HEREDITY

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INTRODUCTION

AMONGST many other problems of heredity, Professor Pearson and his pupils have investigated the inheritance of stature in man. They proceeded by measuring, in a great many instances, the height of a father and one or more of his sons. The average height of all the men measured was about five feet eight inches. It was found that if one considered by itself the group of fathers measuring about six feet, the average height of their sons was about five feet ten. Further, if one took by itself the group of fathers measuring five feet six, the average height of their sons was about five feet seven. That is, tall or short fathers tended to have tall or short sons respectively, but the resemblance as regards stature was only partial. In other words, variations in stature were inherited, but only to a limited extent.

Professor Johannsen of Copenhagen has carried out an investigation on similar lines with regard to the size of the seed in beans. Taking the seeds from a single plant, he separated the large from the small, and planted each lot separately. From the resulting plants, when ripe, he took the seeds and weighed them; he found no difference in the average size of the seed in the two lots. He repeated this experiment several times, and kept on selecting for several generations, but always with the same result. Variations in the size of seed, within a single race, were not inherited at all.

Darbishire has performed the experiment of crossing some ordinary white mice with others of the Japanese waltzing kind. The peculiarity of the latter is their habit of dancing or waltzing—*i.e.* continually turning round in one direction until they are exhausted. The cross-bred mice showed no inclination whatever to waltz—it appeared as though the habit were lost altogether. But these cross-bred mice were mated together and the next generation was reared. A large proportion again showed no tendency to " waltz," but a certain number were found to have the habit just as strongly developed as their original waltzing grand-parents. On counting it was found that there were about three ordinary mice to each one which " waltzed."

In the course of a number of experiments in the crossing of sweet-peas, Bateson and Punnett crossed two individuals of the " Emily Henderson " variety. This variety has always pure white flowers, and the only difference between the two plants was in the shape of the pollen-grains, one having round grains, and the other oval. The cross-bred plants from the two white-flowered parents had deep purple flowers. The seed from these plants was again sown, and in the next generation both white-flowered and purple-flowered plants were found. On counting it was found that there were about seven of the former to nine of the latter.

One might greatly multiply such examples, but those given will serve to show how remarkable, and how apparently contradictory, the facts of heredity are. It is the purpose of the science of heredity to explain all these facts according to one consistent theory.

The science of heredity is at once one of the oldest and one of the youngest of the sciences. The old Greek philosopher and doctor Hippocrates propounded a theory of heredity on something of the same lines as Darwin's, yet most of the writings before the time of Darwin, and a good deal of what has been written since, bear about the same relation to the science of heredity as do the writings of the alchemists to modern chemistry.

It is within the last twenty years or so that the real development of the subject, as an exact science, has begun; and it is not too much to say that more real progress has been made since 1900 than had been made altogether before. Much certainly remains to be discovered, and the answers to many important questions are still unknown or under dispute. It must also be admitted that the very rapidity of progress, especially as it has been made along different lines of investigation, has tended to throw our ideas into confusion. Yet many facts which appeared contradictory have proved to be consistent; order is appearing amid the jungle of facts.

It is a fact, which must have been observed very early in the history of humanity, that like tends to produce like. It may also be said that no two creatures are ever exactly alike. It is the object of the study of heredity to discover the nature and the causes both of the resemblances and of the differences between consecutive generations. The subject is attractive for its own sake, as other sciences are; it is also important by virtue of its bearing on the improvement of the races of economic plants and animals; and there is little doubt that the science will ultimately prove of service by showing the road to a betterment in the inborn characters of man himself.

CHAPTER I

WHY LIKE BEGETS LIKE

MANY attempts have been made to discover the underlying reason for the fact that like tends to beget like. The theories that have been proposed from time to time are both numerous and varied.

Let us first consider briefly what is known as to the actual mechanism by which an organism is produced by its parents. Let us see what is the actual physical connection between parent and offspring.

In sexual reproduction, which is almost universal amongst the higher animals and plants, the union of two elements is necessary before a new organism can be produced. In animals these elements are known as the ovum or egg, produced by the female, and the sperm, produced by the male. The sperm cell is an extraordinarily minute body; the actual size varies greatly, but in many animals it is less than a thousandth of an inch in breadth. The sperm is usually a motile, free swimming body, for all the world like an independent little animal. A common shape is that shown in Fig. 1, where the sperm is seen to have a round "head" and a long, whip-like "tail," the only use of which is for locomotion. Sperms are usually produced by the male animal literally in millions.

The ovum is usually very much larger than the sperm. It is often microscopic, but in birds, where the yolk is the actual ovum, it reaches a very considerable size. The large size of the ovum, however, is due to the fact that it has been stuffed with food for the use of the young animal. There is every reason to believe that the essential part of the egg is contained in the nucleus or germinal vesicle, which bears a very small

proportion to the size of the whole egg. In Fig. 1 is shown the structure of a typical small ovum, showing the germinal vesicle, and a large number of granular masses of yolk. Eggs are usually produced in relatively small numbers, yet certain animals, such as a number of the fishes, produce enormous numbers.

The sperms, having been brought into the neighbourhood of the egg, are, in some way which is not understood, attracted to it. They cluster round the outside of the ovum, and one of them pushes itself into the substance of the egg. One sperm only enters the egg,
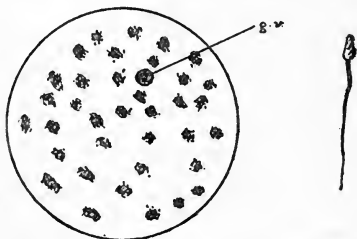

FIG. 1.—The Ovum and the Sperm.   *g.v.* The germinal vesicle or nucleus.

for immediately on the entry of the first, the outermost layer becomes so altered that the others cannot penetrate it. The head of the sperm, leaving its tail behind, gradually travels toward the germinal vesicle, and the two bodies fuse into one. This process is known as fertilisation, and the result is the fertilised egg.

The fertilised egg is endowed with a remarkable energy. It begins to absorb nourishment, either the yolk contained within itself or food obtained from the female parent. The original single cell divides and redivides rapidly, until a hollow ball of cells is formed. Then one-half of the ball is, as it were, pushed inside the other, so that a body like a double-walled cup

is produced. The edges of this cup gradually grow together until only a small opening remains, which is the rudimentary mouth of the new animal. Very soon the backbone begins to be sketched in, the head is moulded off, and the limbs commence to grow out. The whole process is so remarkable that it looks as though an invisible hand were at work, drawing out here, pinching there, and gradually moulding a complete little copy of the parent form.

It must indeed strike one as marvellous that all these possibilities of growth and development are hidden away in a speck of living jelly, several hundred times less in volume than a pin-head.

In plants, the bodies corresponding to the sperm and egg-cells are contained in the pollen-grains and ovules respectively. The structure of the reproductive bodies differs somewhat from what we have described, and the mechanism of fertilisation and the process of development are not the same as in animals. Yet the essential points of sexual reproduction are the same in the two classes of living things.

According to Darwin's theory of heredity, *Pangenesis,* each part of the body gave off minute buds or pangenes, which passed by means of the blood to the reproductive organs. Each egg-cell or sperm came to contain a set of these buds, representing all parts of the body—skin and hair, muscles, bones, heart, kidneys, and the rest. In development, all the elements which had been packed away were simply unfolded and the child therefore came to resemble its parents.

How many such buds would be necessary to give a fair sample, as it were, of such a complex organism as one of the higher animals, it is impossible to say. At any rate, the number would have to be enormous. But many male animals and plants produce thousands of millions of sperm cells in the course of their lives, so that, if Pangenesis were to afford us an explanation of heredity, we should have to suppose the giving off of enormous numbers of complete sets of pangenes.

This sketch of Darwin's theory will be sufficient to

show that it was inherently rather improbable. Darwin, cautious and thorough thinker as he was, saw this very clearly ; yet he was forced to some such theory by what he believed to be good evidence for the *inheritance of acquired characters*. By acquired characters we mean mutilations, modifications due to disease or to use or disuse of special organs.

It will be seen that if such characters are ever inherited, then we must assume some very intimate sort of connection between the various parts of the body and the reproductive organs—some such connection as Darwin assumed in his Pangenesis theory.

We shall return later to this subject ; it has been, perhaps, the most disputed question in the whole subject of heredity, and cannot be said to be yet settled. It is enough to say, in the meantime, that the belief in the inheritance of acquired characters was general in Darwin's time, but is held only by a minority of biologists to-day.

The theory of heredity which is most widely accepted at the present time, and which is, in fact, the only theory that is of much service in helping us to understand the facts, is the theory of *the continuity of the germ plasm*. The development of this main idea has been the great work of the German biologist Weismann. In Weismann's own words, the idea is that part of the germ plasm " contained in the parent egg-cell, is not used up in the construction of the body of the offspring, but is reserved unchanged for the formation of the germ cells of the following generation."

We may illustrate this diagrammatically, as in Fig. 2.

The germ cell G—a fertilised egg—divides into a number of cells, the group A, which constitute a new individual. The white circles may be taken to represent the cells of the specialised organs of the body, bones, muscles, skin, and so forth. The germ cells of the individual A are not formed from the body cells, but *are derived directly from the germ cells of the preceding generation*. The dark circles being taken to represent the germ cells, it will be seen that the line of descent is

from germ cell to germ cell, and that the body cells in each generation are regarded as an offshoot, and as having no function in reproduction beyond that of guarding and nourishing the germ cells.

The process of the setting apart of the germ cells at the commencement of development is not an imaginary one. In several instances it has been clearly distinguished under the microscope.

To endeavour to make this clearer, we may imagine a potter at work. He has a mass of clay ready kneaded by his helper, and from this he cuts off a piece sufficient for a vase. He moulds his vase, which is dried and burnt in the kiln, and can never be turned back into the original soft, plastic clay. But meantime his helper
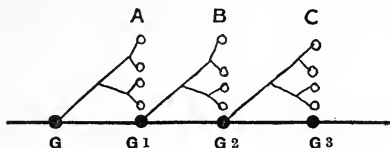

Fig. 2.

has been at work increasing the size of the original lump, so that he can immediately proceed to make another vase from it. The lump of clay, ever growing, ever about the same in character, is the germ plasm. The vases, which we can suppose to be turned out on the same pattern, are the successive generations. Only to make our metaphor complete, the lump of clay would require to be placed inside the developing vase, and to grow there. Besides, of course, the whole process goes on of itself.

The consequences of this theory are far-reaching. The connection between the characters of one generation and those of the next is not direct, but indirect. The son's characteristics do not depend directly on the father's, but indirectly in the sense that both depend

on the nature of the germ plasm from which both alike are formed. Similar material to start with, similar conditions in which to develop—therefore like begets like.

The body simply guards and nourishes the germ plasm. Hence (if the theory of germinal continuity be correct) it appears inconceivable that modifications—adaptions of the body to outside conditions, the effects of education or of the use or disuse of parts—should be inherited. By this we do not wish to imply that nothing can affect the nature of the germ plasm. We know, on the contrary, that many things can. But the effect of any condition on the body cells will not be reproduced, in any representative manner, through the germ plasm.

How far these deductions from the theory of germinal continuity agree with the observed facts of heredity, will be discussed in the following chapters.

CHAPTER II

VARIATION

IF it were an absolute fact that like begets like, instead of a general tendency, it is apparent that there would be no science of heredity at all. All the individuals of a race would be identical in type, and heredity would offer no problem except that of accounting for this identity by some satisfactory theory.

But it is a trite observation, which we need not linger to enlarge upon, that no two things in nature are ever exactly alike. Before entering into the question of how or to what extent these differences are inherited, it is necessary that we should gain some insight into their nature and causes.

In this connection, our first task must be to find some method of describing accurately and briefly such variations as are found. In certain cases this is a very easy matter. Suppose, for instance, that we wished to describe the variation in colour in a certain breed of horses. All that we have to do is to count the number of bays, blacks, greys, &c., occurring in a group of individuals taken at random, and to state the numbers of the respective colours. In this case we are dealing with material which is at once separable into definite natural groups. The colour does not vary by minute stages from black to white, but the variation is, as we say, *discontinuous*.

With regard to a great many characters, however, variation is *continuous*. As regards stature, for instance, men are not separable into so many definite types, but there is a fairly regular gradation in size, from the giant to the dwarf. How are we to measure and represent variation of this kind?

Having first obtained a number of measurements, we proceed to classify the individuals by arranging them in arbitrary groups. We may, for instance, group together all men between five feet six and five feet seven, between five feet seven and five feet eight, and so on. It is desirable to make a considerable number of groups, about ten or a dozen at least, and it would obviously be a roundabout and unsatisfactory method of describing variation merely to state the percentage of individuals falling into each.

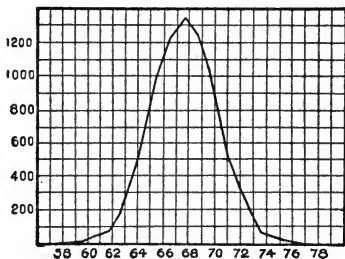Such continuous variability can be well expressed

FIG. 3.

graphically. In order to do this we set off along a base line a number of points to represent, say, the different height classes into which we have separated a number of men measured. We then measure vertically distances to represent the number of men falling into each class.

In Fig. 3 this has been done with regard to measurements of 8585 British men, the vertical lines representing differences of one inch in stature, and the horizontal lines hundreds of individuals.

It will be seen that the class which includes men between 67 and 68 inches is the most numerous, there being over 1300 individuals in it. The numbers in the

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several classes fall off on either side of this central one, and on the whole very symmetrically on the two sides. This falling off of numbers is moderately fast at first, becomes very rapid in the middle portion of each side, and less rapid again towards the base. This curve expresses mathematically the ordinarily observed fact that a large proportion of men are near the average
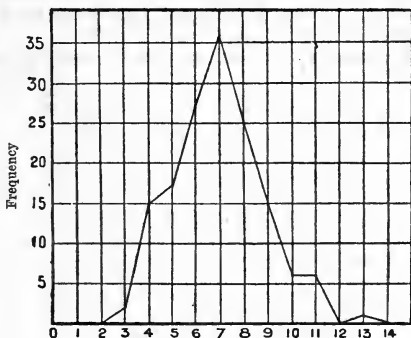

Fig. 4.—Number of Heads.

height, those differing largely from the average being relatively few.

Variability with regard to many of the attributes of living things gives a curve of the same type as that shown in Fig. 3.

But this form of curve expresses also the variability in results that are, as we say, due to "sheer chance," such as the variation in the number of "heads" or "tails" when a number of coins are tossed several successive times. In an actual experiment [1] where fourteen coins were tossed 150 times, the results were obtained which are shown in Fig. 4.

[1] Taken from Elderton, *A Primer of Statistics*, p. 11.

Seven heads was the commonest result, eight and six were less common, and so on, until we reach the classes 0, 1, 12, and 14, which do not occur at all. Our curve in this case is much more irregular than in the previous one, the reason being that in this case we are dealing with a very much smaller number of results, viz. 150, instead of over 8000.

Both of these curves approach, as will be seen by comparison with the ideal type shown in Fig. 5, which is known as the normal curve of variability.

We should get an extremely close approximation to this ideal type if, say, we were to toss a lot of a hundred coins ten thousand times, and plot the result. It is the curve which expresses "probability" in a result which depends on "sheer chance" or on a multitude of small and independent causes, and variability in many characters of living organisms is of this type.

FIG. 5.—The Normal Variability Curve.

The appearance of a giant may be compared to a tossing of ten coins in which all turn up heads. The extreme stature is the result of the many independent factors influencing stature all *happening* to act in one direction, just as the extreme result in tossing is due to the coins having all happened to fall on the same side.

Occasionally, however, variability follows different rules. If, for instance, we were to count the number of "petals" on a series of marsh-marigold flowers, we should find that the commonest number was five, and that there were frequently six or seven, and occasionally eight, but never less than five. The curve representing such variability would therefore be of a quite one-sided type, as is shown in Fig. 6.

Such extreme cases are comparatively rare, but a certain departure from symmetry, or *skewness* as it is

called, is fairly common, and mathematical expressions have been invented to measure its amount.

Sometimes, too, variability curves show two or more distinct summits, which generally indicates that the group of organisms in question is separating into two or more distinct types.

The form of the variability curve, then, gives us a good indication of the *kind* of variability that occurs. But it would evidently be desirable to have some convenient measure of the *amount* of variability.

We might, for example, state the full range of variation. We might say that, in the case quoted before, the stature of the men measured varied between fifty-eight and seventy-seven inches. This, however, would be an unsatisfactory expression of the amount of variability, since it is very much a matter of chance whether the extreme types occur or not.
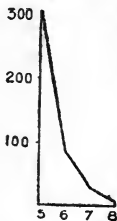
What is wanted is some figure which would be a sort of average of all the individual differences from the mean. It seems somewhat paradoxical at first sight to speak of the average deviation from the mean or general average, but on consideration it will be evident that such an expression may easily be determined. In doing this, one does not consider the differences from the mean as plus and minus, but proceeds simply to add them all together, and to take the average.

This may be made clearer by means of an example. In an actual case,[1] the lengths of 185 nuts were measured, and the measurements arranged in groups as follows. The lengths are given in millimetres, and each class includes all individuals falling within two millimetres of the figure given. Thus the "42" class includes all that fall between 40 and 44.

Length	. . . . .	30	34	38	42	46	50	54	58
Number of nuts	. .	2	7	28	59	49	33	6	1

FIG. 6.

[1] From Elderton, *A Primer of Statistics*, p. 23.

The average length of all the nuts is very nearly 44. In order to determine the average deviation we should have to find the value of the series 2 (44—30)+7 (44—34)+28, (44—38)+59, (44—42)+49, (46—44)+33 (50—44)+6, (54—44)+1, (58—44), and divide the total by 185.

Now, in practice, the *average* deviation is not found to be the most convenient expression, a somewhat different function, known as the *standard deviation*, being more useful. The method of determining this differs from that just given, in that one *squares* the deviation in each case, and after dividing the total of the products by the number of individuals, one extracts the square root of the answer.

Our case would be worked out as follows :—

$$(44-30)^2 = 14^2 = 196 \times 2 = 392$$
$$(44-34)^2 = 10^2 = 100 \times 7 = 700$$
$$(44-38)^2 = 6^2 = 36 \times 28 = 1008$$
$$(44-42)^2 = 2^2 = 4 \times 59 = 236$$
$$(46-44)^2 = 2^2 = 4 \times 49 = 196$$
$$(50-44)^2 = 6^2 = 36 \times 33 = 1188$$
$$(54-44)^2 = 10^2 = 100 \times 6 = 600$$
$$(58-44)^2 = 14^2 = 196 \times 1 = 196$$

Total, 4516

$$\frac{4516}{185} = 24\cdot4; \quad \sqrt{24\cdot4} = \text{about } 4\cdot9.$$

4·9 millimetres, then, is the standard deviation of the lot of nuts measured, with regard to length. And this is a convenient measure of the amount of variation with regard to this character.

In order to obtain comparative figures with regard to different characters, it is usual to express the standard deviation as a percentage of the mean or average. This gives what is known as the *coefficient of variation*. In our case, 4·9 expressed as a percentage of the average, 44, gives a coefficient of variation of about 11 per cent.

If, then, we are in a position to give the mean value of a character, to state the type of curve which the variation follows, and to give the standard deviation or the coefficient of variation we have described the

variation completely, and should be able to compare it with that occurring with regard to other characters.

The mathematical study of variation may perhaps seem rather tedious, and it often appears to have little connection with the real living things with which it deals. But it is of considerable value in the elucidation of some of the problems of heredity with which we shall have to deal.

CHAPTER III

THE NATURE AND CAUSES OF VARIATION

IN the last chapter we have endeavoured to explain shortly the statistical method of dealing with variation. It will be evident that we have considered such differences as occur between the individuals of a race only *in the mass*. We have not attempted to distinguish between the various kinds of differences, or the various groups of causes which we believe to operate in producing them. It is the object of the present chapter to analyse the "sum total of observed differences," and to discuss, as far as possible, the causes of variation.

In the first place we must make a sharp distinction, at least theoretically, between an inborn variation and a modification. Modifications, or "acquired characters," are usually described as the abiding effects of external conditions on the body of an organism; whereas inborn variations are due to changes in the germ plasm. But it is necessary to proceed carefully in considering what these definitions mean. For it is impossible to consider any organism apart from the conditions under which it lives—apart, as we say, from its environment. The inborn characters are expressed only under certain conditions of environment, and acquired characters can appear only when the organism possesses certain inborn tendencies to respond to outside conditions. Thus in a certain sense every character is both inborn and acquired.

But this does not affect the distinction. Given the normal conditions of life within a particular race, the organism would show only its inborn characters. Given

conditions more or less abnormal, such as deficient food, exceptional exercise of a particular member, disease, mutilation, &c., acquired characters would be produced.

If we could take a pair of identical twins, and separate them at birth, giving the one fresh air, abundant food and exercise and education, and rearing the other amid the unhealthy and degrading conditions of our slums, the differences, which would certainly be enormous, would be altogether modification differences. If, on the other hand, we could take two children of different parentage, and rear them under exactly the same conditions, the differences between the two would be altogether inborn.

In practice it is not always possible to distinguish inborn from acquired characters, even when we know fully the conditions under which the organism has lived. But theoretically the distinction between what is " born " and what " made," is absolute.

We may now turn to the inborn variations and endeavour to see how they arise. How does an organism come to differ from its parents, or from the mean of its parents, if it has two, with regard to its inborn characters ?

It seems certain that the great majority of inborn differences between parent and offspring are due simply to new combinations of previously existing characters. It is easy to see that with sexual reproduction, where two parents are involved in the production of the offspring, there is a continual mixing of different germ plasms, and thus almost infinite chances of new combinations.

By way of illustration, we may suppose four sacks of marbles of different colours, say white, black, red, and yellow respectively, to represent the respective germ plasms of four individuals. By mixing the black with the white and the yellow with the red, we get something corresponding to two new germ plasms. If now we take random samples from each lot, say half-a-dozen at a time, and mix the sample from the one lot

with that from another, we will get what corresponds to a new generation. The individuals of this generation will obviously differ from either of their parents; but what is more, they will differ amongst themselves, for some may contain three whites, others four or five, or two, and so on.

This is something like what we conceive to be going on in heredity. We must not compare bi-parental inheritance to an intimate blend of two substances, which would cause any sample of the mixture to be the same as any other sample; for we know that the mechanism of heredity is not of this nature. The mechanism gives large opportunity for different combinations to result from the mating of the same two parents. We shall consider later the laws according to which these re-combinations occur.

In the above example we supposed no new kinds of marbles. Only the combinations of the different colours were new. In heredity it is believed that most inborn variations are due to re-combinations of previously existing characters—that most of our new houses are built of old bricks. It may well be that Shakespeare or Darwin, Goethe or Napoleon, were nothing more than very happy combinations of the traits of their ancestors. Goethe himself recognised this when he wrote the well-known lines :—

> "Vom Vater hab' ich die Statur
> Des Lebens ernstes Führen,
> Vom Mutterchen die Frohnatur
> Und Lust zu fabulieren."[1]

But before we can have new combinations we must start with actual differences. Our experiment with the marbles would have shown nothing, if all the marbles had been white. How do the real differences arise? There are occasions in which something manifestly

[1] "From my father I inherit my stature
And earnest conduct of life,
From my mother my cheerful disposition
And my love for the romantic."

new does make its appearance. The sudden appearance of a novelty is what Darwin called a "single variation," and what is, in modern phraseology, called a mutation. It will be well to give one or two historical instances of mutations.

In this connection we cannot do better than quote Huxley's account of the appearance of the Ancon or otter breed of sheep. He says: "It appears that one Seth Wright, the proprietor of a farm on the banks of the Charles River in Massachusetts, possessed a flock of fifteen ewes and a ram of the ordinary kind. In the year 1791, one of the ewes presented her owner with a male lamb, differing, for no assignable reason, from its parents by a proportionally short body and short, bandy legs, whence it was unable to emulate its relatives in those sportive leaps over the neighbour's fences in which they were in the habit of indulging, much to the good farmer's vexation. . . . The variety appears to have arisen in full force, and, as it were, *per saltum ;* a wide and definite difference appearing at once between the Ancon ram and the ordinary sheep. It is not possible to point out any obvious reason for the appearance of the variety—to use a conveniently erroneous phrase, the variation arose spontaneously." The Ancon ram was retained and used for breeding, and it is interesting to note that its offspring were "either pure Ancons or pure ordinary sheep." The bandy-legged variety of sheep did not prove valuable, and has long ago become extinct, but the history of its origin is interesting.

The oldest recorded mutation occurred in the rather common garden plant, the greater celandine. In 1590, an apothecary in Heidelberg had some plants of celandine growing in his garden, when there appeared amongst the ordinary specimens a peculiar new form, which had its leaves divided into very narrow lobes, and its petals also cut or lacinated. The cut-leaved celandine breeds true from seed and is now widely grown as a garden flower, but all the specimens are descended from the one original plant which arose unexpectedly as a "sport."

The importance of mutations has been emphasised by Professor de Vries of Amsterdam, and he has made a special study of the subject. In the course of much experimental work he was fortunate enough to find a plant which was, as it were, producing mutations right and left. This was the plant known as Lamarck's Evening Primrose, which had been accidentally introduced into Holland from America. De Vries found the plant growing in a deserted potato-field in 1886, and the following year he discovered two peculiar forms, a smooth-leaved form and a type with a peculiarly short style. De Vries removed stocks of these different types to the botanical garden at Amsterdam, and there proceeded to grow enormous numbers of seedlings. Amongst these a large number of new mutations were found—a giant and a dwarf, a form with red-nerved leaves, another with very broad leaves, and several others. Altogether ten perfectly distinct new types were discovered, all but one of which bred true from seed. Some of these mutations were produced many times, others only very rarely.

These examples will serve to show what we mean by the term *mutation*. We have given a few particular instances, but it must not be imagined that only a limited number of cases are known. A great number of mutations have been described, and many of our varieties of cultivated plants and domestic animals have undoubtedly arisen in this way.

It will readily be understood that only the appearance of very marked novelties will tend to be recorded in the ordinary course of events. Small changes will tend to pass unnoticed, and when they occur in conjunction with a considerable amount of other variation they may be indistinguishable even to the trained observer. But it is the modern view of variation that all real changes in the nature of the germ plasm are of the same kind. Whether they be large and striking or minute and hardly perceptible, the changes are all of the nature of mutations—sharp and definite steps from one condition to another. Moreover, it is believed

that actual changes in the nature of the germ plasm are comparatively rare. They are the exception and not the rule in heredity.

It is impossible in our small space to discuss all the reasons on which this idea is based, but some of them will emerge in the sequel.

This conception of variation is very different from that formed by Darwin, who studied the subject very thoroughly. Darwin believed that inborn variation was the rule; that the characters of a species were in a state of flux, so that new variations in one direction or the other could be produced merely by selecting in those directions. One species was formed from another by the accumulation of minute indefinite tendencies in one direction. Darwin emphasised the slowness of the process of change in living things; *Natura non fecit saltum* (" Nature does not leap ") was a favourite aphorism of his. The process of change is no doubt slow in the mass: but we have lately come to the opinion that nature does leap—in fact, that it is only by leaps that change can occur. The slowness of evolution, then, is due to the fact that the leaps are seldom and small.

It is perhaps necessary to say that mutations may be either progressive or retrogressive. The change may be a gain of a new character, but is perhaps oftener a loss of a character which had been gained previously in the history of the race.

Any variation in which a characteristic of a remote ancestor recurs is termed a *reversion*. Certain reversions are due to special cases of recombination, which will be discussed later. But some reversions at least are retrogressive mutations.

As regards the causes of mutations it must be admitted that we are still in almost complete ignorance. We have had enough of speculation on the matter, but the cases in which we can point to any definite cause are extremely few. Even when a connection has been observed between a certain condition and the occurrence of a mutation, it has been impossible to trace the chain of causes connecting the two. This is probably due to

our ignorance of the structure and nature of the germ plasm. Chemists are still far from being able to tell us what living substance is, and until we know this, we shall probably never find out how changes in the germ plasm are brought about.

Quite recently certain investigators have succeeded in producing mutations at will. The American experimenter Tower has produced a number of new types of a certain beetle by subjecting the creatures or their eggs to exceptional conditions of temperature and the like. Macdougall, another American investigator, has caused mutations in plants by injecting chemicals into the seed-cup at the time of the formation of the seeds. More experiments, however, will require to be carried out before any general statement on this subject can be made.

Before concluding this chapter we may discuss briefly two of the disputed questions of heredity.

The first of these is *Telegony*, which is described as the supposed influence on the progeny of a female of a sire with which she had previously been mated. If, for instance, a pure-bred bitch is accidentally mated with a mongrel, it is said that she is spoiled for further breeding. That is, her future offspring by a male of her own breed will tend to partake of the mongrel character. This belief is widespread among practical breeders. For instance, many sheep-breeders' societies have a rule to the effect that a ewe which has been crossed with a ram of a different breed can no longer be considered pure bred, and none of her subsequent progeny can be registered. As regards the explanation of telegony, if it be a fact, it is supposed that the young developing animal exerts some subtle influence on the constitution of its dam. But the mechanism of this influence we cannot even imagine.

The classical example of telegony is that of Lord Morton's mare, which was fully described by Darwin. The mare was mated with a quagga and bore a colt. Afterwards she was mated with a black Arab stallion and bore two colts in succession showing distinct stripe markings.

But further very careful experiments have failed to produce any evidence whatever of telegony. Ewart carried out very extensive experiments with zebras and horses, and obtained no positive results. Pearson has investigated the matter statistically and has also obtained purely negative evidence. One is naturally chary of condemning a belief which is widely held by practical men, but in the total absence of trustworthy cases, one must conclude that telegony is probably a myth.

The second subject is that of maternal impressions. There is a common belief that anything which very strongly affects the imagination of a pregnant mother may have a visible effect on the body of the offspring. This belief is exceedingly old, for we have the case of Jacob setting up peeled wands in front of his cattle, in order to increase the number of speckled cattle, which he was to receive. A similar practice is said to have been followed by certain cattle-breeders in comparatively modern times. An instance is quoted of a pregnant woman having been frightened by an adder, with the result that her child, when born, had a birthmark on its back suggesting the form of a snake.

But, again, it must be said that a few such cases, which may be partly imaginary, and may, when they are real, be mere coincidences, prove nothing; and that carefully planned experiments have always failed to bring forth positive evidence. As regards mental characters, it is perhaps remotely possible that the mother might be able to exert some hypnotic influence on the mind of the unborn child. But the evidence at present justifies no position but that of complete scepticism.

CHAPTER IV

THE INHERITANCE OF ACQUIRED CHARACTERS

As has already been indicated, the question as to the possibility of the inheritance of acquired characters has been, and is, one of the most stubbornly fought in the whole field of biology. This is in part due to the great difficulty of the question itself, and in part to its importance both in practical breeding and in its bearing on our whole theory of heredity.

It is safe to say that at least half the discussion which has taken place on this subject has been a mere matter of words. All sorts of misunderstandings have arisen regarding the real question at issue; and the term "acquired character" itself has been too often used to indicate just whatever a particular writer chose.

We must then, in the first place, endeavour to understand clearly what we mean by an acquired character; but, meantime, in case we should begin to think that there is no real question under dispute, it may be well to state one or two cases which bring out the real difference of opinion.

Suppose that a racehorse is put to stud before having been trained for racing, and begets a number of offspring. The next year he is trained and wins a number of races. The following year he is again put to stud, and mated with the same lot of mares as before. Will the second group of offspring tend to be better racehorses than the first? In other words, will the fact that the racing ability has been developed have anything to do with the possibilities of speed in the offspring? One camp of biologists says "yes," the other says "no."

Herbert Spencer, in the course of a discussion of this subject, quoted the case of his own hands, which were distinctly under the average size. He said, "My father and grandfather were schoolmasters, and their hands were never developed by labour. Therefore I also have small hands." Was this the real reason? Or would his hands have been equally small if his father had been a labourer? Here again we have the definite opposition of opinion.—It has been said that "it takes three generations of idleness to make a pretty hand." Is this an actual fact? Could we distinguish the hand of the aristocrat from that of the navvie's son, provided that neither had himself engaged in physical toil?

To return to the business of defining what we mean by an acquired character, we find this to be no easy matter. It is scarcely worth while to attempt a formal definition, because this involves us in such a tangle of qualifying phrases that it fails to leave us with any clear or definite idea. We shall try, however, to explain what is meant by the term in the course of a few paragraphs.

In the first place, an acquired character is one which is acquired *during the lifetime of the individual*. We can, in a certain sense, speak of a character which has been acquired by a race. For instance, we may say that the domestic fowl has acquired the character of laying more eggs than the wild jungle fowl from which it has sprung. But this has nothing to do with acquired characters in the sense in which the term is used scientifically. One of the commonest misunderstandings of the question might be exemplified by such a statement as that "acquired characters must be inherited, otherwise the special characters of our modern breeds of poultry, which have been acquired through selection, would not be inherited, whereas they are so undoubtedly." This statement involves a loose usage of words. An acquired character is not merely a character which has been acquired. The term is used in a special scientific sense, and we must adhere to this usage if we are to understand each other. Only such characters,

then, are "acquired" as actually make their appearance in the individual lifetime.

Secondly, before we can describe anything as an acquired character, we must be able to point to something more or less abnormal in the environment or habits of the individual which has produced the modification. Suppose, for example, that a person becomes grey-haired at an abnormally early age, and that his children afterwards show the same tendency. This in itself would be no evidence for the inheritance of acquired characters, since the tendency to turn grey at an early age might well have been an inborn variation. But if we could point to a definite inducing cause for the condition, such as a severe illness, its reappearance in the next generation would be either a case of the inheritance of acquired characters, or a very remarkable coincidence.

Thirdly, an acquired character is a change produced on the *body* of an organism, and not directly on its germ plasm. This is the most difficult point of all to grasp, and it is extremely important. Tower has proved that very considerable changes can be induced in a race of beetles by subjecting them to unusual temperatures, and that these changes are inherited. But the changed temperature did not affect the body of the adult beetle itself ; the action was directly on the germ plasm. In this case we are dealing with an induced inborn variation, and not with an acquired character.

It is readily conceivable, however, that certain causes, acting on the body, may produce modifications, and at the same time may produce variations in the germ plasm. But in order to prove the inheritance of acquired characters, we should require to show that the change in the germ plasm actually specifically represents the body modification. If a man is a drunkard, his germ cells may become poisoned and his children be weaklings. But in order to prove the inheritance of acquired characters, we should require to show a reappearance in the offspring of the father's ruined

digestion and red nose. The real question is whether there is an intimate connection between the various parts of the body and the germ plasm; whether a change produced by an outside agency on any particular organ comes to be specifically represented in the germ plasm.

We must now proceed to consider the arguments for and against the inheritance of acquired characters.

In the first place, it is necessary to note that no one is of the belief that acquired characters are always inherited; nothing is more easily proved than that the majority are not. If all acquired characters were inherited, even to a very limited extent, our fox-terriers and hackney horses would have become short-tailed, the foot of the Chinese lady would remain small without artificial devices to keep it so, and children in civilised countries would develop ability to read, write, and speak without any education whatever. Nothing would be easier than to accumulate instances of the non-inheritance of modifications. But all negative evidence must go for nothing if even a few cases to the contrary can be proved. Let us examine some of the positive evidence, and see whether or not it can be regarded as indisputable proof.

Numerous instances have been given of the apparent inheritance of mutilations and the like. A case is quoted of a cow which lost one of its horns by ulceration : it had afterwards three calves which showed, " on the same side of the head, no true horn, but a small nucleus of bone hanging to the skin."

Professor Haeckel quotes a case of a bull having had its tail caught by the slamming of a byre door and squeezed off. The bull subsequently produced tailless calves.

By far the most important evidence for the inheritance of the effects of mutilations is furnished by the experiments of Dr. Brown-Sequard on guinea-pigs. In these experiments operations were performed on the spinal cord and nerves of many individuals. In certain cases these operations were followed by a

peculiar condition resembling epilepsy, and this condition appeared, in some few cases, in the offspring. In one of the most striking cases the sciatic nerve had been cut. The creatures of course lost sensation in their hind limbs, with the result that many of them gnawed off several of their hind toes. From these a small proportion of offspring were obtained which lacked several of their hind toes, or sometimes their whole hind feet.

Instances could be considerably multiplied, and a well-marshalled array of such cases seems difficult to explain away. Nevertheless, when positive results are obtained only in a small percentage of cases, it is necessary that we should look carefully for other possible explanations, and the inheritance of acquired characters is proved only when such other causes are excluded.

The cow with the ulcerated horn may well have had a naturally imperfect horn, which was readily attacked by disease, and the imperfection may have increased by an inborn variation in the offspring.

Brown-Sequard's conclusions, too, are open to criticism. The operations by which epilepsy was produced were very severe in their effects on the nervous system and whole constitution of the animals, with the result that few perfect young were produced. Many of the young were classed as generally feeble, many showed special defects in no way suggesting epilepsy, and a few were epileptic. The appearance of these few amongst a large number of imperfect offspring can hardly be regarded as evidence that the epilepsy, as such, was inherited. In the other case quoted the explanation has been suggested that the toes of the young guinea-pigs were actually perfect at birth, but were afterwards gnawed off by their dams. It is known that rodents occasionally show a tendency to gnaw the tails or feet of their young, and it seems that this might well occur, especially as the habit had been previously somewhat developed.

Again, a number of supposed cases of the inherit-

ance of modifications are doubtless mere coincidences. It is a rather unconvincing explanation of an individual case, perhaps, to call it a coincidence; but such coincidences must occasionally occur, and the probability is that a large proportion of them are recorded.

It must be said, then, that evidence of the inheritance of mutilations is extremely scanty and unsatisfactory. The extreme rarity of supposed cases, in the first place, must make one somewhat sceptical. If modification inheritance were possible we should expect it to occur in a fair percentage of cases. Of alleged cases, many will not bear close inspection, and in most there is some other explanation at least possible. It seems fair to conclude that such few cases as are not open to objection may probably be coincidences.

A large group of modifications may be classed as the effects of use and disuse of organs, and it is perhaps with regard to the possibility of the inheritance of such effects that the greater part of the whole controversy has arisen. Many biologists are of the opinion that mutilations, having often but a very slight effect on the general system, will not as a rule be inherited. But the effects of use and disuse, they claim, burrow deep into the whole organisation, and are thus much more likely to affect the germ cells.

In the process of evolution, many things have occurred which are easy of explanation if we assume that the effects of use and disuse are inherited, and some of them are hard to explain on any other hypothesis.

The hind limbs of the whale long ago ceased to be used, and they have now all but disappeared. The wings of the ostrich have ceased to be used for flight, and they have become greatly reduced. The remote ancestor of our present-day horse began to walk on the tips of his toes, with the result that the middle toe of the five began to bear most of the weight. Since then the middle toe has become very much larger, and the others have disappeared except for two small rudiments.

Generations of giraffes have stretched their necks to reach the foliage of trees, and the neck of the giraffe is grown to a prodigious length. The antelope has been accustomed for centuries to flee from beasts of prey, and has developed in the direction of extreme speed.

Lamarck's theory of evolution was to the effect that races were developed by the accumulation of the effects of use and disuse. And certainly it seems the obvious explanation of the dwindling of the whale's hind limbs, to say that they have become gradually smaller *through disuse*, or to say that the neck of the giraffe has become long through its special use, which involves its being stretched continually.

But we have no proof whatever that these explanations are the correct ones. Moreover, it is possible to explain all the instances given above without assuming the inheritance of modifications. According to Darwin's theory of Natural Selection, the giraffe's neck has become long because through generations the longer-necked specimens have been able to reach more leaves than their shorter-necked fellows, and consequently have been able to live through times of scarcity while the others starved. The longer-necked specimens have continually been preserved by nature, and the race has become long-necked.

Similarly, the fleet antelope escapes from the lion, while his slightly more slow-footed brother is caught and eaten, and the race thereby becomes swifter of foot.

As regards the dwindling of disused members, the explanation of the modern Darwinian is perhaps less convincing. But Darwin says that the wings of the ostrich, for instance, became useless when the ostrich took to running. Hence those individuals which wasted least food and energy in wing-building had the more for leg-building. They had thus the advantage over their stronger-winged fellows and tended to be preserved.

Yet in certain cases such an explanation seems undeniably far-fetched. Take the case of the eyes of cave

fishes. Fishes are found in numerous deep caves, where there is absolutely no light. It is often possible to tell, from geological indications, about how many thousands or tens of thousands of years any particular cave has existed. The eyes of these fishes are invariably more or less reduced, in some cases being nothing more than mere rudimentary and useless specks. It is assumed, of course, that the fishes had normal eyes at the time of their imprisonment. It is found that the degree of degeneration of the eyes always corresponds pretty closely with the length of time that the fishes have been in the cave. The process of losing the eyes seems to be extremely gradual and slow. The inheritance of the effects of disuse is the obvious explanation, and any other must appear both less simple and less probable.

Actual experimental results bearing on this question are very difficult to obtain. Use or disuse is supposed to have only a very slight hereditary effect, so that several generations would have to elapse before this was noticeable. Hence it is not negative proof to say that the parson's son is as strong of arm as the blacksmith's, or the cobbler's as upright as the sergeant-major's. All that we can say from such ordinary observation is that the effects of use and disuse, if they are inherited at all, must be so to a very slight extent. And it would seem almost impossible to devise an experiment to prove more than this.

But the slightest of effects, if cumulative through many generations, would ultimately bring about results of tremendous importance. So that if the inheritance of the effects of use and disuse be ever so slight, it may still be ever so important.

Another group of acquired characters may be described as the direct effects of environment. Changed conditions sometimes produce an effect on the organism which is not, so far as we can see, adaptive; in other words, the change brought about in the organism does not appear to render it better suited to the new conditions. For instance, the colours of the wings of certain butterflies vary according to the temperature

under which the insect passes its chrysalis stage ; also mice which are reared under warm conditions are found to have slightly longer ears and limbs than those reared in colder temperatures.

It will be evident that it may sometimes be difficult to say whether such results are really modifications, or are due to variations induced in the germ plasm. Where we can see the body adapting itself to new conditions we may confidently class the changes as true modifications. But where we observe simply a change, without being able to trace its purpose, we have still to discover whether it began in the body or in the germ cells. This, therefore, introduces a complication.

With regard to the inheritance of such modifications it must be said that the great burden of results is again negative. Alpine plants when brought down to low altitudes become taller, broader leaved, and, in short, lose much of their alpine character. This change seems to be complete in the first generation, and persists as long as the plants remain under lowland conditions. But on returning the plants to their original habitat, the original alpine habit also returns, and remains constant through generations.

Yet in this connection we have one rather interesting case which seems to show just the opposite. In Turkestan there exists a plant nearly allied to our ordinary " shepherd's purse " : from its distribution it appears certain that it has been accidentally spread from the low country to higher altitudes along the line of a very old trade route. The form existing on the higher ground is smaller than that found in the original habitat, and there are other differences. Moreover, the highland form is pink-flowered, whereas the other is white. Now, when the lowland form is transferred to higher districts it becomes exactly like the native variety, even to the pink flower. Changed back, it assumes its original form. But when the highland form is brought down to the home of its ancestors it retains its character, pink flower and all. What could be more obvious than that the change produced by

the new conditions has gradually, in the course of ages, become hereditary ?

There is some evidence, too, that the changes produced in mice by rearing at higher temperatures are inherited in a slight degree. And even more striking results have been obtained by causing species of salamanders and toads to lay their eggs in water instead of on land, by which changes in structure are brought about. But further investigation is required to confirm these results.

There are still other types of modifications which are sometimes regarded as heritable. We frequently hear, for instance, of hereditary disease. Several members of a family die of consumption, and we say that the disease has been inherited. But on examining such a case, it appears that we cannot strictly speak of consumption, or in fact of any disease, as hereditary. Consumption is due to a special microbe, which must somehow be introduced into the system before the disease can appear. Sometimes it may be introduced from the mother before the birth of the child, but even in this case we cannot regard the disease as inherited, since all that occurs is the transference of the parasite from one person to another.

It is known, however, that certain people are much more liable than others to contract certain diseases, and that this *liability* is frequently strongly inherited. But this liability is an inborn quality, so that its inheritance has nothing to do with the present question.

To sum up the main argument, it must be said that there is some presumptive evidence in favour of the inheritance of acquired characters, but that direct experiments have given positive results of only the most meagre and inconclusive kind. Completely negative results have been obtained times out of number, but this of course cannot be taken as negative proof.

Finally, we have the difficulty of conceiving any mechanism which would bring about the inheritance of modifications. At the same time, a process may exist of which we are entirely ignorant.

How difficult of solution this question is, may be judged from the opposite conclusions of different biologists. Delage, an extremely acute and common-sense French writer, concludes that " It is by no means proved that modifications, acquired under the influence of the conditions of life, are generally hereditary, but it seems fairly certain that they are sometimes so. This depends without doubt on their nature." Professor Arthur Thompson comes to the opposite conclusion ; he says : " The question resolves itself into a matter of fact : have we any concrete evidence to warrant us in believing that definite modifications are ever, as such or in any representative degree, transmitted ? It appears to us that we have not. But to say dogmatically that such transmission is impossible, is unscientific."

It seems to us that the latter attitude, the attitude which regards the case for the affirmative as *not proven*, is the most reasonable under the circumstances. It seems impossible to deny that this negative opinion is spreading, and that the position of Delage is becoming less widely held ; and if no strong concrete evidence is forthcoming in the near future, it appears to be probable that the negative position will become generally accepted.

As before stated, the question is one of much practical importance. But even if modifications be not inherited, the environment is still, for practical purposes, a matter of extreme significance. It is unnecessary to emphasise the great influence of environment on man. Education, in its wide sense, is of well-nigh supreme importance both for the individual and for the State. And it should make us but more hopeful of the results of schemes of social reform, if we believe that the slum child is none the worse for the sordid conditions under which its parents have lived.

For the breeder of plants and animals, too, the environment is of first-rate importance, for it often sets a very definite limit to what he can accomplish. Our better varieties of apples and carnations, as well as our

finest breeds of cattle and our best egg-producing fowls, can reach their full perfection only under closely regulated conditions ; and improvement is frequently made possible only when we find means of improving the environment.

Nurture, in the wide sense, must remain a matter of extreme importance for the race even if, as seems likely, its effects pass away with the individual life.

CHAPTER V

INHERITANCE IN PURE LINES

THE term " pure line " is a new one in the science of
heredity. It was first used by Professor Johannsen in
his important paper, " On Inheritance in Populations
and in Pure Lines," published in 1903.

A pure line may be described as including all the
descendants of a single individual, belonging to a race
which is reproduced exclusively by self-fertilisation.
This implies that the germ plasm of any individual has
only one origin. Descent in each generation is from
one parent only, hence there is no opportunity for the
mixing of different germ plasms or for the recombina-
tion of characters derived from different parents.

Inheritance in pure lines is therefore the simplest
possible case, and it will be well to consider it
before we attempt to study those which are more
complex.

Johannsen's original experiments were carried out
with beans and barley. The characters of the former
which he studied were the weight and the relative
breadth of the seed, of the latter the tendency to
blindness, or the occurrence of barren flowers in the
head.

In a random sample of beans, which had been grown
from nineteen different original parents, the size was
found to show ordinary variability. The curve of
variability was very nearly normal, and there seemed to
be every probability that all the beans of the " popula-
tion " belonged to a single type. The average weight
was 478·9 milligrams, and the standard deviation
was 95·3.

But the progeny of each of the original nineteen parents had been kept separated, so that the general population could be separated into its nineteen constituent pure lines. On examining these nineteen pure lines it was found that each had a distinctive average size of seed, and a distinctive standard deviation. The degree of variability in each pure line was considerable, so that it would have been quite impossible to say, with regard to a single seed taken at random, what particular pure line it belonged to. Indeed, differences within a single pure line were often much larger than the difference between the *average* sizes of two distinct pure lines. Variability within each pure line approached the normal type; the average weight varied from 351 to 641 milligrams, and the standard deviation from 64 to 109 milligrams.

In each pure line the seeds were sorted into different sizes, and the lots obtained were grown separately. The progeny from each size of mother-seed were afterwards weighed in order to determine whether the variation in size within the pure line had been inherited. With " Line B " the following results were obtained :—

Size of " Mother " Seeds.	Average Size of Offspring.
350–400 mg.	572 mg.
450–500 „	535 „
500–550 „	570 „
550–600 „	565 „
600–650 „	566 „
650–700 „	555 „

This indicates that variations in the weight of seed, within the pure line, are not inherited; generally speaking, the progeny of the small mother-seeds were just as heavy as those grown from the largest.

A similar experiment was carried out with all the nineteen pure lines, with the same result. Moreover, experiments with the other characters dealt with yielded exactly similar results. In brief, the individual characteristics of the parent did not tend to be repro-

duced in the offspring. The tendency in these was to reproduce the average character of the pure line to which they and their parent alike belonged. This general conclusion has been confirmed by various other investigators with regard to several different kinds of organisms. It seems to apply generally, wherever descent is habitually from one parent only.

As to the causes of variation within the pure line, it seems probable that this is due entirely to environmental conditions. The position of the bean on the plant, the time at which it is formed, and the conditions surrounding the mother plant itself are probably some of these causes. In other words, it appears likely that differences within a pure line are all of the nature of acquired characters, and we have seen that these are probably not inherited.

"A pure line," says de Vries, "is completely constant and extremely variable." This apparent paradox means that variation occurs within a pure line, as everywhere in nature, yet the germ plasm, and therefore the heritage of future generations, remains unaltered.

It is evident, however, that heritable changes within a pure line must sometimes arise, otherwise we could conceive of no method by which the different types could have arisen. But it appears probable that these changes are very rare, and that, when they do occur, they are of the nature of sudden steps from one condition to another—are mutations, in fact.

The pure line conception has brought about a very considerable change in our notions of heredity. It was formerly believed that variation and change were the universal rule amongst living things, and that perfect constancy existed nowhere in nature. Whereas, within the pure line, a perfect constancy, very real although somewhat obscured, exists, and real variations occur only as rare exceptions. According to the old ideas, the characters of a race were continually in a state of flux, and selection in any particular direction could produce change in that direction almost indefinitely. But it will be seen, for example, that if we were to select, in a

general " population " of beans, for large size of seed, a very definite limit would be set to our results ; the ultimate product of selection would be the pure line with the largest average size of seed. A mutation might give us a further increase in size, but selection alone would not produce that steady indefinite increase which it was formerly supposed to cause. The constitution of the germ plasm of a pure race is a perfectly definite and constant thing, and not a quantity varying around a mean. These notions have been found to harmonise beautifully with the results obtained in other departments of the subject.

The principle of the pure line is valuable, not only theoretically, but in the practical improvement of such of our cultivated plants as are habitually self-fertilised. We shall return to this subject when we come to the consideration of the problems of the practical breeder.

CHAPTER VI

INHERITANCE ON CROSSING—MENDEL'S LAW

IN 1865 Gregor Mendel, Abbot of Brünn, in Silesia, published the results of his now famous experiments in the crossing of common peas. His paper appeared in the *Proceedings of the Natural History Society of Brünn*, and it lay buried and forgotten in this publication for five-and-thirty years. Mendel lived before his time, for apparently no one who knew of his paper was capable of realising its importance. In 1900, after the law which Mendel discovered had been simultaneously rediscovered by three separate investigators, the original paper was brought to light.

Many different men had carried out hybridisation experiments previous to Mendel's time. The only generalisations which were reached were that the first cross between two varieties was usually more or less intermediate in character, and usually very uniform ; and that in the following generation there was much variability, specimens being found which very nearly resembled either of the original parents, along with all kinds of intermediate types.

The great advance which Mendel made was in that he did not consider the plant as a whole, but studied the behaviour of each individual character. Further, he carried on his experiments systematically for several generations, and carefully counted the numbers of the different types which occurred.

He selected the common culinary pea for several reasons. It is prolific and easily grown. It is always self-fertilised, hence there could be no opportunity for promiscuous crossing, even when different varieties were grown side by side. Further, there are many

varieties showing very sharply differentiating characters ; the plant may be tall or dwarf, the seeds green or yellow, round or wrinkled, and so forth.

Mendel crossed pairs of varieties showing these sharp differences in one or more points, and noted the manner in which the following generations inherited the special characters of either parent.

It is impossible here to go fully into the technical method of effecting the cross. In essence, the process is to emasculate one flower, which is to form the female parent, by removing the anthers before they have shed their pollen. When this flower is mature, pollen is obtained from a flower of the plant selected as the male parent, and this is brushed on to the stigma or female receptive surface of the emasculated flower. The seeds formed from this flower will produce hybrid plants.

What Mendel discovered from his experiments may best be explained by describing the results of one of them. He crossed a tall form of pea with another of the well-known dwarf type. The difference consists in the one having long internodes or joints between successive leaves, while the other has short. The tall type measured about six feet in height, the dwarf about eighteen inches.

On raising the hybrid plants, the somewhat remarkable observation was made that the plants were all as tall as the tall parent. We usually expect a hybrid or cross-bred to partake somewhat of the character of both parents, but this did not occur. Mendel expressed this fact by saying that the tall condition was *dominant*, the dwarf condition *recessive*.

Mendel allowed these tall hybrids to produce seed in the ordinary way—*i.e.* by self-fertilisation. The following generation, when raised, was found to consist of two classes—talls of equal stature with their tall grand-parent and their own parents, and dwarfs which were just as short as the dwarf grand-parent. There were no intermediate specimens. The dwarf condition which appeared to have been lost in the first hybrid generation thus reappeared in the second. Moreover, the number

of dwarfs in this generation bore a constant proportion to the whole. On counting, there were found to be about 25 per cent. dwarfs, or one dwarf to every three talls.

On further breeding it was found that the dwarf plants, if left to themselves, produced only dwarf offspring—they "bred true," as we say. Here, then, was something new, and something which at first seemed paradoxical. A perfectly dwarf plant is produced by a perfectly tall parent, and the offspring of this dwarf are all, without exception, dwarfs like itself.

When the tall plants of the second generation were left to produce seed by themselves, and the seed of each plant was grown separately, it was found that some produced only tall offspring, whereas others, like their parents, produced both talls and dwarfs. There must, then, have been two kinds of tall plants in the second generation, some which were "pure" in the same sense as their dwarf brothers, others which were "impure" in the sense that they did not produce exclusively tall offspring. It was found that among the groups of offspring there were very nearly two mixed lots to each pure lot, showing that in the second generation there must have been two "impure" tall to each "pure" tall. The mixed groups of offspring consisted, on the average, of 75 per cent. talls, 25 per cent. dwarfs.
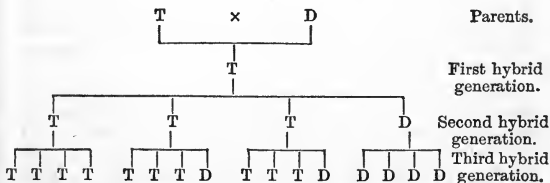
The above scheme may perhaps help to explain these results. In it, the letter **T** represents the tall condition, **D** the dwarf. We will suppose only four

D

offspring from each parent, since the least proportion of one kind that can occur is 25 per cent. Of course if one had only four offspring one might not obtain the proportion shown, since the numbers are subject to chance variations. But with large numbers the proportions were found to approach very closely those given.

We can sum up the results thus. A cross between tall and dwarf gives tall progeny, which however do not continue to breed true with regard to this character. They produce, in fact, about 75 per cent. tall and 25 per cent. dwarf progeny. Of the 75 per cent. talls, 25 are pure, the remaining 50 are impure, and apparently of the same constitution as their hybrid parents. The dwarf plants of the second generation breed true.

In this experiment two striking phenomena have been brought out. The first of these is *dominance*—the complete resemblance of the first hybrid generation to one of the parents, the characteristic of the other parent being entirely suppressed. The second is *segregation, i.e.* the separating out in the second generation—*in definite proportions*—of the characters combined in the cross.

When Mendel's paper was first discovered, it was supposed by many that both dominance and segregation were essential features of Mendelism, and many writers were led to speak of a " law of dominance " and a " law of segregation." But we now know that dominance is quite an irregular phenomenon, and that it was only by accident that complete dominance occurred in all the cases studied by Mendel.

Let us next look at a typical instance in which dominance does not occur. Such an instance is furnished by the crossing of the two forms of primula, known as the " Chinese " and the " star " respectively. The Chinese primula has rather wavy petals, with crenated or ragged edges. The " star " form has flat petals with entire margins, except for a single notch in the tip of each. The cross between these two types is intermediate in form and easily distinguishable from either of the pure

types. The characteristics have, as we say, blended. On rearing the second hybrid generation, 25 per cent. were found to be "Chinese," 25 per cent. were of the " star " form, and the remaining 50 per cent. were intermediate like the first cross. This is illustrated in Fig. 7.

The sole difference between this result and that obtained with the tall and dwarf types of pea, is that in the one case the hybrid individuals were indistin-
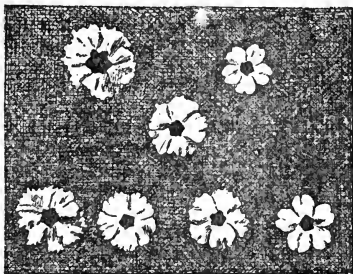
FIG. 7.—"Chinese" and "Star" Primulas with the first and second hybrid generations. (After Punnett.)

guishable from one of the parent types, whereas in the other the hybrids were intermediate in character.

The process of segregation, however, has evidently been the same in the two instances. In both we get the ratio, in the second hybrid generation of—

25 per cent. "pure," like the one original parent.
50 ,, ,, hybrid, like the first cross.
25 ,, ,, "pure," like the other original parent.

The distribution of the parental characters amongst the individuals of the following generations follows, then, a very simple scheme, instead of being, as was formerly thought, the most irregular of all the phenomena of heredity.

What is the explanation of this ratio? The main points were given by Mendel himself, though his theory has been somewhat modified by later writers. It is supposed that the tall pea, for instance, possesses some factor by virtue of which it is tall, while this factor is absent in the dwarf form. All the reproductive cells (ovules and pollen-grains) of the tall pea will possess this factor, while all those of the dwarf will lack it. The hybrid between the two forms is produced by the union of these two different types of reproductive cells. The degree of dominance will depend on the relative potency of the factor for tallness when present in the hybrid condition—that is, when it has been introduced through only one of the reproductive cells, instead of through both.

The essential point is now that the reproductive cells of the hybrid plant do not all receive an "average sample" of the hybrid germ plasm, but that half of them come to possess the factor for tallness, while the other half lack it. The "factor" is not divisible. There is no question of all the reproductive cells bearing "a certain amount of tallness." The factor must either be present or absent, and as a matter of fact it is present in half and absent in half of the reproductive bodies. With regard to any particular character the individual produces germ cells of the same kind as those from which it itself arose. Our hybrid tall plant arose from the union of a "tall" and a "non-tall" reproductive cells, and it again gives rise to these two types in equal numbers.

But how is the Mendelian ratio produced? We have two kinds of female reproductive cells, and two kinds of male. Their union takes place according to what we call "pure chance." If T represent a reproductive cell containing the factor for tallness, and t be taken to represent one in which the factor is absent, then we have T and t pollen-grains and T and t egg-cells in equal numbers. Supposing a certain pollen-grain T, it is evidently an even chance whether it unites with an egg-cell T or an egg-cell t. We therefore get the two

combinations TT and Tt in equal numbers, in a large number of cases. Similarly, with a pollen-grain t, it is an even chance whether any particular combination will be tT or tt. We have then the combinations TT, Tt, tT, and tt in equal numbers. But the second and third combinations are the same, so that we have really only three possible combinations, which occur in the ratio—

$\frac{1}{4}$, or 25 per cent.	T T	. . .	"pure" talls.
$\frac{2}{4}$, or 50 „	T t	. . .	hybrid talls.
$\frac{1}{4}$, or 25 „	$t t$	. . .	dwarfs.

This is our Mendelian ratio.

The case is analogous to a series of tossings of two coins. In a hundred of such tossings we may expect to get fairly nearly the result—

2 heads	. . . .	.	25 times.
head and tail	. . .	.	50 „
2 tails	. . .	.	25 „

Each male or female reproductive cell may be, as it were, either a head or a tail. The "two heads" correspond to the pure tall plants, the head and tail to the hybrid or impure talls, and the two tails results are the dwarfs.

Such is the generally accepted theory of Mendelian inheritance. We are able to test its value by other matings. Suppose, for instance, that we were to cross our intermediate form of primula with the pure "star" type. If A represent the presence of a factor which produces the wavy, "Chinese" type of petal, and a its absence, the pure Chinese type will be AA, and the "star" type aa. The intermediate, hybrid form Aa being crossed with the star form aa, the possible combinations are Aa and aa, with equal chances of each. We might therefore expect 50 per cent. of the intermediate type and 50 per cent. star, which is what actually occurs. We can now give a list of all the possible matings, and the results expected and found. We may represent the dominant condition generally by

D, and the absence of the necessary factor, or the recessive condition, by R

Mating.				Offspring.	
			DD	DR	RR
D D × D D .	.	.	100	...	...
R R × R R .	.	.	...	...	100
D D × R R .	.	.	...	100	...
D R × D R .	.	.	25	50	25
D R × D D .	.	.	50	50	...
D R × R R .	.	.	...	50	50

Let us consider some of the implications of this theory of inheritance.

It implies, firstly, the *purity of the reproductive cells* with regard to the characters which they bear. A particular reproductive cell may carry the factor for tallness or dwarfness, for "Chinese" petals or "star" petals, but the hybrid condition can not be represented in a single reproductive cell. The hybrid condition can be produced only by the union of male and female reproductive cells which are dissimilar with regard to the factor in question.

Secondly, each male or female reproductive cell contains a complete set of factors for determining the characters of an individual. If we have a pure variety of tall, round and green-seeded peas, each egg-cell and each pollen-grain will contain the factors for tallness, and for roundness and greenness of the seed. The result of a cross is therefore the same, whether this or that variety be used as the male or as the female parent. The common beliefs of breeders, that the male is prepotent with regard to certain characters, the female with regard to others, have either no real foundation, or are due to the operation of causes which have nothing to do with heredity, in the strict sense. There appear to be some interesting exceptions to this rule, which we will consider later.

Thirdly, the fertilised egg, and therefore the organism which develops from it, is a *double* structure.

Each character is represented twice over, one of the representatives having been obtained from the male parent, the other from the female. The factors may be in similar or in dissimilar pairs, according to whether the male and female reproductive cells which formed it were the same, or different.

Finally, and perhaps most important of all, Mendelian theory conceives the portion of germ plasm contained in each reproductive cell, as having a perfectly definite structure. If it is derived from a hybrid parent, it may have either of two structures with regard to any one factor, but it cannot be any vague or indefinite mixture of the two. The value of this idea has been compared to that of the atomic theory in chemistry. It was this theory which, by giving chemists the idea of definite chemical substances, made possible the whole science of modern chemistry. There is a close analogy between this and the principle of Mendelism, the principle of discontinuity and definiteness among living organisms.

As regards the real nature of what we have called "factors"—the representatives, in the germ plasm of the characters of the organism—it must be admitted that we know nothing. Indeed, we know so little of the chemical nature of the living substance that it is almost useless even to theorise on the subject. Much laborious chemical research will have to be carried out before the structure of the germ plasm, and its relations to the mature organism, can be understood.

We shall consider later the question of the general application of Mendel's law. In the meantime, we may instance a number of characters which have been shown to be inherited according to the simple Mendelian scheme. Such characters are colour in mice, guinea-pigs, rabbits, fowls, and pigeons; length of hair in certain animals; certain feather characters in birds; leaf form and leaf coloration in certain plants; flower colour in a great number of species; such important practical matters as the presence or absence of horns in cattle, resistance to "rust" disease

in wheat, the shape of potato-tubers, and some abnormal conditions in man, such as the brachydactylous or short-fingered condition ; and many others.

Mendelian segregation occurs, then, in many different sections both of the plant and animal kingdoms, and with regard to characters of many different kinds.

CHAPTER VII

MENDELISM (*continued*)

We must now proceed to consider some more complicated cases of Mendelian inheritance. But before doing so it will be advisable to study the inheritance of two pairs of characters simultaneously.

Suppose that we cross two breeds of cattle differing in two distinct particulars—say, the one is black and
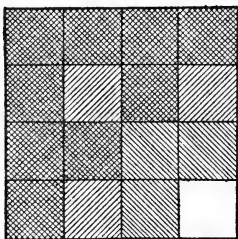
FIG. 8.

hornless, the other red and horned. Black colour is dominant to red, and the hornless condition dominant to the horned. The first generation will therefore be black and hornless. How will the characters be distributed amongst the individuals of the following generation?

If we take a square, and divide it into four equal parts, as in Fig. 8, we may shade three of the quarters to represent the fact that three-fourths of the second generation will be black, and one-fourth red.

The other pair of characters is inherited independently. We must then divide each quarter again into

four, and shade three-fourths of each in the opposite direction to represent the fact that three-fourths are hornless, one-fourth horned. We have now a figure divided into sixteenths. Of these subdivisions, nine are shaded in both directions, representing nine individuals containing both dominants—*i.e.* black and hornless. Three squares are shaded in one direction only, representing three red and hornless individuals. Three are shaded in the other direction only—*i.e.* three individuals will be black and horned. One square only remains unshaded—on the average only one individual in sixteen will be red and horned, and will show both recessives.

To state the matter differently, out of sixteen individuals twelve or three-fourths will be black, and four or one-fourth red. Of the twelve blacks, nine or three-fourths will be hornless, and three or one-fourth horned. Of the four reds three or three-fourths will be hornless, and one or one-fourth will be horned. We therefore have the ratio—

9 with both dominants.
3 with one dominant only.
3 with the other dominant only.
1 with both recessives.

Very close approximations to this 9 : 3 : 3 : 1 ratio have been obtained in a large number of instances.

Of the more complicated instances of Mendelian inheritance, one of the best known and most interesting is that of the type of comb in fowls. The original form of comb, that found in the wild jungle fowl, is the "single" (C in Fig. 9). Other forms are the "rose" (B), "pea" (A), and "walnut" (D). The rose behaves as a simple dominant to the single. The first hybrid generation have rose combs, and of the second 75 per cent. are rose, 25 per cent. single. Pea is also a simple dominant to single, giving the ration 3 pea : 1 single in the second generation. Walnut behaves as a simple dominant to both pea and rose.

If walnut be crossed with single the first generation

have all walnut combs; but the second generation, instead of giving 3 walnut : 1 single, as might have been expected, is composed of walnut, rose, pea, and single-combed individuals in the ratio of 9 : 3 : 3 : 1. Further, when rose and pea are crossed, the first hybrid generation has *walnut* combs. From this it was at first thought that walnut was the hybrid between rose and pea, and that the following generation would give the ratio 1 rose : 2 walnut : 1 pea. This, however,
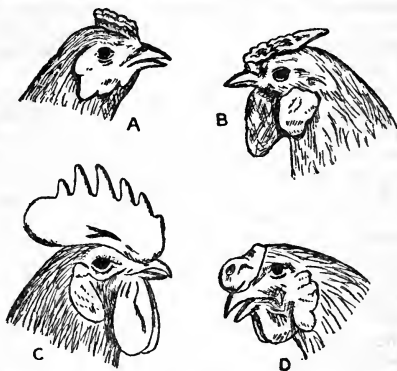
FIG. 9.—Types of Fowls' Combs. A, Pea; B, Rose; C, Single; D, Walnut. (After Punnett.)

did not occur. Instead, the ratio was again 9 walnut : 3 rose : 3 pea : 1 single.

What is the explanation of these rather remarkable results? It is assumed that the rose comb is due to a dominant factor A. The pea comb is determined by a separate factor B, also dominant to its absence. The important point now is that A and B themselves do *not* form a pair of unit characters. Each is dominant to its absence, but the two have nothing to do with each other so far as segregation goes. If A and B are both absent, the fowl has a single comb. If both are

present, the comb is walnut. The one factor is, as it were, struggling to make a rose comb, the other to make a pea, and the result is the walnut form. The walnut type is not a hybrid between the two. It is both pea and rose, and as such may breed true. Our ratio of 9 : 3 : 3 : 1 is produced by the independent inheritance of two pairs of characters, only in this case the two dominants produce a special combined result. So far as the subsequent results are concerned it is immaterial whether both dominants be introduced through one parent, as in the walnut × single cross, or whether one dominant be introduced through each parent, as in the rose × pea cross.

Another interesting case is that of the appearance of the purple colour in crossed "Emily Henderson" sweet-peas, which was mentioned in the Introduction. The facts are that "Emily Henderson" is a pure white variety, the plants being apparently all of one type, except that some have round pollen-grains, others oval. When two of these white-flowered plants are crossed, the progeny are sometimes white-flowered, but sometimes also purple. The appearance of this purple-flowered sweet-pea is a distinct case of reversion; for it is known that all our cultivated forms have been derived from the wild sweet-pea found in Sicily, which has purple flowers.

As before mentioned these plants, when allowed to self-fertilise, produce coloured and white-flowered progeny in the ratio of 9 : 7. The explanation of this remarkable case, given by Professor Bateson, is that two factors are necessary for the production of colour. Neither of these factors alone produces any colour; the two must act together. We might compare the case to that of the action of light on sensitised paper. The one type possesses the basis for colour production, but lacks the developing agent. The other has the factor for developing the basis, but has no basis to develop. Hence when the two types are crossed, colour is produced. In the second generation, nine individuals out of every sixteen will have both dominants and will

show colour. The remaining seven will lack either or both, and will be white. Colour inheritance in sweet-peas is one of the subjects which has been very thoroughly investigated, chiefly by Professor Bateson and his assistants at Cambridge, and many complex relationships have been thoroughly unravelled.

Other striking cases, which were puzzling when first observed, have turned up in the crossing of differently coloured varieties of mice and rabbits. When an ordinary grey rabbit is crossed with a white or albino, grey is dominant. If the first generation greys are bred together, the usual result is the ratio 3 grey : 1 white in the second generation. But sometimes *black* animals turn up in the second generation, the ratio in this case being about 9 grey : 3 black : 4 white.

The explanation which has been suggested for this result is that two factors are responsible for the grey colour. One of these is a general factor for colour, in whose presence colour is produced, and in whose absence the animal is white. We may call this factor C. If only C is present the colour will be black, but there is an additional factor G, which changes the black colour into grey. We may represent the result of crossing diagrammatically by the " chess-board " method which we used before. Taking a square of white paper we may blacken three-fourths of it to represent the fact that 75 per cent. of the second generation will show the dominant character *colour*. Of these, three-fourths will contain the dominant greying factor. We may therefore divide each of the black squares into four, and dot over three parts of each with white, to indicate that 75 per cent. of the coloured animals will be grey, and 25 per cent. black. This gives us the proportions shown in Fig. 10—viz. 9 grey, 3 black, 4 white.

It is interesting to note that of the four white individuals three will contain the factor G. In other words, three will be " disguised greys " and one a " disguised black," the colour in each case being suppressed, owing to the absence of the factor C. What

ought to happen if we cross a pure "disguised grey" with a pure breeding black type? The factor C is introduced by the black parent, the factor G through the white, so that the first generation should all be grey. This supposition has been tested, and is what actually occurs. The production of grey offspring by a black and a white parent is another case of reversion, brought about by recombination of characters on crossing.

A different type of inheritance may be exemplified by the case of black colour in the glumes or hulls of oats, discovered by the Swedish investigator Nilsson-Ehle. Three types exist—white, greyish-black, and deep black. A cross between grey-black and white gives grey-black
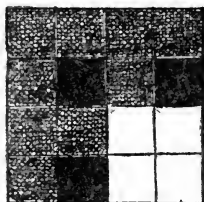
FIG. 10.

hybrids, with normal segregation in the next generation into 3 grey-black : 1 white. Similarly, black and grey-black give black, with normal segregation into 3 black : 1 grey-black. A cross between black and white gives black in the first generation, but in the following generation the ratio obtained is not that of 3 black : 1 white, but is 9 black ; 6 grey-black ; 1 white. The explanation of this is that the black colour is produced by the simultaneous action of two independent factors. Either of these alone produces grey-black, and when both are absent the colour is white. The 9 : 6 : 1 ratio is therefore only a special case of the 9 : 3 : 3 : 1 ratio that we already know.

Cases of this same type have been met with in regard to other characters of oats, and also in maize.

A more complicated instance of the same kind has been discovered by the same investigator. On crossing a certain type of red wheat with a white variety, a hybrid of intermediate shade was produced. On breeding from this, all intermediate shades of colour were produced, ranging from deep red to pure white. It is impossible here to discuss fully the analysis of this case, but Nilsson-Ehle has clearly proved that red colour in the original parent was due to the action of three independent dominant factors. Each factor alone produces a certain amount of red colour; moreover, the shade is only half as deep when it is in the hybrid as when it is in the pure condition. The result in the second generation is that there are six possible shades of red, besides the pure white, forming an almost continuous series. Other consequences of the hypothesis of three factors have been confirmed by experiment. This case is one of the most complex that have yet yielded to Mendelian analysis.

An interesting complication of another sort has been discovered with regard to leaf variegation in the garden snapdragon (Antirrhinum). One variety of this plant has its leaves dotted over with green and yellow, like many other variegated forms. It has long been known that this variety never breeds true, but always throws a proportion of green "sports." On counting a batch of plants, there were found 573 variegated, 286 green, or almost exactly the ratio of 2 : 1. What could be the meaning of this ratio?

On closer investigation of the seedlings, it was found that the actual ratio was 1 green : 2 variegated : 1 *yellow*. A certain amount of green colour is well known to be an essential of ordinary vegetable life, and the yellow-leaved specimens all died as seedlings. The case is therefore similar to that of the hybrid primula—there being produced 25 per cent. of each of the pure types, and 50 per cent. of the hybrid form; only in this instance one of the pure types is incapable of living.

A more remarkable case has lately been discovered by the American experimenter Castle in connection with yellow mice. It has long been suspected that there was something remarkable about them. In the first place, they never breed true. They are somewhat delicate as compared with ordinary mice, they are frequently sterile, and many show a curious tendency to become excessively fat.

If yellow mice are mated with others of the ordinary wild grey colour, the ratio obtained is about 50 per cent. yellow, 50 per cent. non-yellow. This suggests that the yellows are all hybrids, yellow being dominant to grey. When a large number of yellows were inter-bred by Castle the numbers 800 yellow, 435 non-yellow were obtained, which, considering that the death-rate is usually higher among the yellows, indicates the ratio 2 yellow : 1 non-yellow. This ratio is explained by supposing that the pure yellow type, which ought to form one-fourth of the whole, are incapable of sur-viving ; and the supposition is confirmed by the fact that matings of two yellows usually give smaller litters than matings of yellow with non-yellow. It is im-possible at present to say why a pure yellow mouse should be an impossibility, for hair pigment in animals has never been considered indispensable, in the way that chlorophyll or leaf-green is to plants. The reason then remains obscure, but the inheritance of the char-acter itself is explained.

A number of somewhat puzzling complications are grouped as the effects of coupling and repulsion between different factors. There is often a distinct tendency for characters which appear to have nothing to do with each other, to be inherited together or to repel each other in such a manner that a given two rarely occur in one in-dividual. Thus, for example, the "hooded" form of the standard petal in sweet-peas seems to be strongly coupled with certain colours, and occurs only rarely in others. This subject, however, has not been fully investigated.

In other cases there appears to be some selective mating between the reproductive cells. A sperm seems

sometimes to be most strongly attracted by egg-cells of different constitution to its own, and sometimes male and female reproductive cells of the same constitution refuse altogether to unite.

A case of somewhat the same nature as that of the yellow mice has lately been described with regard to one of the mutants of Lamarck's Evening Primrose. It seems that the pollen-grains bearing certain characters, and the egg-cells bearing others, shrivel up and die, so that the inheritance of certain characters must take place through either pollen-grain or egg-cell only. It is believed that the particular form in question is really a hybrid which " breeds true," owing to the fact that the pollen-grains and egg-cells which reach maturity have necessarily different constitutions.

A very puzzling case of what is termed "sex-limited" inheritance has been noted with regard to the peculiar pathological condition in man known as "bleeding." An affected person bleeds profusely and continuously from even the smallest wound, owing to the fact that the blood, for some obscure reason, does not coagulate. The condition affects only men. The sons of bleeders are not themselves affected, and the children of the sons also do not show the condition. It appears only in the sons of daughters of bleeders. Here, then, we have a condition which affects only the male, and is inherited only through the female. The mode of inheritance appears to be Mendelian, but the reason of the complication is not known.

We may here mention the question of the causation of sex itself. It will be evident that the proportions of the sexes usually found, viz. 50 per cent. of each, are what result when a hybrid dominant is mated with a recessive. It appears likely that one of the sexes is produced by the presence of a dominant factor in the hybrid condition, while the other sex represents the pure recessive. As to which sex is the dominant, the evidence from different kinds of organisms is contradictory. The state of affairs probably differs in different types. But the question is admittedly not yet fully understood.

CHAPTER VIII

MENDELISM—GENERAL DISCUSSION

A QUESTION of much importance is the range of application of Mendel's law. Is it, as was at first believed by some, confined in its application to those cases in which very distinct differences are dealt with ? Is it a universal law of inheritance ? Are any real exceptions known ?

From time to time cases have been described which have been quoted as proof that Mendelian segregation does not occur. Most of the apparent exceptions to Mendel's law are cases in which the first hybrid generation is a blend, and where the blended condition appears to be constantly reproduced in the subsequent generations. One of the most commonly cited is that of skin colour in man. The children of a European and a negro, mulattoes as they are termed, are just about intermediate in colour. This, of course, is of little importance in itself ; but if inheritance were according to the simple Mendelian scheme we ought to expect, from a marriage of two mulattoes, the ratio of 1 " white " : 2 mulatto : 1 negro. A family of four in which this ratio occurred would be sufficiently striking to attract attention to say the least. It seems quite certain that segregation on these lines does not occur. It seems, on the other hand, that the children of mulatto marriages are generally again recognisable as about half-bloods, although the shade of colour is occasionally somewhat lighter or darker than that of the parents. It has been observed also that in marriages of two nearly white people, with some negro ancestry, there is an occasional reversion to a much darker shade of colour. In the main, however, skin colour seems to be a character

which "blends" on crossing. A marriage of a white with a mulatto gives "quadroon" children, which are usually recognisable as such, and are generally about intermediate as regards skin colour.

Such ordinary observation, however, is not sufficient to enable us to say that Mendel's law does not apply. It is possible that the case is only slightly more complicated than that of the inheritance of red colour in wheat. And without full and reliable statistics, which are difficult to obtain, we cannot fairly set down this instance as an exception to Mendel's law.

A case in which much better evidence is available, is that of the inheritance of ear length in rabbits. The well-known "lop" variety is characterised by its large size and the extraordinary length of its ears, which causes them to hang down to the ground. In the specimens used by Castle in his experiments the average ear length was about 220 millimetres, while that of the ordinary variety with which they were crossed was about 110 millimetres. The hybrid between these two types had ears about 160 millimetres long, or nearly intermediate between the parent lengths. These rabbits of the first hybrid generation were interbred, but the offspring instead of showing ordinary segregation into 1 long, 2 intermediate, and 1 short, were all about intermediate as regards ear length. Indeed, although the number of individuals was too small to base statistical conclusions on, there appeared to be no greater variation in the second than in the first hybrid generation.

This experiment has aroused a good deal of discussion, and the real meaning of the results obtained is doubtful. It is certain, however, that they cannot be held as demonstrating the absence of segregation with regard to ear length. It may well be that this character depends on a considerable number of independent factor pairs, so that a very large number of individuals would require to be bred in order to have any considerable chance of sensible segregation.

Similar results have been obtained in the crossing

of certain wild species of plants, but the results are not at all convincing.

In general, it seems that where we are dealing with such characters as the excessive length of ear in the "lop" rabbit, which have been produced by continuous selection through many generations, we cannot expect a simple Mendelian result. The end product of the process of selection is probably a combination of many factors, all having a certain effect on the character in question, but independently heritable. The rebuilding of this combination, once broken down by crossing, must necessarily be a difficult process, unless enormous numbers of individuals are raised in the second hybrid generation. We can, then, easily conceive causes which would obscure the fact of segregation with regard to such characters as ear length in rabbits and skin colour in man.

Another objection that has sometimes been put forward to Mendel's law is that while segregation follows in the main the Mendelian scheme, the "pure" types extracted in the second hybrid generation are not absolutely pure, but only relatively so; that they retain a trace of the hybrid character, and have a tendency to "throw back" to it.

In guinea-pigs, for instance, it has been found that the ordinary short coat behaves as a dominant to the so-called "Angora." The hairs of the "Angora" type are very long, this condition being brought about by the fact that they continue to grow indefinitely, whereas the coat of an ordinary guinea-pig definitely ceases to grow after it has reached a certain length. The length of the "Angora" coat is, of course, also limited, as each hair ultimately dies and falls out. But in it there is no definite stoppage of growth. A cross between the two types gives a short-coated hybrid, and the second generation gives segregation into three short-coated, one Angora. But the short-coated individuals, although the growth of their hair definitely ceases, are sometimes distinctly longer coated than their short-haired grand-parents. These individuals with a

modified type of short coat may breed true, and their appearance has been attributed to "imperfect segregation." It seems unnecessary, however, to assume imperfect segregation. The modification of the short coat might be due to the transference of certain independent modifying factors from the Angora. It was found impossible to explain the modification of the short coat by assuming one such factor, but this does not prove that the modification was not due to inheritance on Mendelian lines.

Some of the most puzzling and irregular cases of inheritance have been met with in fowls. We may instance the case of the extra toe which is characteristic of certain breeds. In the first place, it must be noted that the extra toe is not quite uniformally inherited even in pure breeds which have long been selected for this character. In the actual experiment, carried out by Davenport, which we shall describe, a five-toed breed was used which produced about 3 per cent. of four-toed individuals.

When this breed was crossed with a normal, four-toed variety, the five-toed condition was irregularly dominant. A few birds showed five on one foot and four on the other. Altogether, 27 per cent. were four-toed on both feet, and the remaining 73 per cent. showed five toes on either or both. Accepting, for the moment, the fact of this irregularity in dominance, what result should we expect in the next generation ? Twenty-five per cent. ought to be like the five-toed parent breed, which was about 97 per cent. five-toed. This 25 per cent. ought then to be about twenty-four five-toed and one four-toed ; 50 per cent. ought to be hybrids, which we found to be about 73 per cent. five-toed. Our 50 per cent., then, ought to be about thirty-six five-toed, fourteen four-toed. Twenty-five per cent. ought to be like the four-toed parent breed, all four-toed. On adding these numbers we find the expectation to be 60 per cent. five-toed, 40 per cent. four-toed. Actually, the percentages found were 53 and 47 respectively, which, considering that the numbers were small, is

fairly close to expectation. We may conclude that
segregation probably followed the usual rule, but the
reason for the irregular dominance remains unknown.
It is interesting to note that the degree of dominance
has been found to vary in different families, and to be
inherited.

We do not know how frequent such cases are. It
is interesting enough to know that they do not form
exceptions to the law of segregation, but such irregu-
larities must necessarily interfere with the practical
application of Mendelism. It is not impossible, however,
that some fuller explanation of these phenomena may
yet be found.

It is interesting to note the harmony that exists
between Mendelian theory and the facts of "pure line"
inheritance. In a Mendelian crossing, all the indivi-
duals of the first generation are hybrid. In the second
generation, half are hybrid and half are pure with
respect to any particular character. It is easy to see
that if all these individuals reproduce at the same rate,
by self-fertilisation, the number of hybrids will be
reduced to one-quarter in the next generation. The
fraction of the whole population that are hybrid is
thus halved in each successive generation, and the
proportion would soon become negligible. A self-
fertilising population would therefore be expected to
consist of a number of perfectly pure types, showing
no variations of hereditary value. This is exactly the
state of affairs, as discovered by the pure line experi-
menters. It appears fairly certain, then, that segrega-
tion occurs with regard to the special characters of
slightly differing pure lines. We have no means of
knowing whether segregation is according to the Men-
delian scheme, but there is evidently a presumption
that it is so.

In many cases it is impossible to carry out
actual Mendelian analyses of inheritance, owing to
the fact that the distinctions to be dealt with are
too vague and irregular to be readily classified. Most
of the differences between pure lines are of this nature.

Some interesting evidence in a case of this kind has been obtained by East, by means of statistical methods. In one of East's experiments, two varieties of maize were crossed which measured, on the average, 68 and 101 inches in height respectively. This may appear a definite enough difference, but all intermediate heights between these two varieties can be found, and it is impossible to trace any simple kind of Mendelian inheritance of the characters. In the first hybrid generation the average height was 95 inches, and the coefficient of variation was 8·7 per cent. In the second hybrid generation the average height was 82·5 inches, and the coefficient of variation 13·4 per cent. Variability, then, was found to be considerably greater in the second than in the first hybrid generation. This is strong evidence that segregation had occurred.

We know too little as yet to be able to say definitely whether Mendel's law applies with regard to all characters, in all kinds of living organisms. It is certain that it applies to various characters in many species of plants and animals, and it seems doubtful whether any real exception has yet been found.

A secondary point of much interest and great practical importance has lately been discovered by Shull and East, both working largely on maize. It is to the effect that the *vigour* of a plant is influenced, not only by the characters which it possesses, but also according to whether these characters are present in the pure or in the hybrid condition.

It has long been known that inbreeding, or the mating of closely related individuals amongst animals, is very detrimental to the general physiological vigour and the fertility of the breed. Similarly in plants where cross-fertilisation is the rule, enforced self-fertilisation produces much less vigorous offspring than the normal method of reproduction.

It has been found, however, that if maize, which is normally cross-pollinated, be artifically self-fertilised through several generations, the loss of vigour does not continue at the same rate. It is large between the

first and second generations, less between the second and third, and after a few more years a condition of constancy is reached. It is found that further cross-fertilisation between plants of the same strain does not produce an increase in vigour in the progeny. Evidently, then, cross or self-fertilisation as such has no influence on the vigour of the offspring. The loss of vigour is explained as due to the reduction of the strain, at first hybrid with regard to many of its characters, to the condition of a pure line. There is evidence that such pure lines are constant, as others are.

If two such strains are crossed, there is a large and immediate increase in vigour. It is easy to see that the offspring of such a cross may well be more vigorous, on the average, than the original strain propagated continuously by cross-fertilisation. For we now obtain a crop in which all the individuals are hybrid with regard to a large number of characters, whereas in a strain in which crossing is promiscuous the individuals vary greatly with regard to the number of hybrid characters which they contain. In one of Shull's experiments the average yield of two pure, or almost pure, strains of maize was 29 bushels per acre. The first cross between the two yielded 68 bushels, while the original strain of corn, which had been cross-fertilised continuously for five years, yielded 61½ bushels.

The reason why the hybrid condition should be connected with extra vigour, we do not know. But in practical breeding, where vigour is usually one of the greatest desiderata, the discovery should prove valuable.

CHAPTER IX

THE STATISTICAL STUDY OF HEREDITY

In the preceding chapters we have considered the results obtained by the experimental method of studying inheritance, according to which we observe the occurrence or non-occurrence of certain definite characters through several generations in which the matings are controlled. It will have become clear that there are only three possibilities with regard to any particular character—viz. the two pure types and the hybrid. Apart from the relatively unimportant matter of dominance, we cannot in any sense speak of *a degree* of resemblance between parent and offspring, provided that the character in question is determined by one factor pair. There are no degrees of inheritance. An individual must either possess a particular factor pure or hybrid, or lack it.

It was formerly usual to speak of several different kinds of inheritance, of blended, particulate inheritance, and the like. But, as before mentioned, it seems unnecessary to assume several fundamentally different modes of inheritance. It seems probable that Mendelian or alternative inheritance is the general rule.

Nevertheless, it is possible to proceed to study heredity by determining the *average* degree of resemblance between parent and offspring.

In order to get a satisfactory illustration of the method used, it will be best to consider some character showing normal quantitative variability. One of the most fully investigated cases is that of stature in man, before mentioned.

Variations in stature appear to be due to many different causes, no one of which has, by itself, any very

considerable influence. In the first place, there are probably many different hereditary factors having an influence in the matter. The number of hybrid characters as influencing physiological vigour may probably bear some relation to it. Finally, stature is to some extent influenced by environmental conditions, such as nutrition, climate, accidental injuries, disease, and so forth. Such a large group of independent causes tends to produce normal variability.

In studying the inheritance of stature by the statistical method, we make no effort to separate the effects of these various causes, but simply set out to discover the average degree of gross difference or resemblance between parent and child.

Our first business is to make several hundreds of observations of the stature of, say, father and son. This done, we proceed to arrange the figures in groups. Taking, say, all the fathers between 61½ and 62½ inches, we may set them down as a group at 62, and proceed to set down in groups the statures of the sons of these several fathers, finally striking an average of the lot. Thus in the investigation carried out by Professor Pearson and Miss Lee, where over a thousand pairs of fathers and sons were measured, there were seventeen fathers in the 62-inch group. The sons of these, arranged in groups to the nearest inch, were as follows :—

63 inches	.	.	.	.	2
64 ,,	.	.	.	.	4
65 ,,	.	.	.	.	2
66 ,,	.	.	.	.	2
67 ,,	.	.	.	.	5
68 ,,	.	.	.	.	2

giving the average size of about 65½ inches.

One proceeds in a similar manner with all the groups of fathers which in the investigation mentioned extended from 59 to 75 inches, ascertaining the average size of the sons of each group. It is now possible to express these figures graphically. On squared paper, one can set off, say, horizontal distances to represent the several

stature classes of the fathers. One can then measure vertical distances to represent the mean size of the sons of each group. From Fig. 11, where this has been done, it will be evident that the mean size of the sons of 63-inch fathers is about 66·3, of 66-inch fathers about 67·6, and so on. The extreme classes are not included, as the number in each is too small to give a reliable result.
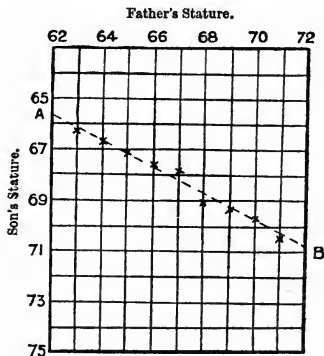
Fig. 11.

It will be seen that the series of points thus obtained falls roughly in a straight line. That the line is not perfectly straight is probably due to the limited number of cases included. We can, however, draw in the straight line (AB) which most nearly touches the whole series of points, and which, in the figure, occupies an oblique position. It will be evident that if the line AB were horizontal—*i.e.* if all classes of fathers had had about the same average size of sons—the inheritance would have been zero ; if, on the other hand, this line had been inclined at 45°—*i.e.* if each class of fathers had tended to have sons of the same average size as themselves—

the inheritance would have been complete. In other words, the degree of inheritance is measured by the size of the angle which the line AB makes with the horizontal. In Fig. 11, the position of this line is just about midway between the horizontal and 45°. The figure representing the size of this angle, as a fraction of 45°, is termed the *coefficient of heredity*, and in the case discussed it works out at 0·51. This means that the size of the son is *on the average* about half-way between the size of the father and the mean size of the race.

The simple method of determining the coefficient of heredity which we have used, assumes that variation is normal, and similar in the parents and the offspring ; also that the line joining the series of points in the figure shows no definite bend. If these conditions are not fulfilled, more complicated methods must be used.

The coefficient of heredity for stature in man is exceptionally high, which indicates either that stature is very largely a matter of heredity, or that environmental conditions usually tend to have similar effects in father and son. The value of the coefficient varies in different cases. It has been calculated, for instance, for the size of litter in pigs, *i.e.* for the number of young produced at a birth by a sow and one of her female progeny, and the figure obtained was 0·07. This indicates that, in the material used, the number of young produced at a birth is largely influenced by causes other than heredity, and that there are only relatively slight inborn tendencies to produce large or small litters.

Galton, who was the pioneer in the statistical study of inheritance, attempted to reduce to one general law the result of his studies of heredity ; that is, he attempted to determine general figures for the average degree of resemblance between parent and offspring, grand-parent and offspring, and so on. Professor Pearson, on the basis of a great deal more experimental work, has stated " Galton's Law " in a modified form. But the fact has emerged that the coefficient of heredity must depend altogether on the nature of the case. Within a pure line, the differences that exist appear to

be due entirely to environmental conditions, and the coefficient of heredity of these is zero. In a mixed population of sweet-peas, on the other hand, where self-fertilisation is the rule and each colour type is produced constantly, the coefficient of heredity would be unity. One should naturally expect many intermediate values, depending on the extent to which the gross total of variability is due to environmental modification and inborn differences respectively.

It is necessary to realise clearly the relation of statistical results, such as we have described, to Mendelian and pure line theory. It has frequently been pointed out that the results of the two opposite methods are not really contradictory. The one, the experimental method, applies to individual cases. It distinguishes sharply between inborn characters and modifications, and it enables us to predict, in any particular mating, the numbers of offspring that will show certain definite inborn characters. But before we can make such predictions we must know, not only the actual characters possessed by the parent organisms, but also their germinal constitutions.

On the other hand, statistical results apply only to populations in the mass. We do not attempt to analyse the gross total of variation, to distinguish between modifications and inborn variations. Moreover, we do not attempt to distinguish between similar individuals of different constitution. We regard all differences as variations, and determine the extent to which, on the whole, in the mass, these variations are inherited. The coefficient of heredity does not enable us to determine what will occur in an individual case. The son of a six-foot father may be anything within the whole range of statures. All that we can say from our statistical investigation is that his height is most likely to be near five foot ten.

Thus the two methods are different ways of treating the subject of heredity, and their results apply in different ways. But it would be a poor apology for the statistical method to say that its results were

merely not opposed to a Mendelian interpretation of the same facts. For Mendel's law and the pure line conception are far simpler generalisations than the statistical laws of heredity. Moreover, they give us an insight into the actual mechanism of heredity which we could never gain by regarding the subject statistically. In fact, it is becoming clear that statistical results have no bearing whatever on the physiological process and mechanism of heredity. Where a Mendelian interpretation is possible, then, it is more valuable, both theoretically and practically, than a statement of a statistical result.

Yet it seems to be the case that, no matter how universally Mendel's principles may be found to apply, there will remain a wide field for valuable statistical investigation ; namely, in those cases which are too complex for Mendelian analysis. It is tolerably certain that such cases will arise in the future, due either to the large number of factors having an influence on a particular character, or else to the obscuring of Mendelian inheritance by the occurrence of relatively large modifications. We have seen that there are three independent factors for such a comparative detail as red colour in wheat, and in the common garden snapdragon the various colour varieties, numbering over a hundred, are produced by the presence or absence of some fifteen independent factors, which have somewhat complex inter-relations. The researches by which these factors have been analysed have necessarily been difficult and laborious, and with a slow-breeding organism, or one which could not be bred in great numbers, the work would have been altogether impracticable. With flower colour, moreover, we are dealing with fairly definite and easily distinguishable characters. If, on the other hand, we were to attempt to unravel the heredity of such a character as size in beans, where many factors are certainly involved, and where the various types are indistinguishable without extensive breeding tests, we should have a problem of much greater complexity.

But even these are not the most complex of the problems of heredity. Consider, for instance, the matter of speed in racehorses. A multitude of different organs, and even certain mental characteristics, are concerned. Further, the presence of certain factors in the hybrid condition appears to be essential to its highest development, for close inbreeding is always detrimental to racing ability. The conditions of development and training have an important influence in the matter, and their effects are inextricably mixed up with the inborn qualities. Again, we are dealing with bi-parental inheritance, and this introduces a complication. And, finally, the horse is a slow-breeding animal, and one which it would be scarcely possible to breed in large numbers for experimental purposes.

Here, then, we have a practical problem of a complexity so great that Mendelian analysis seems out of the question. And it appears probable that many economic characters in animals, which have usually been improved by a long process of selection, are of a similar nature.

It is, perhaps, going too far to predict the actual incapacity of the Mendelian method to cope with such problems, for the method is still in its infancy, and one cannot foresee all its possibilities. Still there seems to be a great probability that such questions are too complex for Mendelian treatment. It is in such cases, where many small causes operate in producing a single result, that statistical methods come to our aid. The coefficient of heredity for speed, could it be determined, would have a distinct practical value.

We may, then, conclude that while all inheritance may well be at bottom Mendelian, and while a description of any particular case in Mendelian terms is simpler and better than a statistical result, yet the latter is valuable if, or as long as, the Mendelian analysis is not found possible.

CHAPTER X

THE PROBLEMS OF THE PRACTICAL BREEDER

THE applications of theory to the work of practical breeding have been indicated here and there, but it may be well to discuss the subject somewhat more systematically.

PLANT BREEDING

Considering first the applications of Mendelism in plant breeding, it will be clear that Mendel's law points out an easy method by which definite characters from two existing varieties may be recombined in one. Much valuable work has been done in the past in this direction, but it has often been accomplished at the expense of a good deal of unnecessary labour. It is with regard to the fixing of new types that Mendelism gives assistance. If the required characters are recessives, they will breed true and will not require fixing beyond the first selection. With dominants, however, it is obvious that ordinary mass selection will give unsatisfactory results, for a considerable percentage of recessives will turn up for a number of years. Mendelism has taught us that the proper method to fix a dominant is to grow the seed of each plant of the second generation separately. The individuals of the groups which show no recessives will contain no hybrids, and will therefore breed true. We can thus obtain our strain fixed and pure almost at once.

To turn to the " pure line " theory, we can say that here enough has already been done to show its great value in practice. At the experiment station at Svalöf, in Sweden, the isolation of pure lines of cereals has

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been carried out on an enormous scale by Nilsson and his assistants. It is interesting to note that Nilsson discovered the pure line method of breeding for himself, before the conception of a pure line was known to scientific workers. From the ordinary varieties of the country, which consisted of mixtures of numerous types of very various productiveness and quality, he has isolated the best pure varieties, and these have proved highly valuable.

It is interesting to note that many of our standard varieties of cereals have been produced from a single ear found growing in some unexpected place. The old agriculturist thus unconsciously produced a pure line, and if it happened to be one of the better types from the common mixed varieties, it proved valuable and was preserved. Thorough systematic search for the best pure lines is a promising method of improvement of such of our economic plants as are continually self-fertilised.

The discovery of Shull and East regarding the increase of vigour on crossing will no doubt have important applications in the improvement of maize, which can be easily crossed or self-pollinated. The method which has been proposed is to use two distinct types, which may or may not be actual pure lines, as parents; to cross them systematically, and to use the cross-bred seed for the production of the commercial crop, a fresh supply being produced each year. This principle would not be applicable with regard to many species of plants, as the type of floral arrangement which obtains in maize is rare.

There are other types of plants in which new theories of heredity fail to suggest any improvement on old methods of breeding. Such, for instance, are those plants which are propagated vegetatively—by sets, grafts, cuttings, or the like. In this case the problem of the improver is simply to *discover* valuable new types. No fixing process is necessary, since, as long as the new type is reproduced vegetatively it will, generally speaking, remain constant, whether it be pure or hybrid.

F

The breeder therefore confines himself to the growing of large numbers of seedlings, and searching amongst them for valuable new types; or else simply to watching for bud variations. Among plants of this type are the potato and a great number of fruit plants and flowers, such as the apple, strawberry, and carnation. It is in such species that perhaps the most remarkable improvements have been made, the absence of any necessity to fix new types having rendered improvement easier and more rapid.

There are other species of plants which are reproduced regularly by cross-fertilisation, or in which cross-fertilisation is at least so frequent that a material loss of vigour occurs when it is prevented, yet in which systematic crossing on the lines described for maize would be impracticable, owing to the male and female organs occurring mixed together. In such cases separation of pure types would be useless, as their vigour would be materially less than that of a mixed, cross-bred "population." In such cases all that can be done, apparently, is to select continuously for the special characters required and also for vigour. In sugar-beet, where a very thorough system of selection has been followed with regard to the percentage of sugar in the root, this has been increased from about eight or nine to seventeen or eighteen. The improvement was fairly rapid at first, but soon slowed down, and now, in spite of the improved methods latterly used, the increase seems to have ceased. In fact, it seems that rigorous selection is necessary to maintain the sugar content at the level which it has reached. This is but what we should expect, for the probability is that one is continually selecting hybrids, and the hybrid condition as such is unfixable.

A similar process of selection, on a somewhat less elaborate scale, is carried out with other species which have a similar method of reproduction to that of the sugar-beet. The method is somewhat costly and laborious, yet science shows us no more simple method of securing the desired end.

Animal Breeding

If we study the history of the development of economic characters in animals, we must reach the conclusion that most of them have been developed slowly, by a long process of selection. Large mutations are occasionally observed ; the Ancon sheep was one ; the bulldog was probably another. But these large mutations are usually mere curiosities, and are preserved as such. The domestic animals must have been selected for certain valuable characters at the outset, and these characters have been slowly improved, either by the accumulation of small variations or by the gradual building up of certain factor combinations. Under these circumstances we must expect simple relations only rarely. The heredity of economic factors will usually be a complex matter. For example, certain breeds of sheep, such as the Merino, have been selected for fineness of wool. Others, such as the Lincoln, have been selected, among other points, for a long and coarser type of wool. Actually, Lincoln wool may be four or five times as long, and about twice as thick as Merino. If these two breeds are crossed, as they frequently are, the hybrid is about intermediate; and in the subsequent generations there is no obvious segregation into Merino and Lincoln types. The second generation is probably more variable than the first, but in any case we have a highly complex relationship. Our theory is not yet perfect enough to deal with such matters. In fact, as regards the ordinary methods of the animal breeder, theory can scarcely go beyond giving general reasons for what was already known empirically. Briefly, the method of the animal breeder is to select individuals showing as nearly as possible the qualities required, to attempt to balance defects in one parent with excellencies in the other, and to mate together individuals which are neither very closely related nor entirely unrelated.

The degree of relationship which is compatible with

fulness of vigour appears to vary considerably in different species, and in the same species under different conditions. The earlier breeders of Shorthorns, working, as they were, with foundation stock of very mixed character, were accustomed to mate together very closely related individuals—sire and daughter, half-brother and sister, and the like, generation after generation. On the other hand, it is safe to say that few turf winners have been produced by matings of animals more closely related than half-cousins. In any case, continued close "inbreeding" invariably leads to greatly weakened constitution, and often to partial or complete sterility.

We may assume with some degree of certainty that this is due to the reduction of many characters to the pure condition—to the formation of pure lines, in fact—for the loss of vigour occurs in the same manner as in plants. Whether these "pure lines" can actually exist we do not know, but in some animals at least, sterility seems to result before this stage is reached.

It is evident that where a certain amount of inbreeding is practised, there will be less opportunity of variation within the strain. For the number of hybrid characters is reduced, and the type is thus partially fixed. Thus a certain amount of inbreeding introduces an element of certainty into the work of the breeder. The mating of almost entirely unrelated individuals gives, on the average, the most vigorous type of offspring. But it is evident that if this method of breeding is continued, the resulting offspring will tend to be very irregular, for there are chances of widely different combinations of factors.

"Breed 'in' to fix type; breed 'out' to secure vigour; in general, compromise"—this may be said to be a summing up of the experience of animal breeders. Theory may be said to have caught up with practice by suggesting reasons for these rules, but it can offer little in addition. One might perhaps prophesy an extension of the present practice of systematic crossing in order to secure both vigour and uniformity, but there are difficulties in the way of such systems of breeding.

CHAPTER XI

EUGENICS

THE final and most important application of our knowledge of heredity must be with regard to man himself. The science which concerns itself with the improvement of the inherent qualities of the human race has been termed Eugenics. Francis Galton was its founder and its greatest prophet.

It has frequently been remarked that what man has done for the domesticated animals, he has never been able to do for himself. Simply by selecting for further breeding those individuals which were most suited to his needs, he has enormously increased the economic value of the various races of domestic animals. Nothing seems simpler theoretically than that some process should be set on foot which would bring about the selection of the better types of humanity and thus improve the average of the race as regards intellect, character, and physique.

The necessity of some such measure is more urgent than might be supposed. It might be held that, while advances are being made in other directions—as regards education, culture, invention, the control of disease, and so forth—the human race could afford to stand still with regard to its inborn qualities. But it appears that under the conditions of modern civilisation there is a tendency for the race to degenerate.

As long as the human species lived under savage or semi-savage conditions, it was subjected, as the species of wild animals still are, to the action of natural selection. Weak individuals would tend to be carried off by disease or starvation; the strong and the cunning increased and multiplied.

The tendency of civilisation, from its very start, has been to prevent the action of natural selection between individuals. Under modern conditions the weak are protected as far as possible, and, beyond a proportion of our lunatics and habitual drunkards, there are few men who find it impossible to rear families. Natural selection, it is true, has not entirely ceased to operate. Diseases, such as consumption, exercise a selective influence, and alcoholism prevents many more from reproducing ; so that the race is probably progressing towards immunity from consumption and towards natural sobriety. But, on the whole, as regards the main important qualities of physical fitness, moral characters, and intellect, natural selection has nearly ceased to operate.

There remains, of course, a genuine struggle for supremacy among the nations, which has the effect of suppressing very decadent peoples ; but its positive result in the way of improving the species generally cannot be large.

With the domestic animals man has replaced natural by artificial selection, and his results have been little short of marvellous. As regards his own species, he has provided no substitute for natural selection.

But this is not all. It is a recognised fact that in most civilised societies the net rate of increase is considerably greater in the lower grades than in the higher ; the lower and in general less desirable classes tend to multiply at the expense of what are regarded as the better types, and the general average is dragged lower in each successive generation.

With reference to the remedy for this state of affairs, some biologists have regarded the elimination of natural selection as a disaster to the race. They have concluded that the remedy is to be found in a return to a state of the sternest individualism, in which there would be no hospitals or charities, so that the weak and the unfit should receive no encouragement. Modern legislation providing for old-age pensions, unemployment insurance, &c., has been deprecated as tending to encourage the weak at the expense of the strong.

But it is certain that a return to conditions of barbaric competition is impossible, even if it were regarded as desirable on scientific grounds ; and it is far from being so by most authorities. Natural selection can no longer be a very potent factor in the improvement of mankind, and whether we have a little more of it or a little less—whether we have an individualistic or a socialistic organisation of society—will make little difference from the Eugenist standpoint.

The essential thing is that some process of artificial selection should be set on foot. It will have become evident from the preceding chapters that the science of heredity can so far give us no hint as to how we should have to proceed in order to produce at will a statesman or a poet, a philosopher or a general, even a champion footballer or pugilist. Except in a few unimportant details, where definite schemes of inheritance have been made out, we should have to rely on the empirical rules of the animal breeder : select desirable individuals, discourage or prevent the reproduction of undesirables, and prevent the mating of close relations. These rules, however, are firmly enough established to leave us without a doubt as to the beneficial results which would follow their application to man.

Schemes of Eugenics, then, may be either positive or negative—they may aim at the encouragement of reproduction in the specially fit, or at its prevention in the specially unfit. It is in the latter direction that the most practical proposals have been made. An eminently sensible one has been that there should be a medical examination previous to marriage, the requirements being a moderate general physique, soundness of mind, and freedom from such diseases as may be communicated to the offspring. It may be that the reproduction of the unfit would not be entirely prevented in this way ; but that obviously undesirable marriages should continue to be countenanced by Church and State is a deplorable state of affairs.

Practical legislative schemes of positive Eugenics seem almost impossible ; it appears that we must look

to the education of the public to ensure the increased reproduction of the specially fit. We might hope for a better state of matters if our professional and middle-class people could be brought to recognise the public duty of reproduction.

We have merely touched upon this wide subject; its full treatment lies somewhat without the scope of such a book as this. But what we have said may be enough to indicate its importance.

A COURSE OF READING ON HEREDITY

STUDENTS looking for a broad general treatment of the subject cannot do better than read Professor J. A. Thompson's *Heredity* (Murray, 1908). The sections dealing with acquired characters and the germ plasm theory are especially good.

Another general work is Dr. Archdall Reid's *Principles of Heredity*, which contains an excellent treatment of certain practical questions in man—disease, alcoholism, and the like.

On Mendelism, Professor R. C. Punnett's *Mendelism* (Macmillan, 1911) is an excellent semi-elementary work. The recognised authority on this subject is Bateson's *Mendel's Principles of Heredity* (Cambridge, 1909).

On statistical theory, Elderton's *Primer of Statistics* is a valuable little book, not dealing with biological problems exclusively. The best larger work which the writer knows is G. U. Yule's *Introduction to the Theory of Statistics* (London, 1911).

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