

CHAPTER III

THE CAUSES OF VARIATION

IN the last chapter the distinction has been explained between continuous and discontinuous variation ; some confusion has however arisen with regard to the terms used in describing these conditions. Continuous variation about a mean (or more accurately modal) condition is sometimes spoken of as 'fluctuation,' but as will be seen below this kind of variability probably includes two very distinct groups of facts. It may include inherent variability arising in the germ-cells, or it may include differences in the adult condition having their origin in different effects of environment during growth. Some writers have used the word 'fluctuation' for this latter condition only.

Discontinuous variation is sometimes called 'mutation,' a word which also has been used in several senses. It may mean the appearance of a form varying discontinuously from the type, or it may be applied to the discontinuous character itself.

A more serious source of confusion is that the term is used by some to denote any discontinuous variation arising 'spontaneously,' by others for cases in which the variety differs from the type in several apparently distinct characters, and not only in one, so that the new form constitutes an 'elementary species.' Since in studying heredity it is usually important to consider distinct characters separately, it may be permissible to use the word for the origin of a form differing recognisably from the type and not connected with it by true intermediates.

It has already been pointed out that very little is accurately known about the causes of variation, and it is not impossible that the different forms of variation have different origins. Most writers agree that the ultimate cause must lie in the action of environment in some form, but as Darwin clearly stated in the *Origin of Species* the environment may act directly or indirectly. In variation of size for example, it is clear that the supply of nourishment, etc., during growth may have considerable influence on the size of the adult, and such variation will commonly be continuous owing to the evenly graded action on different individuals. In these cases the action is direct. If, however, Weismann's theory of germ-plasm and body-plasm is correct, such action may affect only the body and not be transmitted to offspring. It is also possible that the germ-cells may

be indirectly affected, giving rise to variation in the offspring; in such a case, however, there is no necessity that the effect on the offspring should be in any way similar to the direct effect of the conditions on the parent. Nothing is known of the nature of possible effects of environment on the germ-cells; the action may possibly be effective immediately and give rise to variability in the next generation, or it may be that the effects are cumulative and only cause visible changes after several generations have been exposed to the same influences. Galton [13] suggested that the organism may have a certain 'stability,' but *that influences acting for several generations may have a cumulative effect which will gradually alter the equilibrium until it is finally upset and falls into a new condition of stability, giving rise to an apparently sudden variation.* A chemical analogy may make this clearer. If litmus is added to an alkaline solution its colour will be blue. Acid may now be added drop by drop to neutralize the alkali, and suddenly, when the solution becomes acid, the litmus turns red. Examples of variation of which this may possibly be an analogy will be given below.

With regard to the action of environment on the body many facts are known, but it is not certain that they really have any bearing on the question of the origin of variation. For variations so produced are 'acquired characters,' and in many cases at least

there is no evidence that they are inherited. For example, many butterflies have two generations in the year, one of which lives through its whole life-history in the summer and the other passes the winter as a pupa (chrysalis). In some cases the two generations are strikingly different, and it has been shown that by freezing the pupae of the summer brood at the right stage, specimens like the spring brood can be obtained. The difference between the two generations is thus due to the action of cold on the pupa. But the two forms regularly alternate in nature and the effects of cold are not inherited. In plants, some species produce quite different leaves according to whether they are grown in water or in dry soil, but the conditions act on the individual, and do not affect its progeny. In such a case, what is inherited is the faculty of making a certain definite response to definite conditions, and this faculty is present whether the conditions operate or not. In man such diseases as tuberculosis are commonly called hereditary; this however does not mean that the child has the disease because his parent had it, but that the parent had a constitution liable to that disease, and the child inherits a similar constitutional liability. If the parent had never been exposed to infection the child would still inherit the liability, for what is transmitted is not the disease or its effects, but the faculty of acquiring it if exposed. It will be found

that most cases which at first sight seem to support the theory of the inheritance of acquired characters are equally explicable in the view that both parent and offspring are susceptible to the action of the external factor ; what is inherited is not the character acquired, but the innate power of acquiring it.

But it is always possible that some forms of external conditions may act on both the body-cells and germ-cells concurrently, and produce similar effects in each. For example, it may happen that extremes of temperature produce striking colour-variations in certain butterflies. Weismann has pointed out that, according to his theory, in a developing butterfly the determinants for producing colour not only exist in the germ-cells which will transmit the character to the offspring, but also in the embryonic cells of the body which go to produce the coloured parts of the perfect insect. If extremes of heat or cold cause changes in the colour-determinants in the developing wings, so that abnormal colours result, it is possible that the determinants in the germ-cells which transmit the colour-pattern to the next generation will be similarly modified, so that the offspring will show similar abnormalities. This would not be the transmission of an 'acquired character' in the strict sense of the expression, but the simultaneous modification of body and germ-cells in the same manner.

But as mentioned above, it is possible that the same factor acting on body and germ-cells may produce different results in the two cases, so that the individual on which the influences have acted may show one modification and its offspring another. It is also possible that not all the germ-cells will be affected alike, and so among the progeny some will show modification and others not, or some may be differently affected from others; for the conditions of stability of different germ-cells may conceivably be different. Certain experiments on insects give reason for supposing that this is so. The results obtained by Fischer, Standfuss and others from exposing pupae of butterflies and moths to abnormal temperatures, while not entirely concordant among themselves, on the whole indicate that moderate degrees of heat and cold tend to alter in the same way the whole batch of insects treated, often in the direction of varieties of the species naturally occurring in warmer or colder climates. But excessive heat or cold causes extreme variations among only a small proportion of the insects treated, and among the offspring of these abnormal specimens only a small fraction are abnormal, and *some of these have not the same abnormality as the parents.* These observations, together with the fact that the variations produced by heat, cold, and other disturbing factors, may all be similar, suggest that extreme conditions may upset the stability of the type, causing abnormalities to appear,

and that some of the germ-cells may also be altered, but not necessarily in the same manner as the body-cells.

An American zoologist, Tower, describes the production of mutations by the action of environment in a beetle (*Leptinotarsa*). In nature he found about one such variation among 6000 specimens ; when bred in captivity they were more frequent, but when the full-grown beetles were exposed to extremes of heat, humidity, etc., during the maturation of the eggs, the offspring may include a large proportion (over 80 per cent.) of 'mutations.' These were of several distinct kinds, like those rarely found in nature, and when bred together they are stated to breed true. In this case the abnormal conditions produced no effect on the individuals exposed to them, for they already had their final form, but as their eggs were matured under these conditions the action took effect on the eggs, and mutation resulted among the offspring. When part of the eggs of an individual were matured under abnormal, another part under normal conditions, mutation occurred only among the offspring in the first case, all the beetles in the second being normal. It should be noted that as in the experiments with butterflies the effect of changed conditions was not specific ; the same conditions may produce more than one kind of mutation in the same batch of eggs, and some eggs were not affected at all. In both cases the abnormal environment seems to upset

the equilibrium, but the effects may differ in different individuals. It is the nature of the organism or germ-cell affected which determines whether and to what extent the change shall take place; the environment merely supplies the stimulus.

It will be seen that our knowledge of the causes of variation, in so far as these are connected with environment, is very incomplete and unsatisfactory, for although it is fairly clear that conditions may sometimes disturb the equilibrium of the germ-cells and provide a stimulus to variation, yet we have no knowledge of the way in which the stimulus acts *and can make no prediction as to the direction the variation will take.* Before leaving the subject, one other cause of variability must be mentioned—the effect of crossing different races in producing variation. It frequently happens that the result of *crossing distinct races is that the crossed individuals differ from either parent; sometimes in the direction of increased vigour, as was pointed out by Darwin, and other more recent observers; sometimes by the development of characters apparently not possessed by either parent, as in the case of ‘reversion on crossing.’* The cause of this latter phenomenon will be discussed in a later chapter. In the subsequent generations from the cross great diversity may often appear, and Darwin supposed that the mingling of two distinct germinal stocks had an effect in dis-

turbing the equilibrium similar to that produced by change of environment. To some extent this is doubtless true, but recent developments of the theory of heredity have afforded a more exact explanation, in the recombination of the different characters of the two races which are crossed. A fuller account of 'variation induced by crossing' must therefore be postponed until the principles of heredity have been discussed.

One further question should be mentioned before proceeding to the subject of heredity, namely, the relative importance of 'inherent' and 'acquired' characters in making up the sum of characters of a mature individual. It is often assumed, especially in human cases, that the environment has a preponderating influence in shaping the individual. In a certain sense this is true, for many characters can only develop in a suitable environment; muscles must be exercised to be properly formed and the *mind cannot develop its full powers if it is never used*. But the study of variation leads inevitably to the conclusion that the inherent characteristics are all-important, and that the effect of environment is not much more than to give them opportunity to develop. This is perhaps most impressively seen in the case of 'identical twins,' as has been shown by Galton [12]. There is reason to believe that such twins are produced by the division of one ovum, and

even if exposed to different conditions they remain through life much more alike than ordinary brothers who may be brought up under precisely similar surroundings. The same fact is still further emphasised by the study of heredity.