ram but a registered Rambouillet.

Dorset Horn Sheep Breeders' Association.

Rule 6.—No ewe or ewe lambs shall be eligible for entry that have been served with any ram other than a pure bred Dorset Horn from the date thereof.

Michigan Merino Sheep Breeders' Association.

Rule 12.—The product of a registered ewe which shall at any time have been bred to a ram not a registered American Merino, or one eligible to register shall be excluded from registry.

It is of course possible that motives other than belief in telegony have had some influence in shaping these rules, but presumably this belief has been the chief reason for adopting them. At the same time it must be acknowledged that the popular belief in telegony is by no means universal. Thus E. Davenport calls attention to the fact that breeders of dogs are generally credited with a strong belief in telegony. Nevertheless a correspondence which he carried on with dog fanciers failed to disclose more than one case among thirty-seven which affirmed belief in telegony, and twenty-eight of these breeders were positively opposed to it. Since some credence is still given to telegony in popular circles, even if not among scientific investigators, a detailed account of the evidence against it will be presented below.

Lord Morton's Quagga Hybrids.—We can do no better in beginning a discussion of telegony than to refer to the classic example of it, Lord Morton's mare, for this case was accepted at its face value by no less an authority than Darwin.

The details of this experiment are about as follows. Lord Morton bred a seven-eighths chestnut Arabian mare which had never been bred before to a male quagga. The result of the union was a female hybrid which plainly exhibited both in color and in form distinct evidence of its hybrid origin. The mare subsequently passed into the hands of Sir Gore Ouseley who bred her to a very fine black Arabian stallion. To the service of this stallion she bore first a filly foal and in the next year a colt foal. Lord Morton later examined these two colts and as a result of his inspection he wrote as follows to the president of the Royal Society:

> The 2-year-old filly and yearling colt have the character of the Arabian breed as decidedly as can be expected where fifteen-sixteenths of the blood are Arabian; they are fine specimens of that breed, but both in the color and in the hair of their manes they have a striking resemblance to the quagga. Their color is very marked, more or less like the quagga in a darker tint. Both are distinguished by the dark line along the ridge of the back, the dark stripes across the forehand, and the dark bars across the back part of the legs. The dark stripes across the forehand of the colt are confined to the withers and to the part of the neck next to them. Those on the filly cover nearly the whole of the neck and the back as far as the flanks. The color of her coat on the neck adjoining to the mane is pale and approaching to dun, rendering the stripes more conspicuous than those on the colt. The same pale tint appears in a less degree on the rump, and in this circumstance of the dun tint also she resembles the quagga.
>
> Both their manes are black; that of the filly is short, stiff, and stands upright, and Sir Gore Ouseley's stud groom alleged that it never was otherwise. That of the colt is long, but so stiff as to arch upward and to hang clear of the sides of the neck, in which circumstance it resembles that of the hybrid. This is the more remarkable, as the manes of the Arabian breed hang lank, and closer to the neck than those of most others. The bars across the legs, both of the hybrid and of the colt and filly, are more strongly defined and darker than those on the legs of the quagga, which are very slightly marked; and though the hybrid has several quagga marks, which the colt and filly have not, yet the most striking—namely, the stripes on the forehand are fewer and less apparent than those on the colt and filly.

The strength of the evidence in this case can be understood better by reference to Fig. 221, which shows the male quagga which Lord Morton used in his experiments, the hybrid which was produced by the chestnut Arabian mare when bred to this quagga, and the filly which she produced subsequently to the service of a purebred black Arabian stallion.

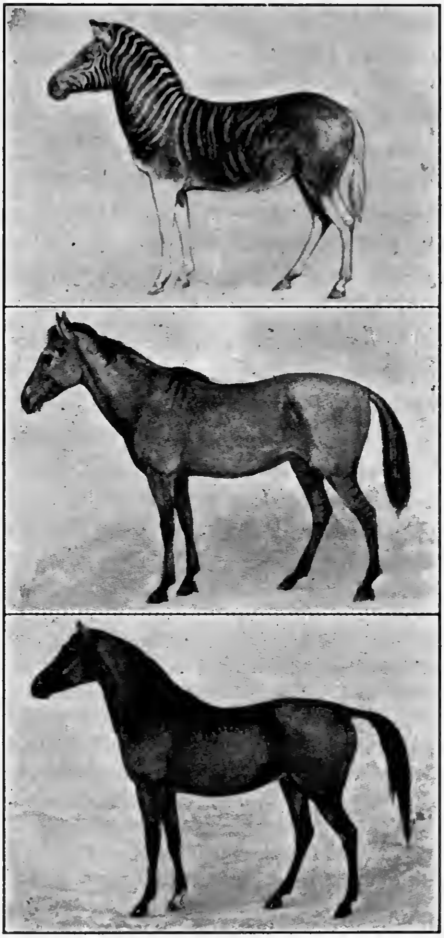


Fig. 221.—Lord Morton's male quagga, a hybrid between a Chestnut Arabian mare and this quagga, and a filly produced subsequently by the same mare when mated to a pure-bred black Arabian stallion. (*After Ewart.*)

But although many scientists have granted the weight of this evidence, later scientific thought has questioned strongly even the possibility of such effect of the male upon the female. Accordingly many adverse criticisms have been made against the validity of this case, some of which, as for example that of J. Wilson, go so far as to deny the hybrid origin of the first foal produced by Lord Morton's chestnut Arabian mare. Those criticisms suggested by Ewart, however, because they are tempered by abundant experimental research, are, perhaps, most just.

Accepting the hybrid nature of the first foal, the question arises as to how common striping may be in horses, especially those of Oriental ancestry. On this point there is abundant evidence as Ewart points out. The old yellow-dun horses of the forest type, which have had much to do in the origin of modern breeds of horses, characteristically possessed a broad dorsal band and zebra-like bars on the legs, and in addition to these markings they often possessed faint stripes on face, neck and withers. In fact evidence points to the belief that a remote ancestor of this forest horse was probably as richly striped as some modern zebras. Even today it is a very common thing among mongrel ponies to meet with individuals which possess distinct markings suggestive of the forest horse. They are not uncommon among Arabian crosses. Consequently we are not surprised when this later filly is compared with the quagga to find that its pattern, rather than suggesting residual effect of the previous impregnation by the quagga, strongly indicates reversion to some ancestral type. The bars on the legs, for instance, were more marked on the hybrid, on the filly, and on the colt than on the quagga. The scanty mane and tail upon which Lord Morton dwells may simply be regarded as additional evidence of reversion.

The Penycuik Experiments.—All the debates which may center around Lord Morton's mare, however, do not carry a fraction of the weight in assigning telegony to the limbo of discarded doctrines of the experimental work of the last two decades. The Penycuik experiments were designed by Ewart to determine whether such a doctrine as telegony were tenable, and, if so, to what extent it exerted influence in animal breeding. They have been carried out on a considerable scale, and included experiments not only with the Equidæ, but also with other animals. In every case Ewart was forced to the conclusion that alleged cases of infection may be accounted for most easily and most satisfactorily as instances of reversion to ancestral types.

To illustrate Ewart bred the Burchell zebra stallion Matopa to a chestnut polo pony. She produced as a result of this mating twin hybrids. The following year she produced a foal to a light chestnut thoroughbred stallion, after which she was again bred to Matopa, and produced a third hybrid foal. Subsequently she produced another foal to the service of a dark chestnut thoroughbred stallion. The three hybrid foals from this mating were all richly striped, in fact the stripes were more numerous, although less conspicuous, than those of the zebra sire. In spite of this fact, however, the two foals produced by mating Valda to the thoroughbred chestnut stallion in no particular, either in color or in form, resembled the hybrid foals. They were chestnut in color without any suggestion of striping, and in liveliness of temperament or vigor of development neither of them resembled in the least the hybrid progeny.

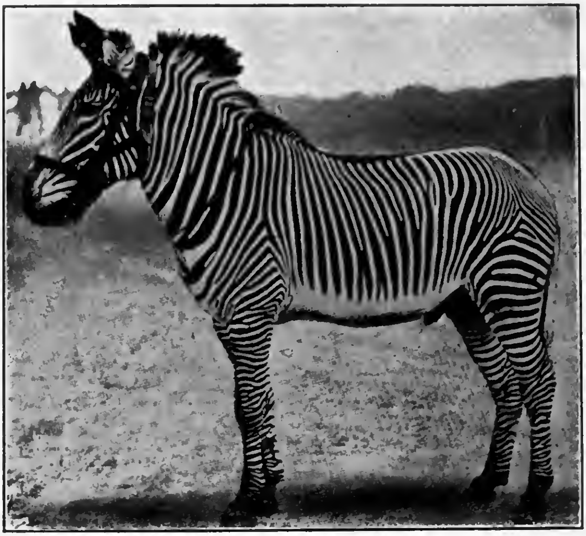


FIG. 222.—Jerry, a male Grevy zebra, *Equus Grevii*, used in U. S. government breeding investigations. (*After Rommel.*)

FIG. 223.—A registered Morgan mare, Baby Gates, used in U. S. government breeding investigations. (*After Rommel.*)

A subsequent experiment is of interest because of the closeness with which it agrees with particulars of the Lord Morton case. Ewart bred

Mulatto, a black West Highland pony, to Matopa and obtained a colt foal Romulus, a beautiful, distinctly striped hybrid. The mare Mulatto was then bred to a black Arabian stallion. To this service she produced a foal which, when examined immediately after birth, showed numerous indistinct markings, so faint, however, that their exact nature was in some doubt. Subsequently Mulatto produced another foal to the serv-

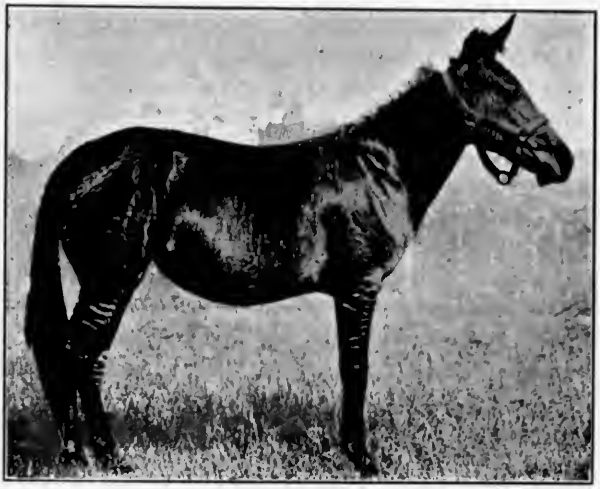


FIG. 224.—Juno, a zebra-mare hybrid produced by mating the Morgan mare, Baby Gates, to the Grevy zebra, Jerry. (*After Rommel.*)

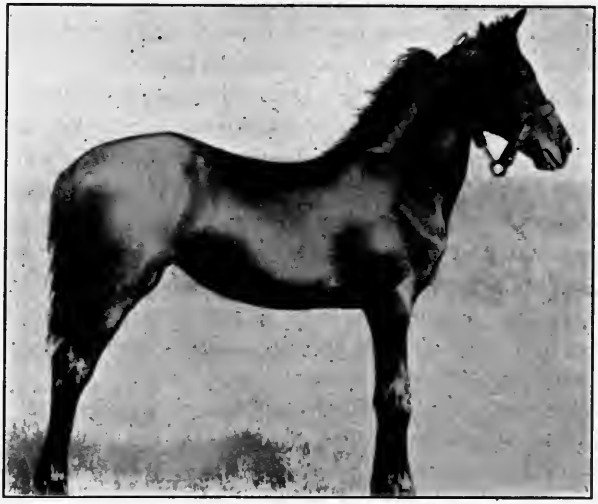


FIG. 225.—Georgia, a registered Morgan filly produced by Baby Gates subsequent to the production of the zebra-mare hybrid Juno, to the service of the Morgan stallion, Pat Murphy. There is no trace of telegony. (*After Rommel.*)

ice of a dark brown West Highland stallion which was also indistinctly marked.

In themselves these foals suggested as strongly that telegony might occasionally occur as did those described by Lord Morton. But Ewart tested the matter further by breeding two dark West Highland mares closely related to Mulatto to the same black Arabian stallion which had sired the striped foal. Two foals were produced, one of which possessed the same sort of indistinct markings as those characteristic of the foals of Mulatto, the other was much more distinctly striped. There can be no question, therefore, that the striping of Mulatto's foals was a consequence of normal hereditary processes having nothing to do with telegony.

Further evidence as to the non-tenability of the doctrine of telegony might be cited from the Penycuik experiment. A vast amount of additional evidence has been obtained from other experiments, some of which have been performed with the distinct object of testing the doctrine, others for different purposes. The experiments of Baron de Parana with zebra hybrids closely paralleled those of Ewart and yielded likewise no evidence in support of the doctrine of infection. The series of photographs shown in Figs. 222 to 225 have been drawn from an article by Rommel describing the work of the U. S. government with hybrids between different species of Equus. Here again there is no evidence that Georgia the Morgan filly which Baby Gates produced subsequently to the production of the zebra hybrid Juno shows any effect of the previous impregnation. The apparent stripes on the body of Georgia, it may be mentioned in passing, are merely her ribs showing through. Similarly there is no evidence that Sweepstakes, the dam of Star Pointer and other pacers, was in any way influenced by the fact that previously she had borne two mule foals. The evidence from mule-breeding establishments, in which thousands of mules have been produced, in every dependable instance is against the doctrine of telegony. Mumford has recorded a large number of concrete cases in support of this position. In a few instances mares had produced as high as ten or eleven mule foals before they were bred to stallions, yet in not a single case was there positive evidence of telegony.

The development of the Mendelian theory of heredity has robbed most of the old evidence for telegony of all its value. An instance which Ewart quotes is of considerable interest in this connection. A tan Dachshund bitch was bred to a tan dog, and produced a litter of puppies having pure white bodies and tan cheeks and ears. Now this bitch had previously borne by misalliance a litter of puppies to a white Fox terrier with tan cheeks and ears. Presumably both the tan Dachshund bitch and dog had long lines of tan or black and tan ancestors; what more natural than to conclude that this was a strict case of telegony? But the breeder to whom the attention of this instance was called remarked that, although the color of this litter was strongly reminiscent of the white fox terrier, the form and general characteristics were otherwise those of pure Dachshunds. Accordingly he traced the pedigree of the dam and found that in the sixth generation it ran back to the kennel of a lady whose hobby was white Dachshunds with tan cheeks and ears. This particular mating had simply given opportunity for the expression of latent factors carried by the tan dogs. It was a perfectly intelligible case of reversion, not telegony at all.

Harmful Effects of Hybridization.—Although we cannot accept the belief in telegony, we must admit that bearing hybrid offspring may sometimes have detrimental effects upon the dam. Thus Ewart quoting from Baron de Parana calls attention to the practice in Brazil of breeders of mules putting their mares to horses after they have reared two or three mules in order to prevent them from becoming sterile. There is a possibility that a hybrid fetus in consequence of its unusual vigor may tax more strongly the resources of the dam and in a sense impoverish her. This is particularly the case in some hybrids like those between the bison and domestic cattle, the production of which is a tremendous drain upon the dam's system and often leads to fatal consequences. But this is not telegony, it is merely a consequence of disturbing the physiological balance in the dam, and has nothing whatever to do with the transference of the characters of a previous sire to offspring borne subsequently to the service of another sire.

Infection of the Male.—The belief in infection of the male is by no means as strong as that in telegony, but occasionally it is met with. Ewart recites an incident of a breeder who refused to allow his Jersey bull to serve Shetland cows for fear that the bull would subsequently carry over old Shetland traits into his Jersey herd. Since we have, however, discarded telegony as applied to the female, there appears to be no warrant whatever for considering it in the male, where an effective mechanism of operation is even less conceivable. Moreover, a vast amount of evidence which has been obtained in Mendelian experiments leaves no room whatever for this belief.

Saturation.—The doctrine of saturation is fundamentally based upon a belief in the cumulative effect of telegony. It holds that successive children of given parents come to resemble the sire more and more in their characters. Although this doctrine has been accorded some importance at times, like the doctrine of telegony it finds no support from experimental evidence. Here again we may point to the evidence from Mendelian experiments, collected for another purpose, it is true, but yielding direct evidence in opposition to the belief in saturation. Moreover, Pearson has collected statistical evidence in human beings with respect to the stature of successive children in the same families. He finds no evidence whatever of saturation, or as he states it of a "steady telegonic influence."

Maternal Impression.—The belief in maternal impression, or in the effect of the pregnant mother upon her growing fetus, is one of the enduring tenets of popular faith. We need not trouble ourselves here with the long series of influences which are supposed to pass from the mother to the unborn child in human beings. Suffice it to state that they are no more varied nor yet more tenable than those cases which have been described for domestic animals.

Many curious cases from that of Jacob's peeled wands[1] down to those of far more recent times might be cited from the chronicles of maternal impression; but like the belief in telegony, they all spring from the unscientific attitude of the popular mind toward isolated instances. We suspect for instance that the famous Biblical herdsman used other methods than that of the peeled wands in order to achieve his remarkable results.

An instance may be given as typical of those which are recounted in support of the belief in the effect of maternal impressions, although in reality it is stronger than most cases. A section of a well-known Scottish herd of Aberdeen-Angus cattle which was separated from an Ayrshire herd by only a wire fence persistently produced, for several successive generations, red and black-and-white calves. But this was the formative period of the breed, and we have already had occasion to mention the diversity of color which characterized Aberdeen-Angus foundation stock. The occurrence of red and black-and-white calves, therefore, is a simple consequence of the cropping out of recessive factors, the Mendelian explanation is adequate and satisfactory. Moreover it is not entirely improper for us to call attention to the utter confusion which would prevail in herds of Aberdeen-Angus cattle, if this phenomenon were of general occurrence. We venture to state that very few breeders of solid-colored cattle have had such trouble from the proximity of herds of Holstein-Friesian, Shorthorn, Ayrshire, and other breeds of cattle, not to mention other sources of contamination which might occur.

But some of the legends of Aberdeen-Angus history are even more curious than this one. It is recorded of the famous breeder McCombie of Tillyfour that he erected a high black fence around his breeding paddock. But it may be expected that McCombie having as his ideal the black polled Aberdeen-Angus cattle used other means of securing a strain breeding pure for the typical Aberdeen-Angus characters.

Like the belief in telegony, the belief in maternal impressions arises from an unscientific attitude of mind toward evidence in general. The

[1] *Cf.* Genesis 30 : 31—43.

particular, unusual instance, because it is so striking fixes itself in the memory and the countless thousands of cases which do not support the doctrine are overlooked. There is something in it akin to the memory of the card player which retains so tenaciously the recollection of an unusual hand, but here it is usually clearly recognized that chance alone is responsible for the good fortune. So also in animal breeding remembrances of strange coincidences are longest borne in mind, but it seems to be a very common fault not to realize that they are after all nothing but coincidences.

Prepotency.—It has been an early observation of animal breeders that some animals possess a superior power of impressing offspring with their characters. This is precisely what is meant by prepotency; a prepotent animal is simply one which has the power to stamp its offspring with its own characteristics. Obviously there is much room here for confusion of thought, but at least the existence of prepotent animals can scarcely be denied. The science of genetics unfortunately has not advanced far enough to be able to state precisely what are the requisites for prepotency, nor has it progressed to such an extent, as some seem to think, that prepotency, like those other popular doctrines which have been considered in this chapter, may be analyzed completely and its untenable features discarded.

The fact of prepotency we say must be admitted, and this position is justified by a study of the history of any of the established breeds of domestic animals. Without exception such breeds all show a narrowing of the ancestral lines to a few favored families due to the superior excellence and transmitting power of the individuals belonging to the family. For prepotency is obviously a family matter.

One of the most notable instances of prepotency is that of the Hambletonian family of trotters and pacers. The progenitor of this family was Hambletonian 10, a remarkable stallion who appears to have inherited his excellent characters from those famous imported sires of the early days of speed development, Messenger and Bellfounder. Hambletonian 10 himself was no mean performer, having to his credit a record of 2:48 ½ as a 3-year old in 1852, at which time the fastest trotting record was 2:28; but it is as a breeder that he has won enduring fame.

E. Davenport has studied with considerable care the relation of prepotency to the development of trotting and pacing horses in the United States. He found that up to and including 1901, a total of 26,327 horses had been admitted to the list of performers, *i.e.*, had records of 2:30 or better. Of these performers, 14,808 traced back to eighty-five grandsires. In other words over 50 per cent. of performers traced back to slightly more than 1 per cent. of the grandsires of the breed. This fact is truly a remarkable demonstration of the relation of prepotency to the development of speed in the American Standard bred. But even more remarkable is the record of the ten greatest producers of speed up to that time. They are given in Table LXIV. Of the ten great sires here listed, one is by Hambletonian 10, eight have Hambletonian 10 for grandsire, and finally Nutwood, the greatest in the list, is by Belmont, by Adallah, by Hambletonian 10. Every one of the ten premier stallions of the breed, therefore, belongs to the great Hambletonian family.

Further evidence as to the existence of prepotency has been given from time to time for many other breeds and for different characters. A typical investigation of this kind has been conducted by Hover for butter-fat production of pure-bred Guernsey cattle. From the advanced registry records for this breed up to December, 1915, Hover found that only thirty-two sires had produced three or more daughters having records equivalent to 600 pounds of butter fat at maturity. Of these thirty-two sires only three had produced more than ten such daughters, and all of these belong to the May Rose family. This same family contains six more of the thirty-two superior sires. Of the rest the Masher family contains seven; the Governor of the Chene family, five; the Glenwood family, five; and the Sheet Anchor family, six. Some of the sires of course belonged to two or more of these families. The results are in no particular different from those which might be obtained with any other dairy breed.

A demonstration of the existence of prepotency, however, is far from a scientific treatment of the subject. While many geneticists admit that prepotency is as yet an unsolved problem, they have not failed to point out several ways in which prepotency might operate. These suggestions have pointed to the relations of dominance and recessiveness, to variations in the potency of factors themselves, and to interrelations within the hereditary complex as providing firm bases for the existence and interpretation of prepotency. We shall discuss each of these briefly below.

The Mendelian Interpretation.—That interpretation of prepotency which refers it solely to the particular characters and the relations of dominance and recessiveness within them may be called the Mendelian interpretation. The simplest expression of this interpretation is found in the relation of homozygous dominants to those which are heterozygous. These two classes are often indistinguishable phenotypically, but the homozygous dominant when mated to recessives impresses its characters on all the offspring, whereas the heterozygous dominant only impresses its characters on half the offspring. The practical bearing of prepotency of this kind may be seen by reference to Pearl's analysis of the inheritance of fecundity in domestic fowls. Here a Barred Plymouth Rock male of the genetic constitution $(ZM)(ZM)LL$ will transmit high laying qualities to all his female offspring regardless of the genotypes of the females to which he is mated, whereas one of the genetic constitution $(Zm)(Zm)ll$ would transmit low egg laying capacity to such an extent that among his daughters even from high producing hens none would fall in the high producing class. For favorable characters the validity of this interpretation depends upon dominance of the determining factors, a condition by no means universally fulfilled.

The Relative Factor Potency Interpretation.—There is some evidence that the potency of a given factor sometimes varies with the source from which it is derived. Pearl has suggested for example that the factor L when derived from the Cornish Indian Game has a lower absolute fecundity value than that of the same factor in the Barred Plymouth Rock. The suggestion amounts to an application of the hypothesis of multiple allelomorphism, a graded series of multiple allelomorphs of differing potencies, or different relations with respect to dominance, being conceived to determine the absolute degree of expression of the factors. We recall here Detlefsen's work with the agouti factor of the wild *Cavia rufescens* which was recessive to the agouti pattern of the tame guinea-pig, and less decided in its phenotypic expression. The conclusions of Goldschmidt that races of the gypsy moth exist which have sex factors of various potencies, such that crosses between them give series of intersexual forms, while less definite with respect to the actual factors involved, provides some evidence in support of the belief that some of the phenomena of prepotency are dependent upon actual differences in the factors themselves.

The Hereditary Complex Interpretation.—The characters for which families are prepotent are evidently often complex, as for example speed in horses, total butter-fat production in dairy cows, beef conformation in cattle, and so on. They must, therefore, depend upon a favorable genetic constitution with respect to series of factors. This interpretation is based upon the conception that factors form physico-chemical reaction systems and it follows the lines which have been developed in the application of this hypothesis to species hybrids. We have pointed out for instance that varieties of *Nicotiana tabacum* impress their total set of characters upon the hybrids with *N. sylvestris* because of the dominance of the *tabacum* reaction system. Certain characters which are recessive within the *tabacum* group are expressed in such species hybrids apparently because of their interrelations with other factors in the *tabacum* group. This idea is also borne out by certain of the Drosophila experiments. Thus Morgan notes that the factor for truncate wings, usually recessive, is dominant in races which have the black factor. The hypothesis rests upon a belief that sometimes factor interrelations determine whether a particular member of an allelomorphic pair shall be dominant or recessive; and that this influence becomes stronger when large sets of factors determine a particular character.

Greater Prepotency of the Male.—There has been a decided tendency to credit the male with greater prepotency than the female. Many investigators have pointed out that extra-biological influences such as the more rigid choice of males and the greater opportunity they have for impressing offspring may account for this belief among animal breeders. Some of the statistical evidence which Pearson has collected on this point seems to indicate no constant behavior in this respect. At the same time it should be noted that phenomena of sex-linkage and crossing-over may play an important rôle here. The operation of the former we see in Pearl's investigations of fecundity in fowls. Here the male is obviously the more prepotent with respect to the transmission of fecundity. The operation of the latter we see in Drosophila experiments Here there is no crossing-over in the male, as a consequence of which hybrid males more often transmit the particular set of factors which determine a phenotype like their own than do hybrid females. While the possibility of extending this phenomenon to mammals appears to have been destroyed by Castle's work with rats, which demonstrated the occurrence of crossing-over in the male, nevertheless as a possible factor in relative prepotency of the sexes it should not be ignored.

Conclusions with respect to prepotency. For the present then we must regard prepotency as an established fact, a phenomenon which has not yet been subjected to scientific analysis. From a biological standpoint, however, it is clear that even with our present restricted knowledge there is room for prepotency based upon the existence of different kinds of relations between factors.

CHAPTER XXXVII

METHODS OF BREEDING

Like modes of research, methods of breeding are the means by which certain results are attained. It is necessary to emphasize this fact, because even yet there is much confusion in the minds of breeders as to the relation which a particular method of breeding bears to results which have been produced by its employment. Not infrequently statements are made to the effect that a certain method of breeding is the cause of the excellence of one race or strain or the inferiority of another. There is a wide difference between the method of producing a given result, and the cause of its attainment. For the sake of clarity of thought we shall endeavor to emphasize this distinction, so far as is possible in the present state of our knowledge, in the discussions which follow.

Phenotypic Selection.—The oldest method of breeding was simply that of mating together the most excellent individuals. In popular phraseology this is the method of breeding from the best—its fundamental postulate is expressed in the old statement, like produces like. We have called it the method of phenotypic selection in order to emphasize the fact that the basis of choice for breeding in this method is the sum total of expressed characters of the individual.

It is not necessary to recount here at any great length the sort of improvement which has been effected in modern breeds of domestic animals by the application of this method of breeding. Let it be sufficient to state that much of the excellence of modern breeds is an earnest of the efficiency of phenotypic selection as a mode of breed amelioration. It may, also, be stated justly that all later methods of breeding; outbreeding, line-breeding, inbreeding, and genotypic selection; are simply refined methods of breeding from the best—they are methods of phenotypic selection plus something else; the something else usually ill-defined, but sometimes, as in genotypic selection, more definitely conceived.

The limitations of the cruder form of phenotypic selection depend upon two primary causes, somatic modifiability of characters and genotypic differences among like phenotypic individuals. Since differences which are due to modifiability tend in the long run to group themselves around a mean in the form of a normal variability curve, it may be stated dogmatically that long-continued phenotypic selection should tend to obliterate them. But it is not enough for the practical breeder to know that eventually a given result may be produced, his time is limited and he, therefore, desires, and rightly, to achieve a given result in the shortest possible time. A case in point is that which we have already discussed in some detail, modifiability in relation to selection for high egg production in the domestic fowl. Here Pearl found that modifiability was so great that simple phenotypic selection of the highest producers for breeding stock resulted in no improvement whatever in laying capacity. On the other hand, the application of a method of breeding which fully allowed for this effect of modifiability and which further took into account the germinal constitutions of the fowls selected for breeding purposes immediately resulted in gratifying improvement. With most characters the influence of modifiability is not so great as in fecundity of fowls. Often in fact modifiability may actually be utilized to advantage by the breeder in determining relative excellence. Thus any system of development which tends to call forth the highest possible expression of the capabilities of individuals tends to widen the differences between superior and inferior individuals. Both good and poor dairy cows tend to give increased milk yield when fed richly, but the increase is often more marked in the good cows. On the other hand, with horses in general it is possible by training to increase speed, but it is a question whether the increase in such a case is more marked in good or poor horses. We may say with confidence, however, that here training by developing the full capabilities of the animal tends to bring its speed up to such a standard that when compared with breed records, the superior excellence of the individual is definitely established. Modifiability, therefore, is on the one hand a factor which tends to decrease the possible effectiveness of the method of breeding from the best; on the other hand, if properly utilized it is a powerful aid in the accurate selection of those individuals which possess the highest inborn capabilities.

When we come to consider the influence of germinal diversity in phenotypic selection, we approach more nearly the problem of the real limitations under which the method of phenotypic selection labors. Here we may distinguish different ways in which germinal diversity may hinder phenotypic selection.

Phenotygic Selection Does Not Distinguish Between Homozygous and Heterozygous Individuals.—To the student of Mendelism this difficulty requires no further comment. It may be pointed out, however, that the difficulty increases as the number of factors for which selection is being practised increases. As with modifiability, however, this difficulty tends to be obliterated by long-continued selection, for such selection inevitably increases the proportion of homozygous individuals within a given phenotype or standard of selection. Roughly it may be said that the rate of increase of the proportion of homozygous individuals is inversely proportional to the number of factors concerned in the selection, for the greater the number of factors the slower is the rate at which the population approaches a uniformly homozygous condition. Theoretically complete attainment of this condition is only reached after an infinite number of generations, but practically the number of generations which is necessary to measure up to within 5 per cent. of the possible limit is much smaller. It is, however, often so large that the animal breeder would prefer to use some other method, if by so doing, he could more quickly reach the desired standard of excellence and stability of type.

At this point, however, it should be mentioned that selection is often made for characters which are recessive, or which give intermediates when in the heterozygous condition. In such cases, of course, the relation between phenotype and genotype is simpler and methods of selection gain in effectiveness in consequence thereof.

Phenotypic Selection Does Not Make Allowance for the Differences Which May Exist Among the Genotypes of a Given Phenotype.—Simple examples of this proposition may be quoted without number. In fowls for example there are dominant whites like the White Leghorn and recessive whites like the White Plymouth Rock. The diverse progeny which is obtained by mating these two breeds together has been described in detail in a previous section. There is some evidence that a similar condition may obtain in cattle with respect to white coat color. White is, likewise, dominant in the horse, and may therefore conceal a large number of latent factors. In the pig the same differences in behavior with respect to white coat color have been noted. There is reason to believe that the same kind of diversity in genetic constitution obtains for economic characters, as for those not so strictly utilitarian. The breeder who follows a method of phenotypic selection should not, therefore, be surprised if crossing different strains results in a disappointing lack of uniformity in his herd. It is not difficult to see that in differences of genotype such as have been noted here, the breeder of best to best meets one of his most perplexing problems.

Phenotypic Selection Fails to Allow for Heterozygosis.—In other portions of this book the assumed effect of heterozygosis on vigor and fertility has already been discussed at considerable length. If a heterozygous condition ever can determine a more vigorous development than the homozygous condition, then the breeding practice of the future will sometimes be materially altered in order to take advantage of this fact. But aside from this possible difficulty there is sometimes a very real difficulty in the fact that selection has set as its standard a type absolutely conditioned by a heterozygous genotype. The striking and ever-quoted instance of this fact is the Blue Andalusian fowl, which no amount of breeding has ever been able to establish in a pure form. If more than one pair of factors is concerned in such a case, the progeny is correspondingly of greater variety—it becomes a case of the Blue Andalusian fowl on a larger scale. It is probable that this condition is not often met with. The only remedy for it is to change the standard of selection.

Pedigree Breeding.—If to phenotypic selection be added the conception of family excellence we obtain the foundation upon which pedigree breeding is based. Pedigree breeding, therefore, is merely a refined system of phenotypic selection; in one form or another it is a very old system of breeding. The principle of pedigree breeding is a laudable one, for it judges the individual not only upon its own expressed characters but also upon those which its ancestors have exhibited. It is, therefore, one more step in the direction of strict genotypic selection.

From an ideal standpoint the effect of pedigree breeding is to emphasize the value of breeding ability. The existence of strikingly prepotent animals must have been a large factor in the development of this method. By insisting upon breeding ability as a measure of excellence, the tendency has been to eliminate the effects of modifiability and heterozygosis, and to favor the selection of the most excellent homozygous individuals for breeding purposes. By so much it has concentrated blood lines within breeds to a few of those which have proven most excellent, and thereby it has amply justified its adoption as a method of breeding practice.

The weakness of the method lies not so much in inherent defects as in the uses to which livestock men have put it. The establishment of herdbooks in which pedigrees are recorded, while undoubtedly an important step in advance in the history of any breed, has tended to emphasize unduly the value of pedigree, often to the extent that individual excellence has not been rigidly insisted upon and even inherent family defects, like the barrenness of the Bates' Duchess Shorthorns, have been regarded lightly. It cannot be too strongly insisted upon that the fundamental basis of pedigree breeding, as well as all other systems of breeding, is individual excellence. No matter how favorable the ancestry, an inferior individual within a family of superior excellence is likely to have lost one or more of the factors upon which that excellence is based. If that is the case, use of such an animal for breeding purposes merely increases the number of animals which lack that portion of the favorable genotype and by so much multiplies inferiority within the family and breed. There are numerous instances in breed history of pedigree fads which have worked to the ultimate disadvantage of excellent families because of the undue prominence given to ancestry in selecting breeding animals.

Breeding Systems Based on Blood Relationship.—The influence that kinship has had on marriage laws in human society is familiar to all educated people. The old Mosaic laws forbade the marriage of closely related individuals, and complex systems of marriage apparently directed against consanguineous marriages are found even among many uncivilized tribes of peoples. Undoubtedly the existence of these systems of marriage in human society has had some influence in shaping the methods which have been adopted by animal breeders, but at most the influence has been small. The most potent factor in livestock practice has undoubtedly been the type of results which has been attained by following one system or another, and the general utility which the given system has in the hands of the average breeder. With respect to the degree of kinship permitted in matings there are three general systems of breeding: out-breeding, in which consanguinity is avoided as much as possible; line-breeding, which is based upon matings of moderate blood relationship; and inbreeding, which is based upon matings of animals closely akin to each other. Each of these methods of breeding will be discussed below.

Inbreeding.—Specifically inbreeding is a system of breeding in which sire is bred to daughter, dam to son, or brother to sister. It is, therefore, based upon the closest possible types of mating. This system of breeding naturally has had its origin in the desire to intensify the blood of notably superior individuals. The most used form of it, perhaps, is that in which a famous sire is bred to his daughters and even at times to the second generation of daughters which have been produced by inbreeding. The method of inbreeding has been particularly useful in fixing types in the early, formative period of the breed. It was the powerful tool which that great breeder of the eighteenth century, Robert Bakewell, employed in the improvement of horses, cattle, and sheep; and with astonishing success. Evidently at that time the popular prejudice existing against inbreeding was even stronger than it is today, as we may judge from the statements of Culley written in 1794.

> The great obstacle to the *improvement* of domestic animals seems to have arisen from a common and prevailing idea amongst breeders—that no bull should be used in the same stock more than three years, and no tup more than two; because (say they) if used longer, the breed will be *too near akin*, and liable to *disorders;* some have imbibed the prejudice so far as to think it *irreligious;* and if they were by chance in possession of the best beast in the island, would by no means put a male and female together that had the same sire, or were out of the same dam. Mr. Bakewell has not had a cross for upward of twenty years; his best stock has been bred by the nearest affinities; yet they have not decreased in size, neither are they less hardy, or more liable to disorder; but, on the contrary, have kept in a progressive state of improvement.

Culley might have written in the twentieth century, for even today inbreeding is popularly blamed for a variety of ill effects. Of these we have discussed decrease in fertility and vigor somewhat, and have reached the tentative conclusion that inbreeding of itself does not always result in diminished vigor and fertility, and therefore in all probability does not stand in any causal relation to it. As a method of breeding, however, it gives abundant opportunity for a race which has any defects whatsoever to express them, for by simplifying the genotypic constitutions of the animals within a family and making them like each other, it tends to increase the proportion of recessive defectives produced in the family. But if no inherent defects exist in the family, then such an effect cannot be produced, and the practice is on the whole to be commended.

The advantages of a system of inbreeding are found in the close approach which this method makes to a strict method of genotypic selection. It overcomes that difficulty of a system of phenotypic selection which arises from the possibility of mating different genotypes which are alike phenotypically. By this method the breeder is assured of genotypic identity in his breeding stock, because they have received their germinal elements from a common ancestor. Accordingly we are not surprised that this method has proven so notably successful in fixing types in the formative period of a breed's existence, because it is just at this time that both genotypic and phenotypic diversities are most common, and the difficulties arising from their existence most baffling. The increase in prepotency which is universally acknowledged to accompany inbreeding is in entire harmony with this interpretation—for by simplifying the genotypic constitutions of the individuals the tendency is to secure more and more individuals which are homozygous for all or nearly all the favorable germinal elements, and which possess in consequence of this fact superior transmitting capacity. The breeder who would add the practice of inbreeding to his operations must learn to cull with a firm hand, however, whenever defects appear for they indicate inevitably that some necessary constituents of the hereditary material have been lost. If he can do this, he has added a powerful instrument for improvement to his breeding equipment.

Line-breeding.—The term line-breeding designates breeding within a given line of descent. By common agreement the term does not include inbreeding; it begins with those degrees of relationship which are just outside the pale of inbreeding. It is, therefore, a system of breeding in which cousins of different degrees are mated with each other.

No system of breeding has been so popular or so generally productive of good results as line-breeding. Like inbreeding, it is a method of breeding which approaches as nearly as present knowledge will permit to the ideal of genotypic selection. Because the individuals which are mated belong to the same line of descent and exhibit similar sets of characters, it is logically just to conclude that they possess similar sets of germinal elements. In this fact we have the whole explanation of the uniformity of progeny which is so characteristic of continued line-breeding.

Line-breeding is popularly credited with all the excellencies of inbreeding and a greatly lessened tendency toward the production of defectives. There is a measure of truth in this belief for line-breeding, by the mating of animals of slightly wider relationship than those used in inbreeding, permits the introduction and intermingling of hereditary elements from slightly different lines of descent. It is in this that we must seek the explanation for the greater success which line-breeding has had among most practical breeders. That explanation is not far to seek, for if the production of defectives depends upon factors which are distributed in Mendelian fashion, and there is no reason to believe that it does not, then any introduction of diverse hereditary elements is likely to result in the neutralization of the defective elements in both hereditary systems, for only under unusual conditions would such elements be identical in the two systems. Along with this tendency toward decreased production of defectives, however, there is the ever present possibility of dissipating the elements characteristic of the ideal family type, of mingling them with others not so productive or desirable. The tendency is by no means so strong as it is in out-breeding, but it is stronger than in inbreeding. It serves again to emphasize the fact that any system of breeding must be based upon matings of superior individuals.

Out-breeding.—Out-breeding is merely a system of breeding best to best, at the same time avoiding relationship in the animals which are mated. While it may tend to avoid completely the disasters which often attended inbreeding, it is subject to all the defects of the old system of phenotypic selection. Chief among these is its tendency toward lack of uniformity in the herd. The harm which it does, however, depends largely upon the breed in which it is practised. Thus among Shorthorns the extraordinary multiplication of individuals of certain families leaves a wide field for the selection of superior individuals distantly related and of the same type, so that in this breed, a form of out-breeding which is really not out-breeding at all, but a very mild form of line-breeding, may be adopted without much danger. Out-breeding, however, is in a sense a harking-back to methods which have been discarded, and although the new breeder may do well to start his operations by avoiding too close affinities, he should steadily endeavor to master the problem of dealing with consanguineous matings sanely and effectively.

Other Systems of Breeding.—Under the chapter on the utilization of hybrids in animal breeding, we have discussed at some length grading and cross-breeding. The former of these methods of breeding provides a simple and practical method for improving livestock on a large scale, and its practice is to be commended. Grading is not to be contrasted with any of the systems of breeding which have been described, but it may be compared on the one hand with pure breeding and on the other hand with aimless scrub breeding. In grading, any of the systems of breeding which have been discussed above may be used, the only requirement is that the sire must always be pure-bred and of the same breed. By rigid selection of females which approach most nearly to the ideal type of the breed from which the sire is selected, grade herds after three or four generations will approach very nearly to the standard of excellence from an economic standpoint at least of pure-breds.

Crossbreeding we have also described in a previous chapter. It is an economic procedure entirely, and is based on the uniting of favorable characteristics of two strains in the cross-bred animals. Along with crossing sometimes comes the increased vigor of hybrids, sometimes striking, other times only slight. Although greatly decried by breeders and advocates of pure-bred livestock, crossbreeding is sound in theory and productive of good results in practice. To reap its benefits, however, it must be followed systematically. The breeder must not be tempted to allow the excellence of cross-bred animals to overcome his better judgment to the extent of permitting their retention in the breeding herd. Increased vigor and size are not alone responsible for the adoption of crossbreeding by some livestock men, but the changing standards of market demands have sometimes favored types of livestock not represented in any existing breed. Two alternatives are then open to the breeder, to establish within existing breeds the type demanded or as it were to synthesize such a type by crossbreeding. The former method is productive of the most permanent good, but it is a slow and expensive project and one requiring the good judgment of an unusually critical breeder. It has its illustrations, however, in the establishment of the Cruickshank family of Shorthorn cattle, the American type of Hereford cattle; and as an outgrowth of crossbreeding in the building up of the Corriedale sheep of New Zealand. Crossbreeding, however, often achieves the same result immediately with existing materials; and, the advantage of a particular cross having been established, it does not require as much skill in operation as the establishment of a pure breeding type. As agricultural science develops we may expect to see crossbreeding for specific purposes much more fully utilized than it is at the present time.

Genotypic Selection.—The method of genotypic selection is a method based on a knowledge of the genotypic constitution of the individuals used in mating. Although but little breeding can be ordered along this line on account of the dearth of knowledge of the actual factors which are concerned in particular character complexes, nevertheless to all practical purposes intelligent application of the methods of line breeding and inbreeding amounts to the same thing. Thus far our knowledge of factors is only extensive enough to apply this method of breeding to relatively simple problems, such as that of producing polled breeds of cattle by the use of polled mutants, mule-footed breeds of hogs, hornless sheep, or particular coat colors in horses, cattle, and swine. Nevertheless it is a very useful conception to add to the stock-breeder's fund of knowledge.

The method of breeding for increased fecundity in poultry devised by Pearl is the best existing illustration of the employment of genotypic selection in attacking a problem of economic importance. We have pointed out how Pearl on the basis of investigations of winter egg production in fowls established the fact that two dominant factors for high winter egg production existed. One of these factors, L, determines the production of pullets which lay somewhat less than thirty eggs during the winter period; the other factor, M, which is sex-linked, adds to this so that birds possessing both these factors lay over thirty eggs during the winter cycle. The breeder's problem, therefore, starting with a mixed flock, is to isolate and breed from individuals of the genetic constitutions $(ZM)(ZM)LL$ for males and $(ZM)WLL$ for females, to the end that the flock will consist entirely of individuals of these genotypes. So valuable are the specific directions which Pearl has given that they are printed in full below.

> 1. Selection of all breeding birds *first* on the basis of *constitutional vigor and vitality* making the judgment of this so far objective as possible. In particular the scales should be called on to furnish evidence. (*a*) There ought to exist, for all standard breeds of fowls, normal growth curves, from which could be read off the standard weight which should be attained by a sound, vigorous bird, not specially fed for fattening, at each particular age from hatching to the adult condition. These curves we shall sometime have. (*b*) Let all deaths in shell, and chick mortality, be charged against the dam, and only those females used as breeders a second time which show a high record of performance in respect to the vitality of their chicks, whether in egg or out of it. This constitutes one of the most valuable measures of constitutional vigor and vitality which we have. If for no other reason than to measure their breeding performance, a portion of the females each year should be pullets. In this way one can in time build up an elite stock with reference to hatching quality of eggs and viability of chicks. (*c*) Let no bird be used as a breeder which is known ever to have been ill, to however slight a degree. In order to know something about this, why not put an extra leg-band on every bird, chick, or adult, when it shows the first sign of indisposition? This then becomes a permanent brand, which marks this individual as one which *failed*, to a greater or less degree, to stand up under its environmental measures of constitutional vigor. (*d*) Many of the bodily stigmata by which the poultryman, during the last few years, has been taught to recognize constitutional vigor, or its absence, have, in my experience, little if any real significance. Longevity is a real and valuable objective test of vigor and vitality, but it is of only limited practical usefulness, because of the increasing difficulty with advancing age of breeding successfully on any large scale from old birds of the American and other heavy types.
>
> 2. The use as breeders of such *females* only as have shown themselves by trapnest records to be high producers, since it is only from such females that there can be any hope of getting males capable of transmitting high-laying qualities.

3. The use as breeders of such *males* only as are known to be the sons of high-producing dams, since only from such males can we expect to get high-producing daughters.

4. The use of a pedigree system, whereby it will be possible at least to tell what individual male bird was the sire of any particular female. This amounts, in ordinary parlance, to a *pen* pedigree system. Such a system is not difficult to operate. Indeed, many poultrymen, especially fanciers, now make use of pen pedigree records. It can be operated by the use of a toe-punch. All the chickens hatched from a particular pen may be given a distinctive mark by punching the web between the toes in a definite way. If one desires to use a more complete *individual* pedigree system, he will find the system described in Bulletin 159 of the Maine Agricultural Experiment Station a very simple and efficient one. It has been in use at this Station for 7 years, with entire satisfaction, on the score of both accuracy and simplicity.

5. The making at first of as many different matings as possible. This means the use of as many different male birds as possible, which will further imply small matings with only comparatively few females to a single male.

6. Continued, though not too narrow *inbreeding* (or line-breeding) of those lines in which the trapnest records show a preponderant number of daughters to be high producers. One should not discard all but the single best line, but should keep a half dozen at least of the lines which throw the highest proportions of high layers, breeding each line within itself.

In the above set of directions two things will challenge the student's interest most, namely the emphasis which is laid upon constitutional vigor and vitality in the selection of breeding birds, and the fact that a system of line-breeding or inbreeding is used in order to increase fecundity.

The relation of the above directions to the genotypic behavior are not difficult to point out. Of females there are two different types $(ZM)WLL$ and $(ZM)WLl$ which are high producers; the remainder are either mediocre or low producers. It is assumed that by trap-nest records, it has been possible to segregate out a certain number of such high-producing hens from a mixed flock of low, high, and medium producers. When these are mated to males from the same lot, a variety of results will be produced according to the genetic constitution of the males. In Table LXXIX are collected the results which follow when females of the two high-producing genotypes are mated with the nine possible kinds of males. Now if the numbers of females of genotypes $(ZM)WLL$ and $(ZM)WLl$ in each pen are approximately equal—in practice those of genotype $(ZM)WLl$ would probably be in excess—then it will be practically impossible to distinguish matings of types (1) to (3) and possibly (4) and (5) unless the number of daughters tested from each pen be relatively large. In this connection we recall the fact, as a further difficulty, that modifiability in egg production is relatively very great. If now an equal number of pens from matings (1) to (5) should happen to have

TABLE LXXIX.—THEORETICAL TABLE TO ILLUSTRATE THE RESULTS OF MATING HIGH-PRODUCING HENS WITH ALL POSSIBLE KINDS OF MALES

Males	(ZM)(ZM)LL (1)			(ZM)(ZM)Ll (2)			(ZM)(ZM)ll (3)		
Females	Females		Males	Females		Males	Females		Males
(ZM)WLL	(ZM)WLl	100% high	(ZM)(ZM)LL	(ZM)WLL (ZM)WLl	50% high 50% high	(ZM)(ZM)LL (ZM)(ZM)Ll	(ZM)WLl	100% high	(ZM)(ZM)Ll
(ZM)WLl	(ZM)WLL (ZM)WLl	50% high 50% high	(ZM)(ZM)LL (ZM)(ZM)Ll	(ZM)WLL (ZM)WLl (ZM)Wll	25% high 50% high 25% medium	(ZM)(ZM)LL (ZM)(ZM)Ll (ZM)(ZM)ll	(ZM)WLl (ZM)Wll	50% high 50% medium	(ZM)(ZM)Ll (ZM)(ZM)ll
Males	(ZM)(Zm)LL (4)			(ZM)(Zm)Ll (5)			(ZM)(Zm)ll (6)		
Females	Females		Males	Females		Males	Females		Males
(ZM)WLL	(ZM)WLL (Zm)WLL	50% high 50% medium	(ZM)(ZM)LL (ZM)(Zm)LL	(ZM)WLL (ZM)WLl (Zm)WLL (Zm)WLl	25% high 25% high 25% medium 25% medium	(ZM)(ZM)LL (ZM)(ZM)Ll (ZM)(Zm)LL (ZM)(Zm)Ll	(ZM)WLl (Zm)WLl	50% high 50% medium	(ZM)(ZM)Ll (ZM)(Zm)Ll
(ZM)WLl	(ZM)WLL (ZM)WLl (Zm)WLL (Zm)WLl	25% high 25% high 25% medium 25% medium	(ZM)(ZM)LL (ZM)(ZM)Ll (ZM)(Zm)LL (ZM)(Zm)Ll	(ZM)WLL (ZM)WLl (ZM)Wll (Zm)WLL (Zm)WLl (Zm)Wll	12½% high 25% high 12½% medium 12½% medium 25% medium 12½% low	(ZM)(ZM)LL (ZM)(ZM)Ll (ZM)(ZM)ll (ZM)(Zm)LL (ZM)(Zm)Ll (ZM)(Zm)ll	(ZM)WLl (ZM)Wll (Zm)WLl (Zm)Wll	25% high 25% medium 25% medium 25% low	(ZM)(ZM)Ll (ZM)(ZM)ll (ZM)(Zm)Ll (ZM)(Zm)ll
Males	(Zm)(Zm)LL (7)			(Zm)(Zm)Ll (8)			(Zm)(Zm)ll (9)		
Females	Females		Males	Females		Males	Females		Males
(ZM)WLL	(Zm)WLL	100% medium	(ZM)(Zm)LL	(Zm)WLL (Zm)WLl	50% medium 50% medium	(ZM)(Zm)LL (ZM)(Zm)Ll	(Zm)WLl	100% medium	(ZM)(Zm)Ll
(ZM)WLl	(Zm)WLL (Zm)WLl	50% medium 50% medium	(ZM)(Zm)LL (ZM)(Zm)Ll	(Zm)WLL (Zm)WLl (Zm)Wll	25% medium 50% medium 25% low	(ZM)(Zm)LL (ZM)(Zm)Ll (ZM)(Zm)ll	(Zm)WLl (Zm)Wll	50% medium 25% low	(ZM)(Zm)Ll (ZM)(Zm)ll

been chosen, then we will obtain the following distribution of males with respect to their genotypes and relative numerical frequencies:

(1)	*(ZM)(ZM)LL*	27
(2)	*(ZM)(ZM)Ll*	30
(3)	*(ZM)(ZM)ll*	7
(4)	*(ZM)(Zm)LL*	9
(5)	*(ZM)(Zm)Ll*	6
(6)	*(ZM)(Zm)ll*	1
	Total	80

In the next generation, therefore, the probabilities are strongly in favor of the selection of males of types (1) and (2) and the trap-nest records should insure the selection of hens which are mostly of the two genotypes given in the table. At any rate matings will be restricted to types (1) to (6), the inferior types (7) to (9) are excluded. Accordingly

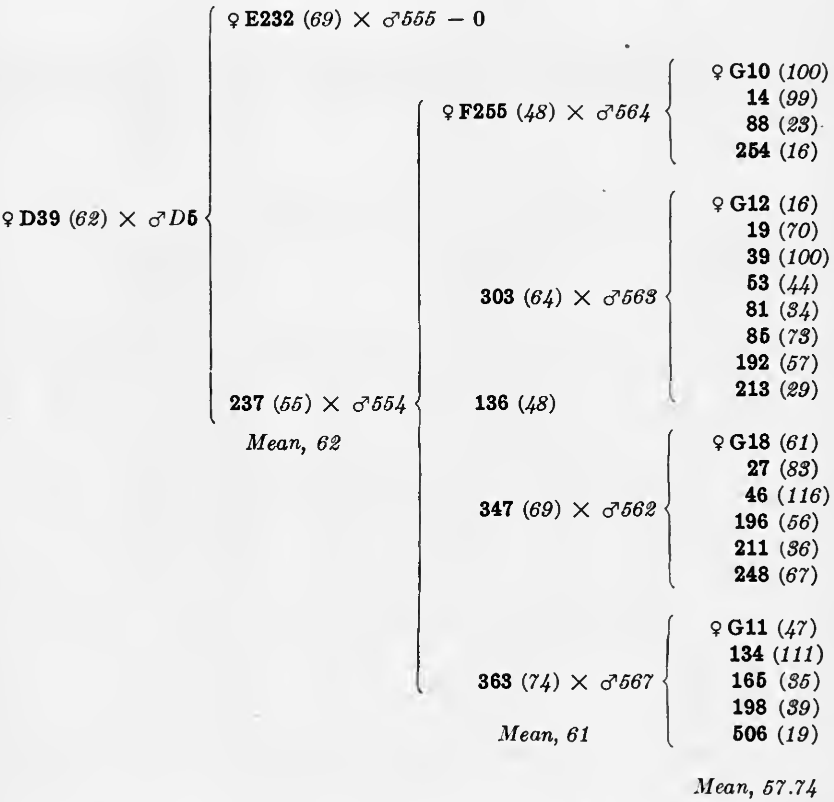


Fig. 226.—Pedigree of line *D5D*39, characterized by high winter egg production. Bold faced figures are band numbers of females, italics of males. Italics in parentheses give the winter egg records. (*After Pearl.*)

this second generation should show a very marked improvement in egg production, if breeding be carried on within the line.

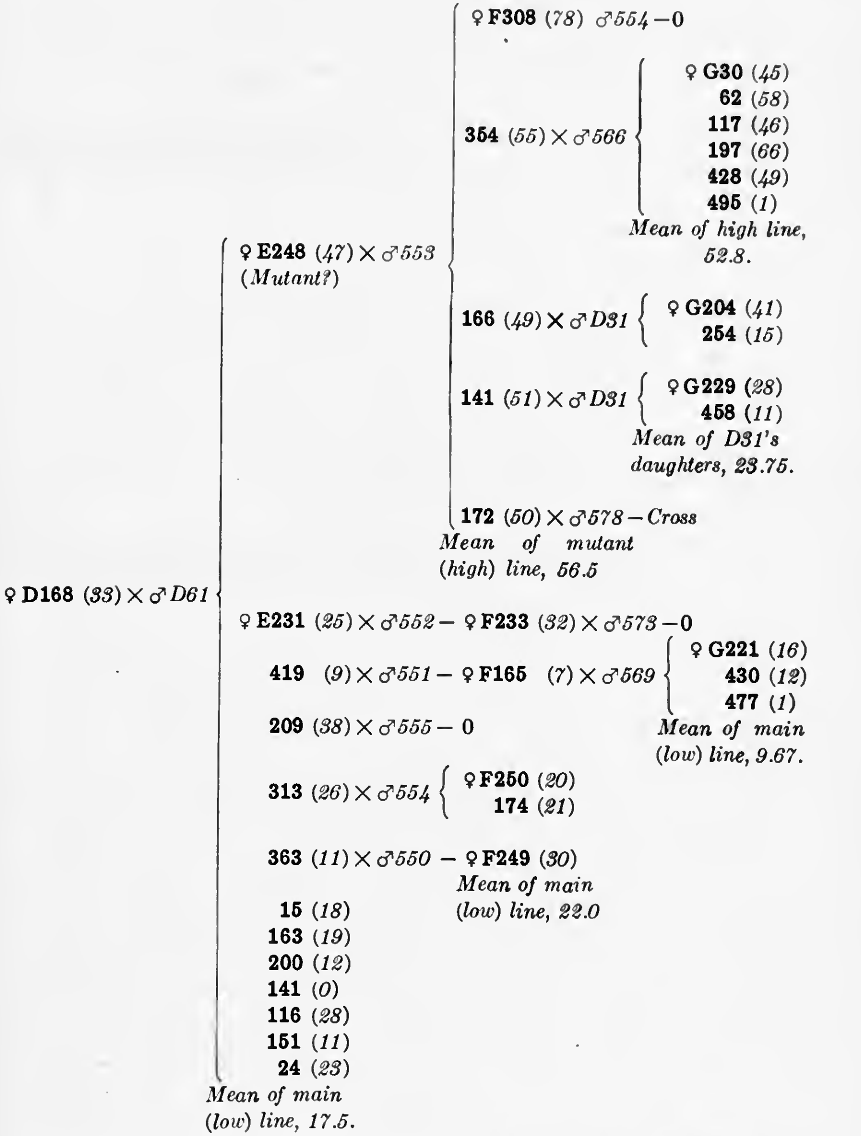


Fig. 227.—Pedigree of line *D*61*D*168, characterized by low winter egg production. Conventions are the same as in Fig. 226. The progeny of the mutant (?) high producer *E*248 is included in this pedigree. (*After Pearl.*)

This method of increasing egg production is not entirely theoretical, but it has actually worked after 9 years of patient selection of high trap-nest performers failed to show any improvement. The two pedigrees given herewith show the type of results which Pearl has secured by an application of this method of breeding. In Fig. 226 is given the pedigree of line *D*5*D*39, a high-producing line. It will be observed that a mean winter egg production of about sixty eggs is maintained throughout four generations. In every case, of course, males were selected for mating of a genotype corresponding to the females. The last generation in this pedigree shows how large a range of phenotypic fluctuation may be expected in breeding operations with fowls.

For contrast with the above line we may present line *D*61*D*168, a low-producing line. The pedigree is given in full in Fig. 227. Here the mean winter egg production of the main low line is about one-third that of line *D*5*D*39. This line is interesting on account of the appearance of a high-producing individual, *E*248, which is probably a product of Mendelian segregation, but may possibly be a mutant. Not only was this individual herself a high producer, but she transmitted her producing abilities to her daughters, so that in the high line of this race, only one individual *G*495, possibly pathological, failed to exhibit a considerably higher winter egg production than the highest individual in the low portion of the line. These two pedigrees illustrate clearly what a systematic plan of breeding may accomplish after mere phenotypic selection has failed completely.

We should not fail to point out as a factor to be considered in interpreting Pearl's directions for breeding poultry for high fecundity, that neither Pearl nor any other scientist claims that the two factors, *L* and *M*, are the only ones concerned in breeding for fecundity. In any mixed flock of birds there must be a number of other factors, which although they may not have as marked an effect as the two primary factors, nevertheless will appreciably affect winter egg production. For this reason the breeder is admonished to use moderate inbreeding or line-breeding, because by too close inbreeding he may inadvertently breed his flock to a homozygous condition for unfavorable modifiers. Line-breeding is necessary, because by this method a like genotypic constitution is assured. Further, too hasty rejection of lines which do not measure up to standard may result inadvertently in the discarding of some line which had greater potentialities than those at first most productive, consequently the warning not to reject all but the best line. Moreover, we suspect that by isolating different high lines and then crossing them and applying the above procedure to the hybrid progeny still better strains might result. The directions which Pearl has given for poultry breeding may be applied with proper modifications to other livestock. They should be carefully studied by every breeder, with the distinct proviso that no rule of thumb, however excellent, can supply the ability for intelligent practical application, an indispensable feature of successful breeding operations.

CHAPTER XXXVIII

METHODS OF CONDUCTING BREEDING INVESTIGATIONS

Any livestock breeder who wishes to carry on breeding operations in an intelligent fashion, particularly if on a large scale, will find it necessary to adopt some definite system of keeping records. Whatever system is adopted it should fulfil at least three requirements: it should be simple; it should be concise, that is it should confine itself to the essential features of the breeding operations; and it should be adapted to the particular conditions of the individual livestock breeder. The last desideratum makes it impossible to outline here any specific plan for keeping written records, consequently certain features of this problem will be discussed so that some definite conception may be gained of the matters with which records should deal.

Judging the Individual.—Of first importance in breeding operations is some method of determining individual worth. In certain cases, as for example, in beef cattle, this depends largely upon visible characteristics, and the breeder has only to build up in his mind by constant association with his livestock an ideal to which he desires to direct improvement in his herd. Whenever he can introduce objective tests, the breeder gains by doing so. The practical breeder has often felt the need of such objective standards of judgment, and from time to time he has attempted to introduce them. Sometimes such tests are very easy to apply, as for instance the speed test in race horse breeding. Sometimes, however, they are more difficult of utilization, as for example, individual butter-fat production in dairy cattle or individual egg production in poultry. Nevertheless even such records may be obtained economically if everything be planned so as to expedite the work connected with them. Methods of keeping dairy records have been devised which enable the dairymen to obtain and record accurately the daily production of his cows by spending about 2 minutes per day per cow in doing it. In Fig. 228 is shown the equipment for carrying out such work and a convenient mode of arranging it. It will be noted that all the necessary equipment is at the hands of the operator, so that no time whatever is lost in obtaining and recording the data. For testing butter fat, composite samples are used and the actual test is often made by some central creamery or appointed milk tester, rather than by the dairyman himself, although the latter method is perfectly feasible.

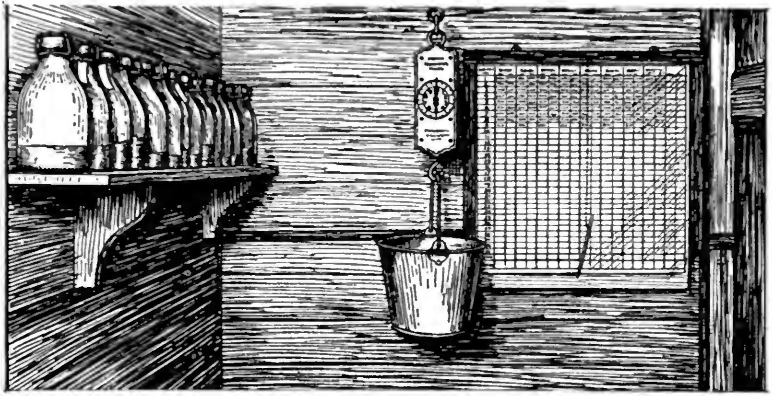


Fig. 228.—Equipment necessary for obtaining individual records of production of dairy cows. (*After Lane.*)

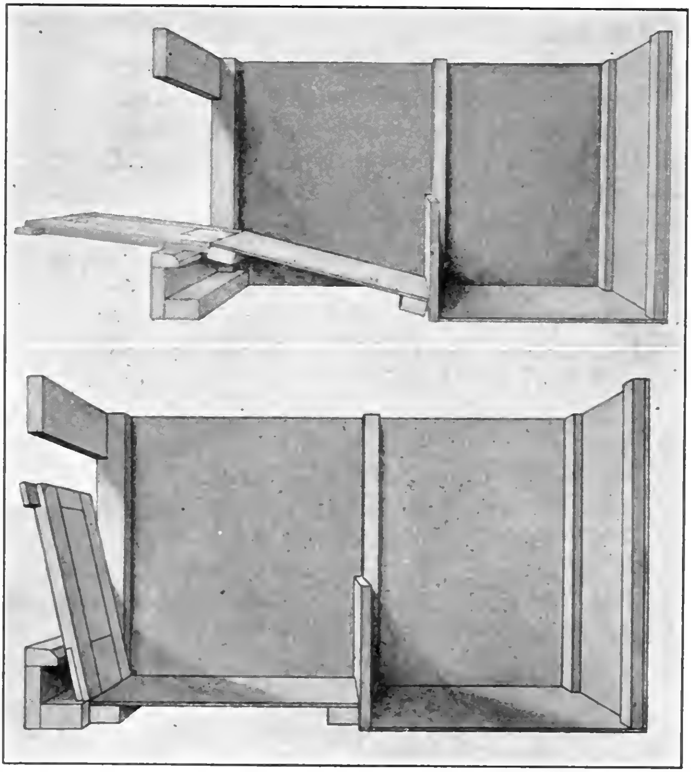


Fig. 229.—Type of trap-nest used in Maine station poultry breeding operations, shown set and sprung. One side removed to show interior. (*After Pearl and Surface.*)

Since so much has been said about the Maine Station investigations of fecundity in fowls, perhaps it would be of some interest to know how records are obtained there. The type of trap-nest in use is shown in Fig. 229. Details of construction need not be taken up here, except to remark that durability of materials is a prime requisite for continuous service. The absence of any springs or other involved contrivances has made it possible to use this type of trap-nest in extensive breeding investigations involving a flock of about 2000 hens. Ten such nests are used in a pen of fifty birds, and an attendant visits the pens at intervals of one hour or more, depending upon the rate of egg laying. Obviously a method such as this is expensive even when reduced to the simplest terms, and it is, therefore, applicable only to the selection and production of breeding stock. It is difficult, however, to conceive of any other accurate criterion which might be adopted.

It should be noted that statistical requirements do not demand that complete records be obtained, for the existence of modifiability and other kinds of individual variability make it impossible in any event to get anything but an approximate record. Accordingly in recording the data of production of dairy cows, for example, it is not necessary to weigh and test the milk every day for the whole period of lactation, but two or three 7-day periods at stated times with respect to the beginning of lactation will give a sufficiently accurate estimate for all practical purposes. Similarly in poultry breeding, Pearl has found that production during the winter period is a sufficiently accurate and distinctive index of the egg-laying capacity of a hen.

Further the danger from unjust comparisons should always be emphasized. A comparison between egg production of hens in the second laying season and pullets would favor the pullets, for pullets ordinarily lay more eggs during the first season than they do as hens in the second season. Moreover different parts of a given season are not equivalent. A pullet lays more eggs in a given length of time during the spring cycle beginning about March 1, than she does during the winter cycle. A cow, likewise, produces more milk during the early part of her lactation period than she does later on, and she reaches her maximum capacity at 5 or 6 years of age. With respect to these points we have reproduced in Table LXVI, the comparative indices which Pearl has calculated and which provide a method of comparing the productions of cows of different ages at different stages in the lactation period. As an additional variable in this case we should include the time at which a cow freshens, whether in spring, summer, or fall, as having a definite influence on herd production of milk and butter fat. We could go on recounting without end such factors which must be considered in making accurate comparisons. The point, however, is sufficiently obvious, namely, that even objective

Tilly Alcartra 123459

Calved October 2, 1908	
Butter 7 days (6 years)	30.20
Milk	632.30
Butter 7 days (5 years)	29.27
Milk	715.40
Butter 30 days	122.71
Milk	3,066.80
Butter 90 days	360.07
Milk	8,793.90
Butter 100 days	396.83
Milk	9,702.80
Butter 7 days (8 months after calving)	19.23
Milk	473.10
Butter 1 year	1,189.04
Milk	30,451.40
(World's yearly milk record)	
Butter 7 days (3 years)	23.15
Milk	613.00
Butter 7 days (8 months after calving)	17.06
Milk	420.00
Butter 1 year	841.23
Milk	21,421.30
Butter 7 days (30 months)	17.39
Milk	490.40
Butter 7 days (8 months after calving)	14.35
Milk	362.10
Butter 285 days	556.20
Milk	14,837.20

Alcartra Polkadot Corrector 30624

22 A. R. O. daughters:	
Geneseo Belle Polkadot	34.39
Milk	733.60
Butter 1 year	916.17
Milk	20,816.20
Alcartra Abbekirk	27.87
13 others from 20 to 27.1 pounds	
10 A. R. sons	
He has 87½ per cent. of the same blood as Ollie Watson Prima Donna, 31.10.	
Brother to the dams of:	
Hilldale Segis	33.17
K. P. Alcartra (3½ years)	30.87
Butter 30 days	121.29
(World's 3-year-old records)	
By a brother to the sires of:	
Sadie Vale Con. 4th	41.06
Four others from 30 to 31.8 pounds.	

Tilly Lou 2d 82057

By a brother to the sire of six 30-pound cows. Her sire is by a son of De Kol Burke, whose 73 A. R. O. daughters include:	
Lint Burke (4 years)	32.76
River Sadie D. K. Burke	32.29
Milk 7 days	920.80
Milk 30 days	3,725.60
Milk 2 years	54,805.20
(World's milk records)	
Five others from 30 to 31.7 pounds, 28 others from 20 to 27.2 pounds; and who is grandsire of Sp. Brook Bess Burke, 34.51 pounds. Five others from 30 to 33.5 pounds.	

FIG. 230.—Pedigree of Tilly Alcartra, world's record milk producer, showing produc-

Chief Phiebe Oak Duchess 28176	
21 A. R. O. daughters:	
Ollie Wat. Prima Donna	31.10
Lillie Geurima 2d	27.46
Wisconsin Bride Phiebe	27.42
Allie Nig. 2d	25.98
Pet Douglas 2d	23.02
Seven others from 20 to 22.9 pounds, 5 A. R. sons.	
From a sister to the dams of:	
Grace Fayne 2d's Hom (World's record)	35.55
Jessie Fo. 2d's Maud Hom	31.17
Three others from 30 to 31 pounds.	
Alcartra Polkadot 50798	
Butter 7 days	29.09
Milk	597.10
Butter 30 days	120.16
Milk	2,605.00
Five A. R. O. daughters:	
Lyndon Al. Polkadot	32.54
Al. Polkadot Ormsby	31.25
Al. Polkadot 2d (3½ years)	22.97
Two A. R. sons.	
Sister to the sire or dams of:	
Sp. Brook Bess Burke	34.81
Snowball Pink 3d	31.69
Ollie Watson Prima Donna	31.10
Heilo Butter Boy Burke 29327	
12 A. R. O. daughters:	
Heilo Oak Burke	23.40
Starlight Burke	20.43
His sire is by a brother to the sires of:	
Urma Burke	35.21
Prin. Hengerveld D. K	33.62
Blanche Lyons De Kol	33.31
Blanche D. K. Hengerveld	33.20
Bloom. Heng. Edith	32.45
Crown Pontiac Josey	32.34
Frenesta Heng. D. K	32.20
11 others from 30 to 32 pounds.	
Tilly Lou 62052	
Her sire is by a brother of the sire of:	
Pauline Alexis (10 years)	32.40
Milk	645.20
Butter 30 days	128.35
Milk	2,629.50
Butter 60 days	238.12
Milk	5,225.10
By a brother to a grandsire of:	
Maplecrest Pon. Girl (4 years)	35.15
Maplecrest Pon. Highlawn (4 years)	30.72
Hattie D. K. Colantha	30.54
Burton High. 2d's Har	30.14
and to the grandam of:	
El. Barn. Mech. D. K	30.49

Phiebe De Kol Burke 25368	
28 A. R. O. daughters:	
Maude Burke	32.03
W. R. Jones 2d's Phiebe	30.18
She will do Uneeda	26.36
Five others from 20 to 25.6 pounds.	
17 A. R. sons.	
Lady Oak 2d 39947	
Butter 7 days	21.49
Milk	492.90
Five A. R. O. daughters:	
Oak De Kol (10 years)	31.54
Lady Oak 2d's Hom. D. K	30.17
Two others with 21 and 27.4 pounds.	
Two A. R. sons.	
Pearl of the Dairy's Joe De Kol 23450	
75 A. R. O. daughters:	
Pearl Ormsby Burke	30.56
Pearl Neth. Vergeus	28.00
32 others from 20 to 26.9 pounds.	
9 A. R. sons.	
Alcartra's 2d's Rose 44430	
Butter 7 days	17.80
Milk	388.90
Three A. R. O. daughters:	
Alcartra Polkadot	29.09
Butter 30 days	120.16
Alcartra Peach	20.42
Two A. R. Sons.	
Phiebe De Kol Burke 25368	
His sire is by a brother to the sire of Aaggie Cornu.	
Pauline (4½ years), 34.32 pounds; the first 34-pound cow.	
Four others from 30 to 33.2 pounds.	
Heilo 4th's Pet 43611	
Butter 7 days	24.92
Milk	632.90
Two A. R. O. daughters, including Heilo Queen De Kol (33 months) 15.60 pounds butter fat, 309.70 pounds milk.	
One A. R. son.	
Iolena Fairmount's Statesman	
13 A. R. O. daughters, including Iolena Margaret, 23.54 pounds butter fat, 472.80 pounds milk; Wait-A-Bit, 19.88 pounds butter fat, 461.10 pounds milk; Angostura, 19.02 pounds butter fat, 446.50 pounds milk.	
Ophelia Diana 46996	22.80
One A. R. O. daughter:	
A daughter of Eunice Clay's Sir Henry and Ophelia Rose 2d.	

tion and breeding performances of her ancestors. (*From Kimball's Dairy Farmer.*)

data must be handled intelligently. In this connection the need of additional comparative tables like Table LXVII for other characters and other classes of livestock should be mentioned. They are not difficult to obtain and undoubtedly they will be available some day.

Pedigrees.—The pedigree of an animal is simply a record of its ancestry, and accordingly the ideal system of recording pedigrees is that system which gives proper emphasis to each animal in the pedigree. The one-time fashionable practice of tracing pedigrees back through five or six or even more generations to some illustrious sire or dam cannot, therefore, be too strongly condemned, for it over emphasizes remote ancestors in certain lines and tends to underrate the importance of a possibility of inferiority in nearer ancestors. As a test of purity of blood, the Arabians require that their horses trace through long lines of descent to the five mares of Al Khamseh; there is, however, no justification for this practice in modern breeding operations.

The pedigrees of pure-bred breeding stock are recorded in herd books. For such animals it is only necessary to consult the herd books in order to trace out their ancestry. However, it is usually more convenient, since the pedigree must be traced through several volumes of the herd-book, to record it in extended form in the herd record. This is not a difficult task; it need be done only once for every animal, and the task is still further lightened by the fact that the individuals of any established herd will have so many common ancestors that they will duplicate one another's pedigrees to a great extent. It is, however, necessary to say a word regarding the method of recording such pedigrees. The following pedigree of Roan Gauntlet, a famous old Cruickshank Shorthorn sire, taken directly from Volume XXII of the "American Shorthorn Herd-book," illustrates a method of recording pedigrees which should not be followed by breeders:

> Roan Gauntlet 45,276 (35,284).—Roan, calved May 19, 1873, bred by A. Cruickshank, owned by Mr. Rennie, got by Royal Duke of Gloster (29,864), out of Princess Royal by Champion of England (17,526)—Carmine by The Czar (20,947)—Cressida by John Bull (11,618)—Clipper by Billy (3151)—by Dandy (6918)—by Tiptop (7633)—bred by Mr. Mason.

The reason why this method should not be followed may be seen very easily in Fig. 232, which illustrates a proper way of recording a pedigree. Here the bold-faced type indicates those animals which were included in the pedigree as given in the herd-book. Of the sixty-two ancestors of Roan Gauntlet in five generations only nine are included in the herd book record. Further the record is defective in that it fails to give any evidence of the type of breeding which was employed in producing Roan Gauntlet. The way this bull traces back to the great

Cruickshank bull Champion of England is the striking feature of his pedigree.

The criticism of the above pedigree is not, it should be clearly understood, directed at the method of recording pedigrees in the American Shorthorn Herd-book, although it is a fair statement to make that the method that has since been employed of recording simply the name of sire and dam is more economical and just as satisfactory. Even by the old method, however, the pedigrees are so recorded that the entire set of ancestors may be determined. The point, however, is simply this, that such pedigrees should not be used as standards of judgment of ancestry, but rather those of the type shown in Fig. 230.

Fig. 231.—**Tilly Alcartra. No. 123459, Holstein. Production for one year, 30451.4 lb. milk containing 951.2 lb. butter fat (average test 3.12 per cent.).**

The addition of other data to the pedigree indicative of the value from a breeding or productive standpoint of the animals therein listed adds greatly to its value, particularly to the new breeder who is not yet fully familiar with the great names of breed history. The pedigree of Tilly Alcartra 123,459, the record-breaking Holstein-Friesian cow portrayed in Fig. 231, is given in Fig. 230 along with data relative to the performance and breeding value of the animals whose names appear in the pedigree. A pedigree worked out like this one is a much safer guide in judging merit than one which gives data proving that the animal in question traced in the fourteenth generation three times to some famous sire of ancient history. Performance should be insisted upon all along the line, and when three or four generations of some subdivision in a notable line fail to bring forth performing individuals, it is high time for the breeder to suspect that something has been lost in that line of descent, something that a pedigree, however excellent in remote ancestors, cannot supply.

The Coefficient of Inbreeding.—We would call attention to Pearl's coefficient of inbreeding as an instance of another refinement which has been advocated for use in practical breeding operations. Pearl proposes that inbreeding be used in a generic sense to include all cases in which some of the matings in the pedigree were of related individuals. In order to indicate degree of inbreeding he suggests the use of a coefficient of inbreeding of the form

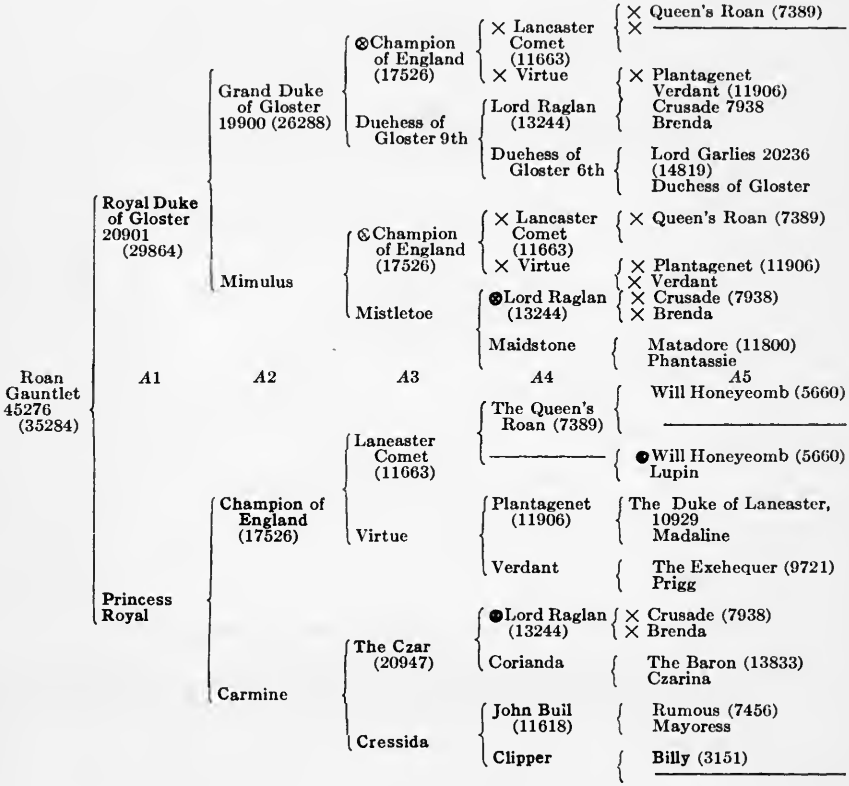


FIG. 232.—Pedigree of Roan Gauntlet, a famous Cruickshank Shorthorn bull.

$$Z_n = \frac{100\,(P_{n+1} - Q_{n+1})}{P_{n+1}}$$

which is essentially a mathematical expression of the relation in per cent. between the maximum number of different ancestors which an individual might have in a given generation, and the amount of repetition which has occurred in its ancestry.

In the above formula for Z, the coefficient of inbreeding, P_{n+1} denotes the maximum possible number of different ancestors which an individual might have in matings of the $(n + 1)$th generation and Q_{n+1}, the actual number of different ancestors which he has. For an application of this coefficient we take the pedigree of Roan Gauntlet as given in Fig. 232. It gives the following series of values for Z:

$$Z_0 = \frac{100\,(2 - 2)}{2} = 0 \text{ per cent.}$$

$$Z_1 = \frac{100\,(4 - 4)}{4} = 0 \text{ per cent.}$$

$$Z_2 = \frac{100\,(8 - 6)}{8} = 25 \text{ per cent.}$$

$$Z_3 = \frac{100\,(16 - 10)}{16} = 37.5 \text{ per cent.}$$

$$Z_4 = \frac{100\,(32 - 19)}{32} = 40.625 \text{ per cent.}$$

To determine these values we have started with the A_1 generation in which $p_1 = 2$ and of necessity $q_1 = 2$ also. The value of Z_0, therefore, must be 0 in all cases. In the A_2 generation $p_2 = 4$ and $q_2 = 4$, also, because all these four animals are different and have not previously appeared in the pedigree. The value for Z_1, therefore, is 0. In generation A_3, $p_3 = 8$. Champion of England appears twice in this generation, and since he has appeared already in A_2, the two reappearances in A_3 are crossed out. Counting the remaining individuals in this generation, we find $q_3 = 6$, and consequently $Z_2 = 25$ per cent. Now this $Z_2 = 25$ signifies not only that Roan Gauntlet in the third ancestral generation has 25 per cent. less than the maximum possible number of different ancestors, but also that in any generation further removed he must of necessity have at least 25 per cent. less than the maximum possible number of ancestors. In the next following generation, A_4, $p_4 = 16$. In determining q_{n+1} we strike out Lancaster Comet and Virtue, sire and dam respectively, of Champion of England. It is worth while noting here that these two animals are automatically eliminated in this generation because of the reappearance of an animal in a lower generation in this same line of descent. Reappearances at the apex of a line of descent are called *primary reappearances* and are marked ⊗ in this pedigree, whereas reappearances which are determined by the primary reappearance of an individual in a lower generation are called *secondary reappearances* and they are marked with the sign ×. It is only necessary to determine primary reappearances in calculating the coefficient of inbreeding, for secondary reappearances may be accounted for by simply doubling the total number of reappearances in the next lower generation. Continuing down the A_4 generation we meet with Lord Raglan as a primary reappearance as the sire of Mistletoe and further down as the sire of The Czar, also. The total number of primary and secondary reappearances in A_4 is, therefore, 6; and since the expression $p_{n+1} - q_{n+1}$ is merely a measure of the total number of reappearances, the value of $Z_3 = 6/16 = 37.5$ per cent. In A_5 we know the total number of secondary reappearances will be $6 \times 2 = 12$. There is one primary reappearance, that of Will Honeycomb, which must be added to this value, making the total number of reappearances in this generation thirteen. This gives the value $Z_4 = 40.625$ per cent. If we have, therefore, at hand an extended pedigree of an animal it is a simple matter by this method to determine its coefficient of inbreeding for any number of generations.

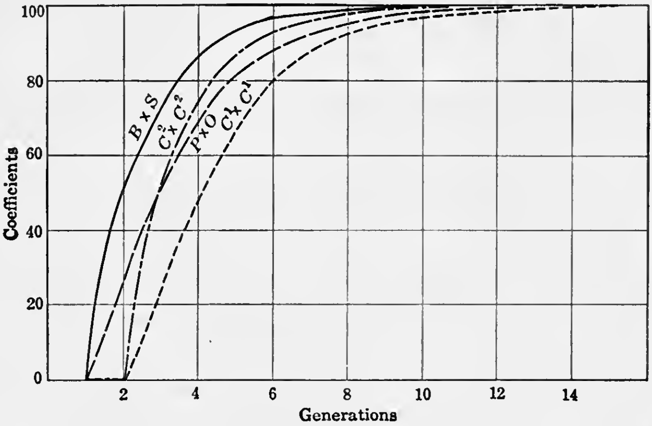


Fig. 233.—Curves of inbreeding: $B \times S$, continued brother × sister matings; $P \times O$, continued parent × offspring matings; $C^2 \times C^2$, continued double-cousin matings; $C^1 \times C^1$, continued single-cousin matings. Continued matings of uncle × niece give a curve identical with $C^1 \times C^1$. *(After Pearl.)*

In Fig. 233 are shown a number of curves of inbreeding which show graphically the rate of concentration of blood lines with different types of matings. Continued brother × sister matings give the maximum values for the coefficient of inbreeding. In this connection Pearl calls attention to the similarity of form of the brother-sister and double cousin curves and of the parent-offspring and single cousin curves.

The Coefficient of Relationship.—Obviously it is necessary for determining the significance of the coefficient of inbreeding to know how the reappearances occur in the pedigree. Thus if animals appear on both sire's and dam's line of descent sire and dam are related in some degree. But it is possible as Pearl points out to have a high coefficient of inbreeding without any relationship whatever between sire and dam. In fact, specifically the limiting value of the coefficient of inbreeding where sire and dam are totally unrelated lags only one generation behind the value for continued brother-sister matings. Pearl, therefore, proposes to determine not only the coefficient of inbreeding, but also a coefficient of relationship which shall express mathematically the degree of kinship existing between an individual's parents. We again take the pedigree of Roan Gauntlet as an illustration of the method of calculation employed. We obtain the following series of values:

$$\begin{array}{ll} Z_0 = 0 & K_1 = 0 \\ Z_1 = 0 & K_2 = 0 \\ Z_2 = 25 & K_3 = 50 \\ Z_3 = 37.5 & K_4 = 75 \\ Z_4 = 40.6 & K_5 = 75 \end{array}$$

The values for K, the coefficient of relationship, were determined in the following fashion. In A_3 on the sire's side, Champion of England which has already appeared on the dam's side reappears twice. The maximum possible number of animals different from those on the dam's side in this generation is four. Since two of these are identical with an individual which has already appeared on the dam's side, $K_3 = \frac{2}{4} = 50$ per cent. In A_4 the double primary reappearance of Champion of England in A_3 automatically determines a total of four secondary reappearances, and to these are added two primary reappearances of Lord Raglan. In A_4, therefore, $K = \frac{6}{8} = 75$ per cent. In A_5 there are no additional primary reappearances involving both sides of the pedigree, consequently the value of K remains at 75 per cent. It seems wise for breeders to use these coefficients in order to gain precision in the use of terms, if for no other purpose.

Of course the use of inbreeding coefficients does not alter the problem of inbreeding from a biological standpoint. That problem is concerned with the effect of mating closely related animals. It has already been pointed out that the coefficient of inbreeding may be high when there is no relationship between sire and dam as, for example, when a closely inbred Jersey cow is bred to a closely inbred Holstein-Friesian bull. Such matings are of course not a part of the problem of inbreeding as it is understood in practice. For a precise expression of this problem we must look to the coefficient of relationship. A coefficient of relationship of 50 per cent. for A_3 would probably be a fair mathematical requirement for inbreeding as conceived in practice. A coefficient of relationship of this magnitude includes double cousin matings as well as those of brothers with sisters and parents with offspring, but this appears to be a fair inclusion, if reference be made to the curves of inbreeding given in Fig. 233. For further details of the applications of these coefficients reference must be made directly to Pearl's work.

Marking Individuals.—The problem of marking individuals often is difficult where large numbers of individuals are involved. When very small herds are kept in which the animals may be known individually this matter is not very important, because the animals may simply be given a distinctive name, and any notes which it may be necessary to make may be recorded under that name. But when individuals become more numerous, it is usually necessary to have some safe and effective way of distinguishing them. For cattle aluminum ear tags of various kinds are often used, and these may be obtained stamped with any numbers which are desired. These may be used for smaller animals, also, or the ears may be punched in various fashions. A method used by Dr. Bell in sheep breeding experiments is illustrated in Fig. 234. By the use of eight holes with place values such as are indicated in the diagram, it is possible to identify 256 sheep according to the following combinations:

Fig. 234.—Method of identifying sheep by holes punched in the ears. (*From the Journal of Heredity.*)

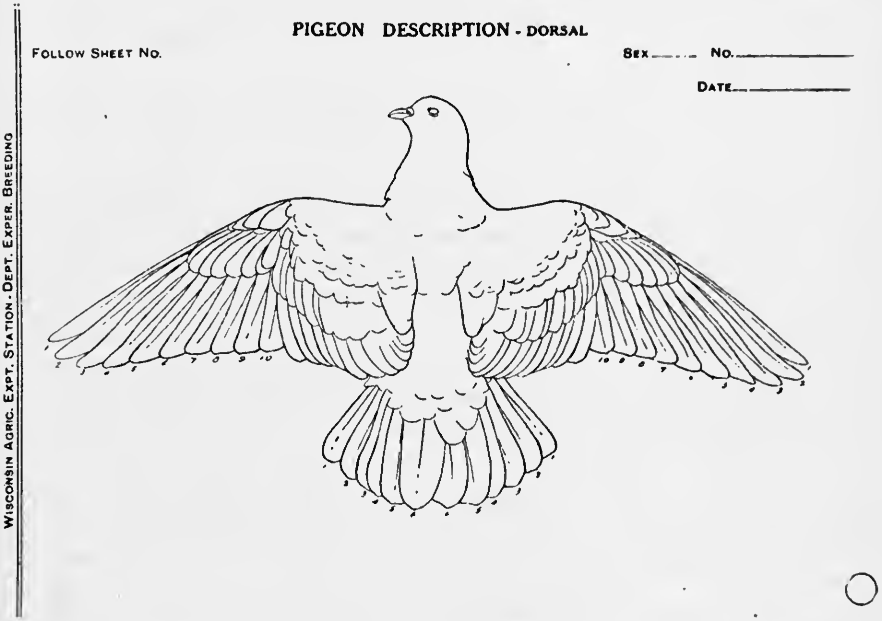
Total sheep identified by 0 hole	1
Total sheep identified by 1 hole	8
Total sheep identified by 2 holes	28
Total sheep identified by 3 holes	56
Total sheep identified by 4 holes	70
Total sheep identified by 5 holes	56
Total sheep identified by 6 holes	28
Total sheep identified by 7 holes	8
Total sheep identified by 8 holes	1

This is a very simple mode of identification, and by means of a rubber stamp with a sheep's head outline or description sheets having such a head as that shown in Fig. 234 printed upon them, it is very easy to record accurately the designation which has been given to any particular sheep. The method can of course be used with other animals, and it avoids the difficulty of loss which sometimes is met with in using ear tags.

Poultry may likewise be marked in two different ways either with web punches or with aluminum bands which fit around the shanks. For large numbers the latter method is preferable.

Recording Data.—The keynote of any system of recording data should be simplicity. This requirement must be met in scientific work; it is, however, particularly important in practical breeding for herdsmen have but limited time at their command for keeping records.

The time necessary for recording data may often be very much curtailed, if properly devised, printed forms are used. They are superior to other less accurate methods of registering data not only because they make it easier to set down the data, but because by having items indicated on the sheets or cards, it is very easy to see at any time just what data remain to be determined. The methods in all cases should be those which are best adapted to the particular conditions which obtain in the case in hand. We may summarize in brief the requirements of a good system of record keeping by discussing the several features of it.



PIGEON DESCRIPTION - DORSAL

FOLLOW SHEET NO.

SEX____ NO.________

DATE________

WISCONSIN AGRIC. EXPT. STATION - DEPT. EXPER. BREEDING

FIG. 235.—Pigeon description sheet in use in experimental breeding at the Wisconsin Agricultural Experiment Station. (*Devised by Leon J. Cole.*)

The Individual Sheet.—By the individual sheet is meant a sheet upon which is recorded vital data for a particular individual. This sheet should have places for recording such data as the date of birth of the individual, its date of death or disposal, from whom acquired and to whom disposed of, and other data of a similar character. This sheet may conveniently have on its back a pedigree blank for recording all the ancestors for at least four generations back. A separate sheet of this kind should be made out for at least each breeding individual; individuals which are not to be kept for breeding purposes may be noted on other specially devised condensed blanks, which give only the necessary essential data respecting them.

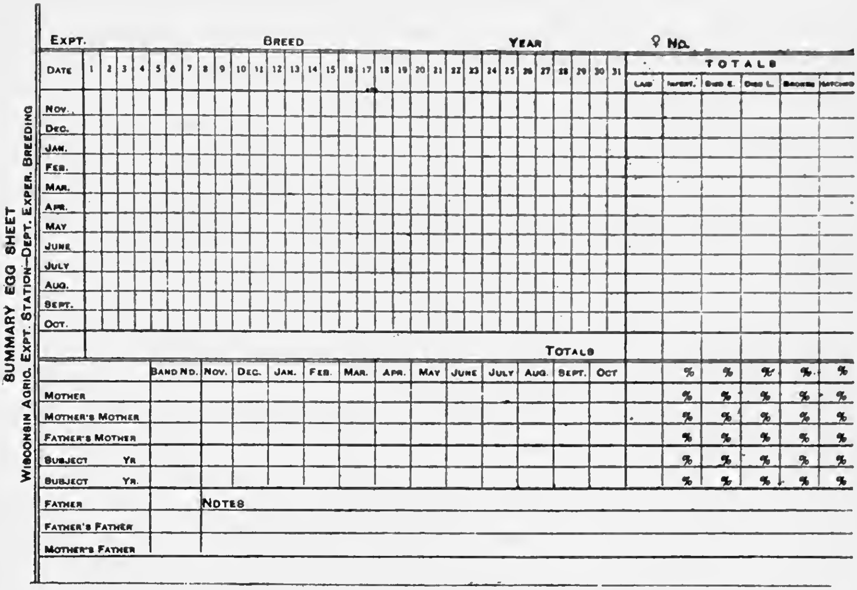
The Description Sheet.—The purpose of the description sheet is to provide space for notes bearing upon the characteristics of the animal in question, short items which may be jotted down from time to time whenever they occur to the breeder. This sheet should also bear whatever extended individual descriptions may be necessary. In many cases, the use of a printed outline such as that shown in Fig. 235, which is used in the investigations of pigeon breeding at the Wisconsin Station, aids greatly in making such descriptions definite and detailed without much labor. An outline form for instance will aid materially in recording the extent and position of black and white areas in Holstein-Friesian and other cattle which usually have broken colors.

The Progeny Sheet.—For recording matings and progeny a special sheet is often useful, although it is often possible to provide space for this data on the individual sheet. This blank will generally be used in the form of a follow sheet to accompany other sheets of each breeding female. Space should be provided for recording dates of service, name of sire used, date of delivery, sex of offspring, and other vital data of this type. There should be a place for recording the disposition of the offspring; if added to the breeding herd, a cross-reference should be made to its individual sheet.

The Performance Sheet.—The performance sheet is necessary only when the data obtained under this heading are relatively extensive as is the case in milking records of dairy cows or egg records of hens. This sheet should be devised in such a fashion as to permit the recording of data quickly and accurately. In Fig. 236 is reproduced a summary egg sheet such as is used in breeding investigations at the Wisconsin Station. It will serve as a type of the kind of sheets which may be used in recording data of performance.

Sheets for Special Purposes.—If the breeder is following out any particular type of operations which require special data it should be an easy matter to devise sheets which will help him in that matter. As an illustration we give in Fig. 237 a reproduction of a sheet used at the Wisconsin Station in an investigation of multiple births in cattle.

General Considerations.—Any system which is adopted should be convenient. For that reason a loose leaf system, because it is not bulky and offers the maximum freedom in rearrangement and filing, will probably prove most satisfactory in practical work. Such systems have



SUMMARY EGG SHEET

WISCONSIN AGRIC. EXPT. STATION—DEPT. EXPER. BREEDING

EXPT. BREED YEAR ♀ NO.

DATE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	TOTALS					
																																LAID	INFERT.	DIED E.	DIED L.	BROKEN	HATCHED
NOV.																																					
DEC.																																					
JAN.																																					
FEB.																																					
MAR.																																					
APR.																																					
MAY																																					
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AUG.																																					
SEPT.																																					
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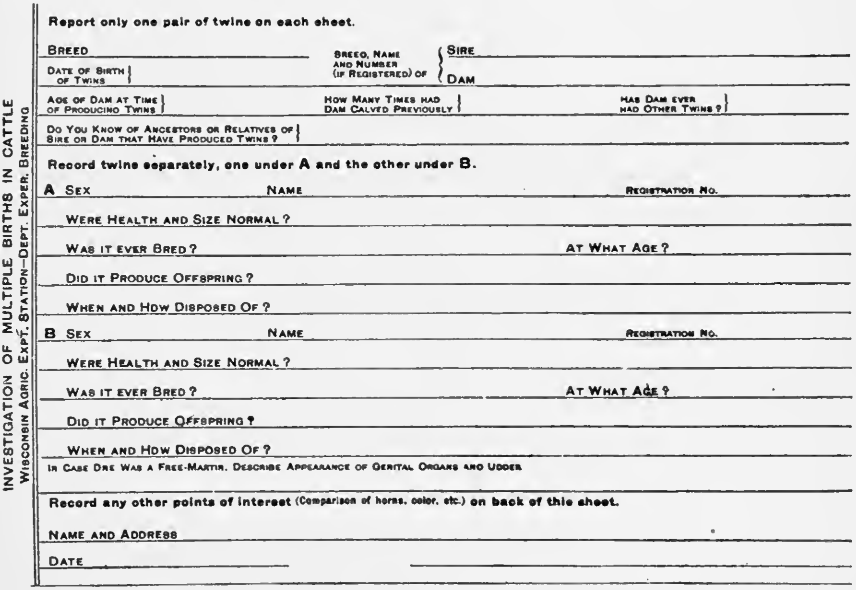
	BAND NO.	NOV.	DEC.	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT		%	%	%	%	%
MOTHER															%	%	%	%	%
MOTHER'S MOTHER															%	%	%	%	%
FATHER'S MOTHER															%	%	%	%	%
SUBJECT YR.															%	%	%	%	%
SUBJECT YR.															%	%	%	%	%

FATHER		NOTES
FATHER'S FATHER		
MOTHER'S FATHER		

FIG. 236.—Summary egg sheet in use in experimental breeding investigations at the Wisconsin Agricultural Experiment Station. *(Devised by Leon J. Cole.)*



INVESTIGATION OF MULTIPLE BIRTHS IN CATTLE

WISCONSIN AGRIC. EXPT. STATION—DEPT. EXPER. BREEDING

Report only one pair of twins on each sheet.

BREED

BREED, NAME AND NUMBER (IF REGISTERED) OF } SIRE

DAM

DATE OF BIRTH OF TWINS }

AGE OF DAM AT TIME OF PRODUCING TWINS } HOW MANY TIMES HAD DAM CALVED PREVIOUSLY } HAS DAM EVER HAD OTHER TWINS ? }

DO YOU KNOW OF ANCESTORS OR RELATIVES OF SIRE OR DAM THAT HAVE PRODUCED TWINS ? }

Record twins separately, one under A and the other under B.

A SEX NAME REGISTRATION NO.

WERE HEALTH AND SIZE NORMAL ?

WAS IT EVER BRED ? AT WHAT AGE ?

DID IT PRODUCE OFFSPRING ?

WHEN AND HOW DISPOSED OF ?

B SEX NAME REGISTRATION NO.

WERE HEALTH AND SIZE NORMAL ?

WAS IT EVER BRED ? AT WHAT AGE ?

DID IT PRODUCE OFFSPRING ?

WHEN AND HOW DISPOSED OF ?

IN CASE ONE WAS A FREE-MARTIN, DESCRIBE APPEARANCE OF GENITAL ORGANS AND UDDER

Record any other points of interest (Comparison of horns, color, etc.) **on back of this sheet.**

NAME AND ADDRESS

DATE

FIG. 237.—Printed form used in investigation of multiple births in cattle at the Wisconsin Agricultural Experimental Station. *(Devised by Leon J. Cole.)*

been devised for the use of practical breeders. Various aids such as different colored sheets for different purposes help to make these systems still more convenient. Obviously for the sake of convenience sheets should be of the same size so that they may all be filed in the same style of binder. The sheets which have been illustrated in this account are of size 5 by 8 inches and are very convenient for most purposes.

Coöperative Breeding.—Most farmers who raise livestock cannot afford themselves to keep a good bull for breeding purposes for the few cows they have, or still less a stallion for the few mares which they may need for their farm labor. Since such a large proportion of stock-raisers are in this class it becomes a grave question as to how these farmers may be provided with the advantages which accrue from the use of pure-bred sires. Any plan which has for its purpose the raising of the general average excellence of livestock must take account of these farmers, for taken all together they own a very large proportion of the livestock in the country, and in the future they will own an increasingly larger proportion of it. One of the best ways of meeting this difficulty is by forming coöperative associations among the farmers themselves for the purpose of purchasing pure-bred sires. There is no reason why a given section of country should find it necessary to have a different breed of horses or cattle or swine on every farm, consequently the first step in the formation of such a company should be to agree upon the particular breed and type of bull or stallion which should be purchased. Thereafter under no circumstances should this decision be changed, but the farmers should endeavor to grade their herds up to the highest standard of that breed. A definite plan such as this would work an enormous improvement within a few years in the character of the livestock in a given rural district.

In passing it may be mentioned that it has often been found advisable and feasible to lend government aid to the improvement of livestock. This has been particularly the case in European countries where long decades of breeding have reduced types within a given district to a fair degree of uniformity, so that the government might follow a simple uniform practice in dealing with a given district. The success which such a policy may achieve is testified to by the popularity of the Percheron and French Coach horses, breeds to which the French government has lent considerable official encouragement. These are, however, details to be worked out in every section; the important point in every case is to follow up thoroughly and consistently for a considerable period of time whatever scheme is adopted.

CHAPTER XXXIX

CONCLUDING REMARKS

Although we have discussed a deal of material in this account of genetics in relation to animal breeding, it must be apparent to any student that we are still woefully lacking in detailed and precise knowledge. In fact, as yet we seldom have accurate information with respect to the most simple and easily determined matters, such as growth curves in the various breeds and races of livestock, comparative production curves, and the like, the obtaining of which is largely a matter of routine. Such data are not even genetic data, strictly, but they are so necessary for the application of genetics to animal breeding that genetics proper must almost mark time until they can be obtained. The necessity of having accurate standards of judgment obviously need not be debated before an intelligent audience.

Our dearth of detailed knowledge is particularly noticeable, however, in the field of genetics proper. It has been said—and there is much justification for the statement—that our knowledge of heredity is not secure with respect to any character until it has been found possible to analyze it and determine the factors which enter into it. If such a criterion then be applied to our knowledge of heredity in horses and cattle, for example, we have little cause to congratulate ourselves upon the extent of our accurate knowledge; for in either of these animals the number of factors accurately known could be counted on the fingers of both hands. It is a far call from such a state of affairs to that obtaining in *Drosophila ampelophila* in which knowledge has been derived concerning about 150 factors, many of which have been arranged in a systematic, coördinated scheme. Our knowledge is very meagre especially with respect to those factors which affect primarily economic characters in domestic animals, such as milk production in dairy cows, fertility, vigor, and like characters or character-complexes. Here we have a very good beginning in Pearl's analysis of winter egg production in domestic fowls; but compared with the amount of information yet to be gained we see how long is yet the road to be travelled. But this beginning which Pearl has given us is very encouraging; it leads us to feel confident that our knowledge of accurate details of heredity will be pushed further and further.

For after all in spite of our present dearth of detailed knowledge of heredity in domestic animals there is no real cause for discouragement. It is not yet two decades since the rediscovery of Mendel's law of heredity; and the most rapid progress has been made within the last five years. It is not, therefore, at all strange that we have not yet obtained extended data from experimental research; in fact, most of the Mendelian data we now have on the larger domestic animals is of the interpretive kind, that is, the conclusions have been drawn from records already in existence. Experimental research such as has been employed in the study of the inheritance of coat color in rodents, has not yet been carried out to determine the relations of the various coat colors and patterns in horses and cattle; the best that has been found possible thus far is the study of herdbook records and breeders' notes.

The Need of Research.—Students know too well how difficult it is to make due allowances for all the variable factors which may enter into a given body of data. Consequently, however simple the conditions may be, those conclusions which are based on records as crude as those of herd books and breeders' notes are subject to a great deal of uncertainty. Moreover, it is usually impossible under practical conditions to find matings which have been carried out in such a way as to give crucial tests of a given hypothesis of factor relations. We have emphasized this difficulty in the discussion of Mendelian inheritance in domestic animals, pointing out that very often alternative interpretations could be made of the crude data extant; interpretations which could be very easily subjected to a crucial test in the case of accurate scientific research. In the domestic animals, as in Drosophila, the ideal goal of genetic analysis should be that which determines accurately the mode of inheritance and expression of as many Mendelian factors as is possible. The task is difficult, but the increasing knowledge of heredity in lower forms will immensely simplify its execution.

The time and expense necessary for carrying out studies of heredity has often deterred investigators from attacking problems in higher animals because the possibility of economic application of the results has seemed to be remote or almost certainly nil. But this is not the point at issue, as may be clearly seen when the interrelations between factors are considered. Accurate determination, for example, of the various factors and factor interactions in the heredity of coat color in cattle would give a secure and definite basis from which to prosecute other investigations more intimately concerned with problems of economic importance. It is even highly justifiable to commend such investigations, because the problem is then first approached in its simplest form. There is grave question as to the advisability of plunging pell mell into difficult problems before the simpler ones have been solved, were it not for the fact that simultaneous attack may be made in such investigations both against the more obvious and the more obscure questions.

Since work of this kind requires relatively large funds and consecutive attention during many years, it is the kind of research which is eminently suited to the facilities provided by agricultural experiment stations. In the present state of knowledge in genetic enquiry, investigations in heredity to be of value must be planned and directed by carefully trained men such as should make up the research staff of experiment stations. Undoubtedly as the need for this type of research becomes felt more strongly, as it inevitably will when agricultural methods become more intensive, special facilities will be provided such as are particularly adapted to genetic research. We cannot well apply genetic principles to their full value before we have definite genetic knowledge.

The Service of Genetics.—At the present time genetics can without question render an important service to animal breeding, for excellent as may be the art of the skilled practical breeder it remains a regrettable fact that it is neither practised nor known by the great body of practical breeders in this country. The great fundamental conception of genetics that heredity is the primary guiding hand in determining the characteristics of the individual, whether physical or mental, has not become a part of the fund of knowledge of the general public. The firmly grounded belief of the geneticist that the phenomena of heredity have a definite knowable basis are still flouted by the less informed among our practical brethren, not only in speech but also in deed, for nothing is more pitiable than the blind hope manifested among some of them that something good may come out of their hit-or-miss methods of breeding. Superiority does not arise from inferiority in animal breeding; planless breeding operations are not less deplorable than lack of systematic action in any other department of rural activity.

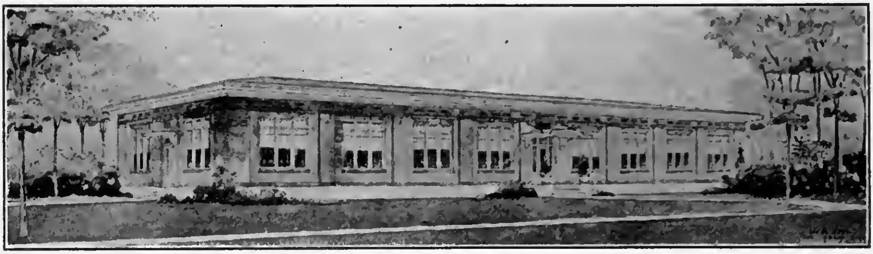


Fig. 238.—Laboratory devoted to genetic research at the University of Illinois.

It is here indeed more than in any other fashion that genetic instruction finds its justification. For as more and more men become familiar with the laws of heredity and by inference and example broaden the circle of those who begin to appreciate the significance of those laws, it must inevitably follow that general breeding practice will thereby be gradually raised. It is not possible for a geneticist, however broad his knowledge, to map out rules of procedure in breeding operations such that success must inevitably follow their application. Such procedure is not to be commended; it is not even scientific, by very nature. For intelligent application of the principles of genetics, which is the ideal of the scientific animal breeder, presupposes a knowledge of such principles; the service of the geneticist, therefore, should be to determine principles and to indicate insofar as may lie within his power the significance of these principles.

Fig. 239.—Genetics laboratory (for general course) College of Agriculture, University of California.

It is in this direction that the study of genetics is not only advisable but needful, for it provides as it were the framework to which the breeder may add the necessary empirical elements for the construction of his finished plan of procedure. And he will find as he becomes more and more familiar with that framework that it is not a mere indifferent edifice to which he may attach things here and there as convenience dictates, but that it is a coördinated and interrelated structure which provides definite places for different kinds of things, so that when they are fitted in their proper places they tend that much to add to the completeness and unity of the whole structure. It is a fortunate breeder who is able to approach his problems from such a point of view.

The Need of Other Knowledge.—Proficiency at any sort of game may be gained only by practising the game. No amount of reading and study of methods of play will suffice to make a good card player or a billiardist; it is required that the player be able to put the principles to effective use if he would achieve any measure of success. It is not far different in the practice of animal breeding. Genetics provides merely the principles of a game, the effective employment of those principles necessitates a thoroughly grounded knowledge of a wide range of matters pertaining to the technique of rearing, training, mating, and what not of the particular type of animal which is being bred. We might say somewhat enigmatically that successful animal breeding requires a knowledge both of *principles* and *principals.* He who has studied genetics has only begun the study of the broader subject of animal breeding. Ordinarily it would be a much safer procedure to entrust the future of a carefully built-up herd of pure-bred livestock to the sympathetic care of the herdsman trained in the old school rather than to the most thoroughly trained genetic investigator in the land.

For after all success in animal breeding depends very largely upon the ability of the breeder to build up in his mind an ideal type; and there is no more reason or assurance that such a type will arise full-formed in the mind of the breeder than that any other good thing may be obtained without effort. Here indeed is a rare opportunity for good sound judgment to work toward a definitely appointed end. For the ideal type of the breeder will in a sense be a composite of many types, in determining which the particular force of any one factor must be weighed with consummate skill. Thus to take a single illustration, that of the ideal type of beef Shorthorn, we may point out some of the types which must be welded so to speak into one. There is first the market type of beef cattle; broad, deep, built upon the plan of the parallelogram, carrying a maximum percentage of high priced cuts, and a minimum percentage of offal. In the second place we may consider the feeder's type of beef cattle. He desires an animal which will lay on flesh rapidly and economically. Consequently he looks for a bright and alert, but not overly active disposition, and a high degree of functional excellence in the digestive system and body in general, such that the animal will consume a maximum amount of food and convert it into flesh of the proper quality. Perhaps as a slight compensatory allowance here the feeder permits a slight increase in volume of digestive and other vital organs with a consequent increase in percentage of offal for the sake of more economical gains. In the third place we must consider the breeders' type of beef cattle. Here questions of the regularity of breeding, of the type of cow best suited for the production of young, of the ability of cows to provide sufficient nourishment for their offspring, of adaptability to the conditions of climate and to the other environmental features of the locality in which they are produced, and many other considerations enter in. Finally we have the ideal breed type to consider: the animal must possess those characters which distinguish Shorthorns as a breed from other beef breeds such as Aberdeen Angus, Galloway, or Hereford cattle; and very likely it will be necessary in order for it to meet with favor that it display those particular characteristics of the Shorthorn breed which mark it as belonging to some favorite family or strain. We have seen how difficult it is to deal with Mendelian experiments involving differences in five or six definite, allelomorphic pairs of factors; how much more difficult must it be to deal with all the variable considerations which enter into the discussion of the method of constructing an ideal beef type of Shorthorn cattle. And yet even in the face of all these requirements the results of intelligent, systematic breeding operations are surprising in excellence and uniformity of product. When we consider this fact we can only become more strongly convinced of the definite, knowable operation of the laws of heredity.

But these factors which enter into the determination of ideal types are largely considerations outside the pale of genetics proper. These are the matters which must be added to a knowledge of genetics in order to complete the equipment which would be at the command of the animal breeder. To this knowledge, also, must be added information bearing on the technique of managing breeding herds in order to realize the full returns which it should be possible to secure. This information will include a large and varied range of topics such as the methods of feeding breeding stock and of developing young stock, the determination of the proper number and use of service animals, methods of coping with disease of various kinds; a knowledge of methods and appliances by which the greatest possible use may be made of particularly excellent animals, such as by artificial insemination, and a thousand and one items to recount which would only make this discussion more tedious and uninteresting. But these elements are none the less essential to the equipment of the successful animal breeder.

So we come to the end of our account of genetic principles in animal breeding, realizing very keenly the limitations in our knowledge, and the inadequacy of the principles of genetics alone and unsupported to serve as a working equipment for the practical animal breeder. But we take a deal of courage and satisfaction out of the fact that a consideration of those principles has a proper and important part to play in animal breeding, first by the emphasis which it lays upon heredity as a factor in production, and secondly by the firm foundation of coördinated principles which it provides as a guide to procedure in breeding operations. It is necessary thus to emphasize the importance of heredity as a determining factor in production, because of the erroneous ideas which are held by the generality regarding the fact of heredity; it is wise to study genetics as a guide in breeding practice, because any knowledge which is reduced to a basis of known principle or is coördinated with principle is that much clearer of comprehension and more assured of intelligent application. But with all this the study of genetics has failed of its highest purpose, if it has not encouraged in the mind of the student the open attitude toward truth and the healthy skepticism of the true scientist. For after all problems of animal breeding are problems which should be approached in nothing less than a spirit of scientific research, problems of infinite complexity but of intense interest as well.

GLOSSARY

Aberrant.—Deviating from the normal range of variation of the group in which it is placed.

Aberrations (Chromosome).—Irregularities in chromosome distribution during mitosis or meiosis.

Acquired Character.—A modification of bodily structure or habit which is impressed on the organism in the course of the individual life.

Aleurone.—The protein granules found in the endosperm of ripe seeds. In maize the aleurone is confined to a thin layer adjacent to the pericarp.

Allelomorphs.—Factors occurring in the same locus in homologous chromosomes, and for this reason producing "contrasting" or "alternative" characters.

Allogamous.—Requiring two individuals to accomplish sexual reproduction; also applied to plants which are normally cross-fertilized even though capable of self-fertilization.

Amphimixis.—The mingling of hereditary units of two parents in sexual reproduction.

Antitoxin.—A substance, formed in the body of animals inoculated with certain bacteria, which has the power of neutralizing toxins formed by the corresponding organisms.

Atavism.—The appearance of grandparental characters in an individual; contrasted with reversion, which is the appearance of a more distant ancestral character.

Autosome.—Any other chromosome than the sex-chromosomes.

Autogamous.—Requiring only one individual to accomplish sexual reproduction; normally self-fertilized plants.

Biometry.—The branch of science dealing with the statistical investigation of organic differences.

Biotype.—A group of individuals all of which have the same genotype. Homozygous biotypes generally breed true but heterozygous biotypes do not.

Blastogenic.—Originating in the germ-plasm.

Bos.—A genus of hollow-horned ruminants having simple horns in both sexes, typical of the family Bovidæ and the sub-family Bovinæ, containing the oxen or cattle.

Breeding.—The art of improving plants and animals, or the experimental investigation of genetics by testing, hybridizing and selecting.

Bud Mutation.—A mutation occurring in the very early history of a bud such that a branch is produced which differs genetically from the remainder of the plant.

Bud Sport.—A branch, flower or fruit which differs genetically from the remainder of the plant.

Calycine Flower.—A peculiar hose-in-hose type of abnormality.

Capon.—A castrated male fowl.

Castration.—The act of removing the sexual glands.

Cell.—One of the independent protoplasmic bodies which build up an organic tissue.

Character.—One of the many details of structure, form, substance or function which make up an individual organism.

Chimera.—A mixture of tissues of different genetic constitution in the same part of a plant.

Chlorophyll.—The vegetable pigment which gives the characteristic color to ordinary green plants.

Chromatin.—The most permanent and characteristic constituent of the nucleus; so called on account of the readiness with which it becomes colored by certain dyes.

Chromomeres.—The chromatin granules, which are sometimes arranged like the beads on a necklace.

Chromosome.—A definite aggregation of chromomeres.

Cleistogamous Flowers.—Those in which development is arrested in the bud but which are fertile. The more perfect flowers of the same plant are often nearly or quite sterile. This peculiar dimorphism is known to occur in about 60 genera.

Clone.—A group of individuals produced from a single original individual by some process of asexual reproduction, such as division, budding, slipping, grafting, parthenogenesis (when unaccompanied by a reduction of the chromosomes), etc.

Contabescense.—An abortive condition of the stamens and of pollen; of very common occurrence in hybrid plants.

Crossing-over.—Exchange of chromatin material between homologous chromosomes.

Cross-over Gamete.—A gamete containing one or the other of a pair of homologous chromosomes which have interchanged parts by crossing-over.

Cytology.—The branch of biology which treats of cells, especially of their internal structure.

Cytoplasm.—That portion of the protoplasm of the cell outside the nucleus.

Dam.—A female parent, referring to mammals; generally with sire as the male parent.

Development.—The complete process of growth of an individual.

Differentiation.—The process of producing specific parts or substances from a general part or substance.

Dimorphic.—Comprising two distinct forms.

Diœcious Plants.—Those having the two different sexes on different plants, thus insuring cross-fertilization.

Diploid.—The number of chromosomes normally found in the somatic cells of a species; twice the gametic or haploid number.

Dominant.—Applied to one member of an allelomorphic pair, having the quality of manifesting itself wholly or partly to the exclusion of the other member.

Drosophila.—A genus of fruit flies, *D. ampelophila*— the pomace or fruit fly.

Embryogeny.—Early development of an egg leading to the formation of an embryo.

Embryology.—The science which treats of embryogeny.

Endosperm.—The substance stored in a seed adjacent to the embryo for its early nourishment.

Epistatic.—Applied to a factor or gene which conditions a certain character when present in a genotype which contains a factor or factors in other loci affecting the same character; for example, the factor *P* for purple aleurone in maize is epistatic to *R*, the factor for red aleurone; contrasted with hypostatic.

Equidæ.—The horse family.

Equus.—The typical genus of the family Equidæ.

Evolution.—The general name for the history of the steps by which any living being has derived the morphological and physiological characters which distinguish it.

Factor.—An independently inheritable element of the genotype by the presence of which some particular character in the organism is made possible; gene. Sometimes referred to as genetic factor or unit factor to avoid possible misinterpretation.

Fecundity.—The potential reproductive capacity of individuals; the ability to produce mature ova or sperm.

Feral.—Run wild, having escaped from domestication and reverted to a state of nature.

Fertility.—Ability to produce normal, living young; the opposite of sterility.

Fertilization.—The union of male and female sex cells.

Filly.—A female colt or foal. A young mare.

Fluctuations (Fluctuating Variations).—The slight differences normally found in organisms and attributed *either* to environmental influences or to recombinations of genetic factors.

Fetus.—An animal embryo in the later stages of development.

Forehand.—That part of the horse which is before the rider.

Gamete.—A mature male or female sex cell.

Gametogenesis.—The process of development of mature sex cells from the primordial germ tract.

Gene.—See factor.

Genetic Factor.—See factor.

Genotype.—The constitution of an organism with respect to the factors of which it is made up; the sum of all the genes of an organism.

Genus (pl. Genera).—In botany and zoology a classificatory group ranking next above the species, containing a group of species (sometimes a single species) possessing certain structural characters different from those of any others.

Germ.—In contrast with soma, the germ-plasm.

Germ Cells.—Cells specialized for sexual reproduction; the ova and spermatozoa in animals, the egg cells and pollen grains in plants.

Germ-plasm.—That part of the cell-protoplasm which is the material basis of heredity and is transferred from one generation to another.

Geotropic.—Turning or inclining toward the earth.

Graft-hybrid.—A shoot or plant produced by grafting one kind of plant upon another and whose characters are intermediate between the characters of the two components.

Graft-symbiont.—One member of a graft union.

Gynandromorph.—An animal in which one side exhibits female characters and the other side, male characters.

Haploid.—The number of chromosomes normally found in the gametes of an individual; one-half the somatic or diploid number.

Heifer.—A young cow that has not had a calf.

Hereditary-complex.—The total set of factors in any species conceived as a reaction system in which the factors display harmonious interrelations with one another.

Hermaphrodite.—Being of both sexes.

Heterosynapsis.—As applied to the sex-chromosomes, the pairing of an X- and a Y- or a W- and a Z-chromosome.

Heterotypic Division.—The meiotic or true reduction division by which homologous chromosomes are separated into different gametes.

Heterozygosis.—The condition of an organism due to the fact that it is a heterozygote; the state of being heterozygous; the extent to which an individual is heterozygous.

Heterozygote.—A heterozygous individual.

Heterozygous.—That condition of an individual in which any given genetic factor has been derived from only one of the two generating gametes. Both eggs and sperms produced by such an individual are typically of two kinds, half of them containing the factor in question, the rest lacking this factor; consequently the offspring of heterozygous individuals usually consist of a mixture of individuals some of which possess the corresponding character while others lack it.

Homosynapsis.—As applied to the sex-chromosomes, the pairing of two *X*- or two *W*-chromosomes.

Homozygosis.—The state of being homozygous; the extent to which an individual is homozygous.

Homozygote.—A homozygous individual.

Homozygous.—That condition of an individual in which any given genetic factor is doubly present, due usually to the fact that the two gametes which gave rise to this individual were alike with respect to the factor in question. Such an individual having been formed by the union of like gametes, in turn generally produces gametes of only one kind with respect to a given character, thus giving rise to offspring which are, in this regard, like the parents; in other words, homozygous individuals usually breed true.

Hormone.—A substance secreted or found in some organ or tissue and carried thence in the blood to another organ or tissue which it stimulates to functional activity or whose functions it inhibits.

Hybrid.—The offspring of animals or plants of different genotypes, varieties, species, or genera.

Hypertrophy.—An enlargement of a part of the body from excessive growth or multiplication of its elements.

Indigenous.—Native, not exotic.

Inter se.—Between or among themselves.

Interference.—Protection from coincident crossing-over of loci on either side of the point of crossing-over.

In utero.—In the uterus or womb.

Lethal.—Destructive of life.

Linkage.—That type of inheritance in which the factors tend to remain together in the general process of segregation; "gametic coupling" of the older terminology.

Locus (pl. loci).—A definite point or region in a chromosome at which is located a genetic factor or gene.

Lymantria.—A genus of moths.

Meiosis.—See reduction or heterotypic division.

Metabolism.—The sum of the chemical changes within the body, or within any single cell of the body, by which the protoplasm is either renewed or changed to perform special functions, or else disorganized and prepared for excretion.

Mitosis.—Indirect cell division, the characteristic method of multiplication of somatic cells, in which each chromosome is halved longitudinally, one-half passing to each daughter cell.

Monœcious Plants.—Those having both sexes in the same plant.

Morphology.—The branch of biology concerned with the outer form and internal structure (without regard necessarily to the functions) of animals and plants.

Multiple Allelomorphs.—Factors occupying the same locus of homologous chromosomes; the characters conditioned by such factors.

Mutant.—An individual of a genotypic character differing from that of its parent, or those of its parents, and not derived from them by a normal process of segregation or by crossing-over.

Mutation.—The result of a change in genotypic nature independently of normal segregation or of crossing-over; strictly an alteration in the fundamental nature of a genetic factor.

Non-cross-over Gamete.—A gamete containing a chromosome which has not been affected by crossing-over.

Non-disjunction.—The failure of the two members of a pair of homologous chromosomes to disjoin in the reduction division so that both pass into the same gamete.

Normal Allelomorphs.—The factors conditioning the characters of the wild or normal type of a species as contrasted with the factors which condition mutant characters.

Nucleoplasm.—The protoplasm in the nucleus.

Nucleus.—The more or less centrally situated cell organ containing the chromatin which has come to be known as the hereditary substance *par excellence.*

Ontogeny.—The development of the individual as opposed to phylogeny.

Ovules.—The macrosporangia of flowering plants; the female sex cells with the immediately surrounding parts; the future seeds.

Paramecium.—A ciliated protozoan.

Pedigree.—List of ancestors; genealogical tree.

Peloric Flowers.—Regular flowers borne on plants which normally have irregular flowers.

Pericarp.—In flowering plants the seed vessel or ripened ovary; in maize each seed is morphologically a fruit and the seed covering is termed pericarp.

Petiole.—Leaf stalk.

Phenotype.—The sum of the externally obvious characters of an individual or a group of individuals.

Phyletic.—Pertaining to ancestral species or groups.

Phylogeny.—The history of the evolution of a species or group; distinguished from ontogeny.

Phylloxera.—A genus of plant lice; usually of gall-making habits.

Phylum (pl. Phyla).—A primary division or sub-kingdom of the animal or vegetable kingdom.

Physiology.—The sum of scientific knowledge concerning the functions of living things.

Phytomer.—A plant-part or plant-unit; one of the structures or elements which, produced in a series, make up a plant of the higher grade. The ultimate similiar parts into which a plant may be analyzed are units consisting of an internode and a node with its leaves. Each unit may reproduce its like or the entire plant.

Polled.—Hornless.

Pollen.—The male sex cells of flowering plants.

Polydactylous.—Having extra fingers or toes.

Polyphyletic.—Derived from several phyla; having several different lines of descent.

Prepotent.—Able to impress individual characteristics upon offspring to a marked degree.

Probable Error.—An arbitrary term used to designate the amount that must be added to or subtracted from the observed value to obtain two limiting figures of which it may be said that there is an even chance that the true value lies within or without these limits.

Protein.—Complex organic substances containing nitrogen, *e. g.*, albumin or white of egg.

Pure Line.—A group of individuals derived solely by one or more self-fertilizations from a common homozygous ancestor. Sometimes erroneously applied to groups of individuals believed to be genotypically homogeneous (a homozygous biotype or a clone) without regard to their method of reproduction.

Quagga.—A zebra-like animal from South Africa. Named from the sound of its cry.

Recombination.—The uniting of parental factors in individuals of the second or later generations after a cross.

Reduction Division.—One of the last two divisions in gametogenesis, when homologous chromosomes are dissociated and pass into different gametes; the heterotypic division, meiosis, the mechanism of segregation.

Recessive.—The opposite of dominant.

Reciprocal Hybrids.—Hybrids the sexes of whose respective parents are reversed.

Regression.—In biometry, the avarage variation of one variable for a unit variation of a correlated variable.

Reversion.—The appearance of a distantly ancestral character in an individual, as the production of purple-flowered sweet peas by crossing two whites.

Scurs.—Abortive horns.

Segregation.—The process by which genetic factors become dissociated to different gametes by the mechanism of the reduction division.

Sex-chromosome.—The accessory chromosome which has come to be associated with one or the other sex, or one member of a pair of morphologically or physiologically distinct chromosomes which carry a factor or factors for sex.

Sex-linked.—Applied to factors located in the sex-chromosomes or to the characters conditioned by them.

Sex-ratio.—The proportion of males and females in a population.

Sire.—The male parent of a beast; generally with dam as the female parent.

Soma.—Body; especially in contrast with the germ or germ-plasm.

Somatic.—Pertaining to the body as contrasted with germinal which pertains to the germ cells.

Somatic Segregation.—Appearance of genetically diverse tissues in the same individual due usually to mutation in a somatic cell or, possibly, rarely to chromosome aberrations, or, in a few questionable cases, to some unknown cause.

Somatogenic.—Originating in the soma.

Somatogenesis.—See Development.

Species.—That which is specialized or differentiated recognizably from anything else of the same genus; collectively those individuals which differ specifically from all the other members of the genus and which do not differ from one another beyond the limits of (actual or assumed) individual diversity.

Spermatozoon (pl. Spermatozoa).—A mature male sex cell in animals.

Spindle.—The nuclear division figure.

Sterility.—Lack of ability to produce normal, living young; the opposite of fertility.

Stereochemistry.—A branch of chemistry which considers the spatial arrangement of the atoms composing a molecule.

Stirp.—As contrasted with body or soma, the germ or germ-plasm.

Strain.—A group of individuals within a variety which constantly differ in one or more characters from the variety type.

Synapsis.—Non-technically, the conjugation of maternal and paternal chromosomes preceding the reduction division.

Taxonomy.—The department of science which embodies the principles of classification, especially systematic classification of organisms.

Teratology.—The phase of morphology concerned with the naming and classification of abnormalities.

Tetraploid.—Quadruple the haploid or double the diploid number of chromosomes characteristic of the species.

Toxin.—A poison produced in animal tissues.

Triploid.—Treble the haploid or once and one-half times the diploid number of chromosomes characteristic of the species.

Unit Characters.—Those characters which behave as units in heredity.

Unit Factor.—See Factor.

Vaccine.—The modified virus of any specified disease introduced into the body by inoculation with a view to prevent or mitigate the disease or to confer immunity.

Variate.—A single magnitude determination of a character.

Variety.—A group of individuals within a species which constantly differ in one or more characters from the species type.

Vegetative Mutation.—A mutation occurring in any somatic cell.

Zygote.—A fertilized ovum or the product of the conjugation of gametes; hence, for brevity, an organism resulting from fertilization.

Zygotic.—Of or pertaining to a zygote.

Zygomorphic.—Irregular flowers which are divisible into similar halves in only one plane.

LIST OF LITERATURE CITED

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