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ADAPTATION AND MUTATIONS

A LECTURE TO THE SCIENCE MASTERS' ASSOCIATION,
JANUARY 5, 1934

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THE word adaptation, like nearly all the words which have come into use in evolutionary discussions and have been bandied about in controversy during the last seventy years, has acquired in the course of time more than one meaning. It is sometimes used for the process of becoming adapted, necessarily a hypothetical process, about which we can know nothing except by inference. I want to use it here in a different sense ; for an observable fact, the state of being adapted, of conformity between structure and function, which can be recognized or appreciated by a sufficiently careful examination of a living being, in just the same way as if we were to examine any piece of mechanism, like a bicycle, without preconceptions, as a child or a savage might examine it. We could, with sufficient care and patience, see that the different parts, the chain or the pedals or the bearings, were specially designed for what they had to do, and would do it worse, or fail altogether, if they were made differently.

As such, adaptation is an observable fact, and I believe it is no exaggeration to say that it is the most striking and obvious fact observable throughout the animal and plant kingdoms. But there is one circumstance which stands in the way of its receiving its full weight in those theoretical discussions and works on general biology in which questions of principle are discussed. It is almost impossible with any brevity to exemplify the notion of adaptation. Just because adaptation consists, even in the simplest cases, in a multiplicity of correspondences between one sufficiently complicated system, the organism itself, and another equally complicated, the environment in which it finds itself. It is, indeed, just this multiplicity that makes the thing recognizably adaptive. So that, even in the simplest cases that one can think of, such as a cat's

School Science Review, 15: 294-301, (1934).

claws, the adaptiveness cannot be properly appreciated without rather lengthy consideration of such concomitants as the retractible mechanism, the protective pads, the neuro-muscular adjustments underlying the quick snatching movements of the forelimbs, and the geometrical advantages of the way the claws are themselves curved. And each of these points carries its full conviction only after somewhat careful study.

In general, adaptation is easy enough to notice, but very difficult to observe or to describe properly. And the weight to be given to adaptation as a general fact is not to be appreciated by the attenuated abstracts which find their way into works of general discussion, but only by following the full detail of the descriptions and experiments published in those comparatively few cases which have received the detailed investigation that they deserve. Such cases, I mean, as the description recently given before the Royal Society by Dr. Wigglesworth of the climbing organ found on the foot of some species of South American bugs ; or of that mud-boring larva described by Poulton which, to avoid the pupa into which it will form itself being exposed when the mud dries up and cracks, by patient circumambulations predisposes it to crack round a circular cylinder, in the midst of which the pupa will lie safe from attack.

Now the attitude taken up towards adaptation by contemporary zoologists exhibits a profoundly interesting cleavage of opinion. In genetical circles, where mutationists chiefly predominate, adaptation is so little emphasized as to be scarcely mentioned, save with a half-contemptuous reserve, as of one defending himself from the charge of really believing in fairy tales. In Lamarckian circles, on the other hand, one may hear certain adaptations not only emphasized but, one might say, triumphantly brandished as indisputable proofs of the Lamarckian contention. One reason for this contrast is obvious. The mutationist has no explanation to give of adaptation as an observable fact; the furthest he can go towards recognizing it is in the lukewarm theory of preadaptation, in which a new form is supposed to arise spontaneously, and, if it has the good fortune to discover an unoccupied environment to which its new characters happen specially to fit in, to establish itself there as a successful species.

On the contrary, adaptation, or the striving to improve adaptation, is the mainspring of the Lamarckian theory, and in this it resembles Darwinism. For, on these two theories, evolutionary progress is taken to consist merely in the gradual perfection of adaptations, while all other changes which supervene, leading to the formation of new species, genera or families, are merely adventitious by-products of the process of becoming better adapted,

Though they agree in this important matter of making the tendency towards improved adaptation the mainspring of evolutionary change, Lamarckism differs profoundly from the selectionist theory, not only in the way that is well recognized, in postulating heredity for some kinds of variation not usually regarded as inherited, but in the whole basis of its evolutionary argument. For Lamarckism is not really a theory of evolution at all, but a theory of the production of mutations, and of the causes which are competent to bring mutations about, If it were true, as Lamarck was ready to assume, that the desires of animals, or their subconscious strivings, were competent to produce heritable changes in the germinal material, or if, as some neo-Lamarckians more materialistically assert, functional use and habit were capable of producing such effects, we should know something more than we do about the causation of mutations, but it would still be questionable whether the mutations so caused were capable of producing any evolutionary effect. In this matter the selectionist is in quite a different logical position. As far as his theory is concerned, he is quite indifferent as to the cause of mutations, so long as they are produced somehow, with the rather minute frequency necessary to maintain a stock, or pool, of heritable variability. Given that heritable variability, it can be seen, or rather, I should say, it can be rigorously demonstrated, that differences in the rates of death and reproduction will produce a constant modification of the species, in whatever directions lead to a more perfect adaptation to the circumstances in which it exists. The interest of the selectionist is centred in the complicated chain of causation which lies between the occurrence of the mutations, and the evolutionary changes which are in progress. But this gap is bridged, in the Lamarckian theory, and, indeed, in all alternative theories, such as those which go by the names of Orthogenesis or Nomogenesis, by the easy, but questionable, assumption that the prevalent direction in which mutations are taking place determines the direction in which evolutionary progress must supervene.[1]

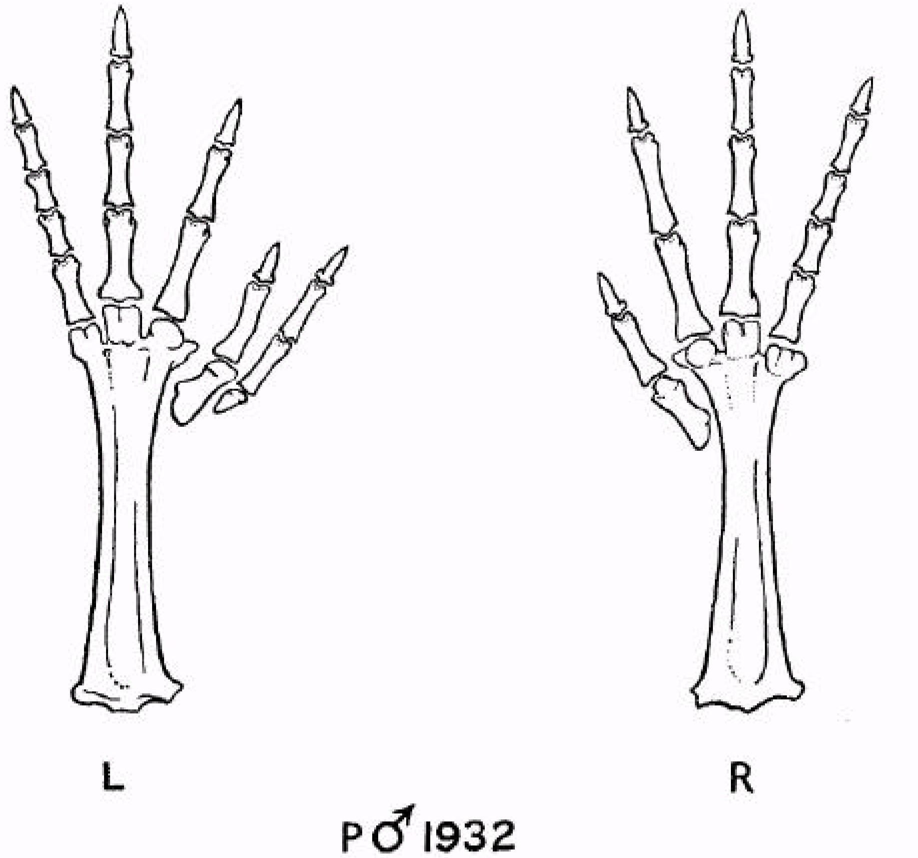
[1]A clear expression of this "obvious" assumption was quoted by W. Bateson in 1909 : "As Samuel Butler so truly said : ' To me it seems that the "origin of variation," whatever it is, is the only true "origin of species." '"

To take a concrete example, if it could be proved that the mutations taking place in the crocodile were predominantly such as tend to lengthen the neck; whether these were caused, as a Lamarckian might suppose, by the efforts of the animal to lengthen its neck being more frequent or more violent than its efforts to shorten it; or whether, on the orthogenetic view, the species had been endowed with some kind of inner urge towards producing mutations of this kind, it might still be denied that this fact afforded any solid ground for believing that the average length of the neck would in fact increase from generation to generation. It is not obvious that any phylogenetic change at all will be produced, or that it will not take place in the opposite direction, and it is only by assuming that this is obvious that Lamarckism, Orthogenesis and Mutation-theory can claim to be theories of evolution, rather than merely theories of the origin of mutations.

That it is not obvious I can illustrate with a fairly typical mutation, that of polydactylly in poultry, which I have been breeding for the last few years. The typical manifestation is an extra toe growing outside the hallux. As often as not, in my material, this is supported by an additional metatarsal, similar to that of the hallux, but unlike the hallux, the additional toe has two phalanges as well as a claw. It is not a mere twin of the hallux, such as one might suppose would arise, if, owing to some check in development, growth had taken place from two centres instead of from one. The bony structure is illustrated in the figure (page 298).

What makes this mutation interesting from an evolutionary standpoint is the complete uniformity, in their structural units, of the feet of other birds. There must be more than ten thousand species of birds, and although the feet of a hawk, a parrot, or a duck differ greatly in the sizes, positions and curvature of their components, the bones are the same in all. I believe the only exceptions that exist in the whole group consist in the simple loss of two toes in the ostrich, and of one toe in some of the other struthious birds. Apart from this, evolution in the structural components of the foot has simply not taken place, although the class is a large and varied one, and must have been in existence for some 50,000,000 years.

Now it would be straining the possibilities of coincidence to assume that the domestic fowl is the only bird in which the structure of the foot is liable to mutation, or that the human period is the only one in which such mutations occur. Indeed, I understand that polydactylly has been found also in ducks and in pigeons, though I do not know how far these mutations are similar to the one we have in poultry. We can only avoid a gratuitous assumption, of high improbability, by admitting that at least thousands of species of birds have from time to time shown mutations in their bony structure right outside the limits of variability of normal members of the entire class. Indeed, we should have to go as far



Diagrammatic drawing of the skeleton of the feet of a heterozygous cock. The right foot is entirely normal, the left shows full development of the extra hallux.

as the toads to find an extra hallux as a normal structure. Whether this has any connection with the mutant toe in poultry it is impossible to say, but it is at least clear that the mutant activity of the kind under consideration, within the class of birds, has been entirely fruitless of any evolutionary consequence.

A single example, however clear, must be insufficient to bring home the full conviction, which the study of mutations gives, of their general inefficacy as causes of evolutionary change. A very large number of mutations have, however, been found in the different species of *Drosophila* which have been bred experimentally. About 300 are known in *D. melanogaster*. None of these can be regarded as probably advantageous in the wild environment. The great majority are very obvious defects and deformities affecting principally the wings and eyes, but sometimes the body and legs. Beyond these, however, there are a much larger number which are completely lethal, in that the mutant fly is incapable of developing beyond the larval stage, and often even beyond the egg. If it could be assumed that the mutations observed in *Drosophila*, i.e. the largest and most frequent of those occurring in that species, pointed the direction of its evolutionary progress, we should have to assume that the flies of this genus were degenerating to a flightless, sightless and finally inviable condition. If we do not believe this, we must admit that the greater part of the mutational activity to be observed is completely ineffectual in regard to evolutionary consequences. In asserting this, however, there is no reason to deny that a minority of mutations, especially those which are rarer and slighter in their effects, may contain the ingredients out of which adaptive improvements will, in the future, be built up. Just as it is the existing fund of heritable variation, supplied by the mutational activity of the past, which is the means by which any selective modification now in progress is made possible. It is only of the majority of mutations that it can be said that their effect is deleterious to the individuals in which they occur, and would be deleterious to the race, were they not being constantly eliminated by counter-selection.

It is sometimes said that civilized man is in racial danger because natural selection has been abolished, and because, in consequence, the deleterious mutations which must continually be taking place will accumulate and become more frequent. Now, without in the least admitting that natural selection has been abolished in civilized man, there is every reason to think that the mutations to which he is exposed are as disastrous as in other species. Many mutations in man are known, causing physical deformity, deafness, many defects of the eyes, some involving complete blindness, idiocy and insanity; and it is certainly important that the frequency of these defects should not be allowed to accumulate. There is, however, no reason to suppose that the mutations causing these defects have, individually, in any case, an especially high mutationrate ; and with mutation rates of the order with which we are familiar in experimental material, something like 1 in 1,000,000 in each generation, the accumulation of such defects from this cause must be exceedingly slow. Indeed, there is every reason to think that the incidence of defect could be decreased, rather than allowed to increase, by a common-sense policy of encouraging defectives, and members of defective strains, to refrain from parenthood, and by putting facilities, such as sterilization, within their reach to enable them to do so.

The danger to civilized man, as it seems to me, does not lie in the supposed abolition of natural selection. What has been, to a considerable extent, abolished, is only the death-rate of infants and children, between birth and the reproductive ages. Changes in the death-rate at ages subsequent to reproduction are, of course, without evolutionary effect. But the death-rate is only one of the agencies through which natural selection acts. Reproduction in man shows enormous variability both among individuals and between different classes of the community. The magnitude of these differences is sufficient to bring about genetic changes in the whole population in the course of only a few generations, whereas, in the case of most wild species, it is probable that even in the course of several hundred generations only very small genetic changes are brought about. Instead of saying that natural selection has been abolished, then, it would probably be true to say that it is acting on civilized man with unparalleled violence, the intensity being a hundred or a thousand times greater than is usual with other species.

We may recognize the exceptional violence of selective modification in man by means of two sociological observations. One is the differential birth-rate between different occupational groups. It is probably true at the present time that the entire group of occupations yielding incomes of more than £250 or £300 a year is producing less than half the number of children needed to replace their parents. It is a familiar fact, also, that into this occupational group are being continually drafted the ablest and most enterprising children selected from every stratum of the population. The improvement and extension of the educational system, and, indeed, every step of progress that is made towards the ideal of giving to ability, wherever it may arise, the fullest opportunity of a professional career, only make it more certain that the elimination of professional stocks constitutes the elimination from the race of just those qualities which we recognize as most valuable in the working of a civilized society,

As some of my readers may already know, I have proposed elsewhere[1] that a rational account can be given in terms of known biological facts of how it is that natural selection is acting in civilized man in so dangerous a way. We do our best, with considerable, and, I believe, increasing success, to ensure the social promotion of persons gifted with qualities of value to society, and we thereby produce a natural contrast, entirely harmless in itself, between the innate abilities of persons born in different strata of society. But socially valuable qualities are not the only ones which, in our economic system, raise a family from a less to a more affluent class. Infertility, whether due to physiological or temperamental causes, and whether acting through the postponement of marriage, or the limitation of births, is, and has for centuries been, a cause of social promotion. So that we have every reason to anticipate, theoretically, and on the same grounds, two verifiable observations : (i) that the children of the better-paid classes shall, on the average, be more gifted, and (ii) that families in these classes shall be smaller than in the population at large. The opposite inferences are also verifiable, if we take not the most prosperous, but the least prosperous, section of the population, to compare with the remainder. What civilized society has succeeded in doing is to harness the most powerful of selective forces, namely, that engaged in the elimination of infertility, to the task of eliminating that whole body of qualities which we consider most valuable to society.

Whether the remedy for this peculiar biological situation is to be found, as I suggest in the book referred to, in a contributive system of family allowances, I must leave to readers of that book to judge. Perhaps I may express the hope that those who are inclined to reject this particular solution should at least go into the matter sufficiently carefully to satisfy themselves that the biological difficulties can be met by any preferable alternative remedy.

[1] *The Genetical Theory of Natural Selection,* by R. A. Fisher, Sc.D., F.R.S. Oxford: The Clarendon Press, 1930.