ORGANIC EVOLUTION

OUTSTANDING DIFFICULTIES AND POSSIBLE EXPLANATIONS

(1) The selection of infrequent mutations and the inheritance of acquired characters could not alone account for evolution.

THE theories of evolution associated with the name of Charles Darwin have been keenly criticised in recent years, and in some respects these attacks are sure to produce permanent results. This must be in a measure the fate of all scientific enquirers who break new ground, and that it would be so in his case was doubtless anticipated by the author of the *Origin of Species*. The criticisms of Darwin's works have, however, not infrequently been unjust, an injustice which has sometimes arisen from ignorance of the aims which he had in view. His objects were to show in the first place "that species had not been separately created, and secondly, that natural selection had been the chief agent of change, though largely aided by the inherited effect of habit, and slightly by the direct action of the surrounding conditions[1]." The first of these objects, that is, the establishment of a belief in descent with modification, was always held by my father to be the more important of the two; for I once heard him say, if a recollection of about fifty years' standing may be trusted, that "after

[1] *Descent of Man.* 2nd Edition, Vol. I. p. 92.

all, evolution is the great thing, not natural selection." The public do not now realise how few persons admitted the truth of this "great thing" when he began his enquiries; and as to scientific men, they now look on organic evolution as being such a well established fact that their attention is directed only to questions concerning those methods by which evolution may have been brought about which are still disputable. In consequence they sometimes forget that Darwin was entirely successful in what he regarded as his main object.

If we turn to the secondary objects which the author of the *Origin of Species* had in view, namely the discovery of the ways in which descent with modification has been slowly brought about in the past, we see that since his day great changes have taken place in the generally accepted opinions concerning the inherited effects of habit. Weismann succeeded in nearly destroying for a time all belief in the racial effects of use and disuse, whilst now the pendulum is swinging somewhat back again towards the acceptance of the inheritance of acquired characters as a factor in evolution. It is not my intention now to touch on this controversy, or to discuss to what extent, great or small, use and disuse have been the direct causes of evolutionary changes, except merely to state my reasons for holding that in respect to many or most structures the inheritance of acquired characters must at all events have been aided or controlled by natural selection in order to have produced the organic forms now in existence.

In the first place the amount of use to which in bygone times different structures of the same organism were being put cannot in many instances have

tallied with the need for their growth in order to have produced the innumerable complex adaptations now found in nature. To illustrate this point, the development of the maternal instincts may be cited as a single example. Amongst many animals we find that the mother's affection for her young forces her to risk her life freely for their protection, whilst it does not so completely overcome her sensations of fear as to prevent her from abandoning her progeny when the danger becomes extreme. This balance of instincts seems to make for the survival of the species, and it may, therefore, have been produced by natural selection. But there seems no reason why a state of things tending to promote survival should have resulted from the inherited effects of use; for the relative strength and duration of the sensations of fear and affection do not necessarily bear any relationship to the need for the development of these qualities in such a way as to assist in the struggle for existence.

A more important difficulty in the way of those who seek to attribute evolutionary effects to the *unaided* influence of the inheritance of acquired characters may be illustrated by reference to the growth of muscles through the stimulus of exercise. If the growth of a muscle due to exercise in any one generation merely resulted in the *same* amount of growth following on the average the *same* amount of exercise in the *next* generation, this would be the result which we should anticipate judging by the ordinary laws of inheritance; and we should find in this fact no explanation of the process by which the muscle had been evolved so as to have attained its present dimensions and, therefore, no clue to the process of

evolution. To afford such a clue, must not the inheritance of acquired characters mean in this instance that the growth of a muscle through exercise in one generation would result in that muscle being *more* developed in the coming generations after having received the *same* amount of stimulus from exercise? Muscles are, however, used in every generation, and if this were the only relationship which existed between exercise or use and racial development, would it not follow that in every animal each muscle would always be bigger than was that same muscle in the preceding generation? If there were no other agency at work but the inheritance of acquired characters, would not the inevitable evolutionary result be an indefinite increase in the size of every muscle? In many cases obviously this would have produced extremely harmful results of a kind that are in fact seldom found in nature; and it must, therefore, be assumed that some other agency has always been at work preventing these evil consequences from arising. Can any other brake but natural selection be suggested as that by which this tendency for use[1] to cause an indefinite racial increase in the size of all the structures used has been brought to a standstill?

But even if natural selection be accepted as having been an efficient co-operating agency in preventing overgrowths in the evolutionary process, our difficulties are not thus all cleared out of our path. Structures have often grown less and less as the generations succeeded each other until they quite disappeared; and, to account for this disappearance,

[1] For the inheritance of acquired characters to have produced very wide evolutionary effects, must not 'use' include the growth or development of all organic structures?

'disuse' has often been suggested as having been the cause. Even if it be admitted that without selection disuse may form the basis of a rational explanation—and possibly the only rational explanation—of the disappearance of some *useless* structures, we yet have to account for innumerable instances in the evolutionary process of *useful* structures having merely become diminished in size without having vanished. Those who in such cases also rely on 'disuse' as having been the cause can hardly have considered what meaning they wish to be attached to the words they use; for the structures thus held to have been diminished in size by 'disuse' must in many cases have been in constant 'use' in every generation. But if we should decide to adopt unusual meanings for our words, making the 'disuse' of a muscle merely imply that it is not being as much used, and 'use' imply that it is being more used than was that same muscle in the *previous generation*, then we shall find that use and disuse as thus defined may very likely be properly relied on when laying the foundations of a theory of organic evolution which is at all events logical. To illustrate this point allusion may be made to the suggestion that internal secretions form the connecting link between the structure and the germ-plasm by means of which use and disuse are made to produce hereditary effects. If the average growth of a muscle in a given generation resulted in the production of a certain quantity of the appropriate secretion, and if this particular *quantum* of the secretion were such as to produce no effect on the germ-plasm, then in an evolutionary sense the organism would be in a state of equilibrium as far as the development of that particular muscle was concerned. But if a greater

use of the muscle, besides increasing its size, were to make it produce a greater amount of the secretion, and if the *additional amount* of the secretion produced above the *quantum* were so to affect the germ-plasm as to make the muscle become larger in the next generation after the same amount of use, then this acquired character would be inherited. In the same way we can conceive that a reduction in the size of the muscle through lessened use might also be a heritable character in consequence of the secretion being produced to an amount below the *quantum*. It would, however, still have to be admitted that an increase or a decrease in use above or below the original amount of use would lead to an indefinite increase or decrease in the size of the muscle unless this tendency were checked by some such agency as natural selection. In fact there must exist some method of restoring racial equilibrium when an organism has again come to be well suited to its surroundings, a restoration which would be accomplished if the different secretions came to be produced only in such quantities as to have no effect on the germ-plasm. May not this result be brought about by natural selection in the following manner? Let it be assumed that the size of the *quantum* of the secretion which does not affect the germ-plasm is a variable quality or differs amongst the different individuals of the species[1]. Taking the case of a muscle which had been increased in size by the inherited effects of use up to a point where a further increase would on the whole be harmful, natural selection would then begin to come into play by eliminating not only those individuals which would in any case possess exception-

[1] The sensitiveness of the germ-plasm might also be the variable.

ally large muscles, but also those in which the production of the secretion was exceptionally large. Would not this process go on until, by the survival of individuals both well suited to their environment and producing such a *quantum* of the secretion as would not affect the germ-plasm, a state of equilibrium had again been established?

Thus we see that by assuming the efficacy of either secretions, pangenesis, or any other connecting link between use and disuse and racial development, a system of inheritance of acquired characters does become a logical possibility. Judging by the way in which useless characters have disappeared, and considering the necessity for some mechanism resulting in a restoration to a state of equilibrium, evolution as the result of use and disuse seems likely to have been an exceedingly slow process; a conclusion which in no way tells against a belief in this method of producing racial changes. It has, however, been claimed that the inheritance of acquired characters is the simplest explanation of evolution; but if it necessitates the admission of the efficacy of natural selection, and if natural selection has to be brought into play in this complex manner, this claim becomes at least very doubtful.

In the foregoing discussion on the inheritance of acquired characters I have tacitly assumed the absence of any vitalistic principle or continuous modification of the action of the forces of nature. To discuss the validity of making any such assumption would open out a subject too wide here to be dealt with; and I will only say that what I have assumed does not necessarily involve the belief that science alone can solve the riddle of the universe. As to the direct

effects of environment, that is as to mutations directly caused by the action of external conditions on the germ-plasm, this is a factor on which Neo-Lamarckians have to rely to a considerable extent; and here it is even more evident that they have to choose between placing reliance on selection as a necessary co-operating agency and trusting to some vitalistic principle. If mutations directly due to environment were only to make their appearance in directions making for survival, it would be necessary to hold that their production was guided by some unknown external agency or by some *sentiment interieur*, to use Lamarck's phrase. But to rely on any unexplained law limiting mutations due to environment to such as do make for survival is almost to abandon a belief in organic evolution; for the essential feature of such a belief is to hold that descent with modification has been brought about by natural causes all of which might still be operative. Those who believe that evolution is now explicable must, therefore, maintain that the nature of these environmental mutations has no relationship to the survival of the species, and that it is only natural selection which makes them play a useful part in the evolutionary process. In fact it seems that the chief function of use, disuse, and the direct effect of environment has been to create mutations on which selection was able to act effectively. The main point here insisted on is, however, that for the foregoing reasons, together with others which I am incompetent adequately to discuss—such, for example, as those based on the wonderful instincts of worker bees—we must hold that the inheritance of acquired characters and mutations due to environment cannot alone account for the appearance of all the

existing forms of organic life. Rule out selection and evolution becomes inexplicable.

We must, therefore, next consider whether selection can in truth do all that is necessary to make up a complete theory of organic evolution. The controversies concerning the part played by natural selection have often turned on whether the mutations which are necessary to serve as a basis on which it could act have been large and infrequent (and to these the term mutation has often been exclusively applied), or small and frequent (which have been inaptly described as continuous variations). Adopting the word 'mutations' to cover all original modifications in the germ-plasm, I am not here concerned to enquire what part has been played by large mutations in the evolutionary process, but merely to indicate as briefly as possible why they cannot supply all that is needed in the way of explanation.

The difficulty of always relying on large mutations, which never do occur frequently, becomes most readily apparent when studying those cases of adaptation which must have necessitated modifications of a suitable kind having taken place nearly simultaneously in several different parts of the same organism; the classical instance being the increase in the weight of the stag's antlers and the necessary increase in strength and size of the neck and shoulders to bear the greater burden. It has not, I think, been as a rule sufficiently clearly realised how extraordinarily seldom all the necessary mutations would occur at the same time in the same individual. Imagine, for the purposes of illustration, a mutation which occurs on the average once in every thousand organisms; that is such a mutation that, if it occurred in man, would show itself in about fifty thousand inhabitants

of the United Kingdom. Then it can be demonstrated that, if dealing with mutations which are in no degree correlated, it would be as likely as not that we should have to wait for over ten thousand generations for four of these mutations to appear in these islands simultaneously in any one individual. That all four of these large mutations would, when they did appear, all be of about the right relative magnitude to produce proper adaptation, would be very improbable. And even granted that such a prodigy of adaptation would appear at extraordinarily rare intervals, the newly appearing Mendelian factors would become widely scattered amongst different organisms after a few generations of random mating; the proper adaptation would no longer exist; and if the changes of character were in themselves harmful when standing alone, these mutations would be eliminated by selection during the immense period of time which would elapse before they would all be again united in one individual. Whatever it may be which produces a change in one structure is no doubt likely to produce changes in other structures also. But unless we can assume that all the changes due to one mutation will be so related to each other as to produce the needed adaptations (as the result of some *sentiment interieur*?) the arguments against the efficacy of large mutations which are based on probabilities, though changed in form, yet are not invalidated by the fact that several parts of the organism are often simultaneously affected; for the greater the number of structures suitably affected by one mutation, the rarer would be the occurrence of such a mutation. It follows that if trusting entirely to the effects of large and infrequent mutations, every adaptation must have been the result either of a number of mutations each