Adaptation.[1]

By Prof. D. M. S. WATSON, F.R.S.

THE only great generalisation which has so far come from zoological studies is that of evolution—the conception that the whole variety of animal life, and the system of inter-relationships which exists between animals and their environment, both living and non-living, have arisen by gradual change from simpler or, at any rate, different conditions.

Evolution itself is accepted by zoologists not because it has been observed to occur or is supported by logically coherent arguments, but because it does fit all the facts of taxonomy, of palæontology, and of geographical distribution, and because no alternative explanation is credible.

Whilst the fact of evolution is accepted by every biologist, the mode in which it has occurred and the mechanism by which it has been brought about are still disputable. The only two 'theories of evolution' which have gained any general currency, those of Lamarck and of Darwin, rest on a most insecure basis; the validity of the assumptions on which they rest has seldom been seriously examined, and they do not interest most of the younger zoologists. It is because I feel that recent advances in zoology have made possible a real investigation of these postulates that I am devoting my address to them.

Both Lamarck and Darwin based their theories on the assumption that every structure in an animal had a definite use in the animal's daily life or at some stage of its life history. They understood by adaptation a change in the structure, and by implication also in the habits of an animal, which rendered it better fitted to its "organic or inorganic conditions of life". Thus, for Darwin at any rate, a general increase in the efficiency of an animal was an adaptation. But amongst his followers the term came to imply a definite structural change of a part or parts by which an animal became better suited to some special and characteristic mode of life. The adaptation of flowers to ensure fertilisation by definite species of insects is a characteristic case. Such definite adaptations can only be shown to exist by very long continued observation of the animal under its natural conditions of life. In the post-Darwinian literature the suggestion that such and such a structure could be used for some definite function is too often regarded as evidence that in fact it is actually so used. My colleagues amongst the palæontologists are, I am afraid, offenders in this way.

Even if it can be shown that the structure of an animal is such that it is specially fitted for the life which it in fact pursues, it does not necessarily follow that this structure has arisen as a definite adaptation to such habits. It is always conceivable, and often probable, that after the structure had arisen casually, the animal possessing it was driven to the appropriate mode of life.

The only cases in which we can be certain that adaptation in this true sense has occurred are those, unfortunately rare, in which we can trace in fossil material the history of a phylogenetic series, and at the same time establish that throughout the period of development of the adaptation its members lived under similar conditions.

It is not unusual for a student of fossils to discuss the habits of an extinct animal on the basis of a structural resemblance of its 'adaptive features' to those of a living animal and then to pass on to make use of his conclusions as if they were facts in the discussion of an evolutionary history or of the mode of origin of a series of sediments.

In extreme cases such evidence may be absolutely reliable: no man faced with an ichthyosaur so perfectly preserved that the outlines of its fins are visible can possibly doubt that it is an aquatic animal, and such a conclusion based on structure is supported by the entire absence of ichthyosaurs in continental deposits of appropriate ages and their abundance in marine beds. But if extremes give good evidence, ordinary cases are always disputable. For example, there is, so far as I know, not the least evidence in the post-cranial skeleton that the hippopotamus is aquatic: its limbs show no swimming modification whatsoever, and the dorsal position of the eyes would be a small point on which to base assumptions.

Most palæontologists believe that the dentition of a mammal, and by inference also that of a reptile or fish, is highly adaptive, that its character will be closely correlated with the animal's food, and that from it the habits of an extinct animal can be inferred with safety.

Here again the extreme cases are justified; the flesh-eating teeth of a cat and the grinding battery of the horse are clearly related to diet. Crushing dentitions, with the modification of skull and jaw shape and of musculature which go with them, seem equally characteristic. I had always believed that the horny plates and the jaws of the platypus were adapted to hard food, and that that animal possessed them, whilst the closely allied *Echidna* was toothless, because it was aquatic and lived in rivers which might be expected to have a rich molluscan fauna that could serve as food. But the half-dozen specimens the stomachs of which I have opened contained no molluscs whatsoever, and seem to have fed on insect larvæ, the ordinary soft bottom fauna of a stream. I do not know whether this is an accidental occurrence, dependent on a special abundance of insects in the Fish River in late spring, or whether it really represents the normal food. Nothing but continued observations made throughout the year can justify any statements about this case.

In the face of this uncertainty, can we make use of the character of the dentition of fossil vertebrates for the determination of the nature of their food, and thus by building up phylogenetic series investigate the gradual development both of habit and their adaptation? One without the other is valueless. The classical case of the horse is, of course,

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familiar to everyone. From the time of Huxley the story of the gradual increase in depth of crown of the molar teeth and in the complexity of the pattern formed by the worn edge of the enamel which coats the cusps of the molars has been held to show a steady improvement in mechanism which enabled the Equidæ to take advantage of a wide extension of grass land which was assumed to have occurred in Miocene times.

This assumption in its ordinary form, however, rests on the basis of an inadequate analysis of all the factors involved. The modern horses are bigger than those of the Eocene: an ordinary hackney weighs about fifty times as much as *Eohippus venticolus*. Thus, the modern horse will wear away in a day fifty times as much tooth as its ancestor; but the surface area of its cheek teeth is only about fifteen times as great, so that without a deepening of the tooth crown by three and a third times it would have a shorter life. Actually the crown is deepened about thirteen times, so that its potential longevity is increased to about four times that of *Eohippus* on the assumption that the abrasive qualities of the food of the two animals have not changed. Dr. Matthew has produced evidence to show that in *Merychippus*, the Miocene genus of horse, tooth change took place at a younger age than it does in modern horses; the implication being that the potential longevity was less than it now is.

Thus the fact that *Equus* has proportionately some four times as much tooth as *Eohippus* may mean no more than that it lives longer, and its marvellous dentition may not be adaptive in the sense that it is specially modified for the trituration of a new type of food. It may represent no more than a reaction to the requirements of a large animal. I believe that most adaptations the history of which can be traced in fossil material are of a similar kind.

Whether a change which enables a mammal to become larger and to have a greater potential longevity is an adaptation may be disputed. Certainly it is very different from the usual conception of a structural change fitting an animal for a definite type of life in particular circumstances.

There are, however, a few cases where we are, I think, on firmer ground. The slow and steady improvements in limb structure which go on in the mammal-like reptiles from Lower Permian to Lower Triassic times take place in animals which do not exhibit a steady increase in size, which indeed cover nearly the same range of sizes at the beginning and end of the story.

In the earliest of these animals the upper arm projected at right angles to the body, and the forearm lay at right angles to it, nearly parallel to the ground. The track was very wide, the stride absurdly short, and only one foot could be moved at a time, whilst some of the muscles were devoted entirely to the support of the weight of the body, leaving the whole propulsive force to be supplied by the remainder, or rather by such of them as were not concerned with returning the limb to the position it occupied at the beginning of the stride. From these slow and clumsy ancestors we may trace the gradual acquirement of the structure found in *Cynognathus* or in a mammal; where the arm moves nearly parallel to the principal plane of the animal, the stride is greatly lengthened and every muscle contributes both to the support of the body and to its propulsion. Here we have a case where we can observe an improvement of an animal mechanism which definitely enabled an animal to move faster than its ancestor.

Such general improvements in the mechanism of an animal's body, which are the only adaptations which can be proved to have occurred, differ so greatly in scale and in their general nature from that detailed fitting of an animal to some particular niche in its environment which Darwin believed to occur, that it is important to investigate whether there is any general occurrence of such special relationship of structure and habit, and whether if it occurs it is rightly to be regarded as of adaptive origin. It is, I believe, in the first part of such investigation that a good deal of the future value of physiological work in zoology lies.

The physiological work which is at present being conducted by zoologists falls under two main heads. It may be concerned with the explanation in physico-chemical terms of definite life processes, such as fertilisation or cleavage, the activities of cilia or the nature of muscular activity. Such work is of value to zoology because it increases our knowledge of the cell and all its parts and of the things which may control its activities. It will become essential for an understanding of the factors which underlie morphogenesis, that is, of those factors some of which are carried as material bodies in the chromosomes.

The other type of physiological work is that which, like the classical 'experimental physiology' of the medical school, is devoted to an attempt to understand the functioning of the different systems of organs and ultimately of the whole body of an animal. I believe that such studies hold out the greatest promise of results of any in zoology. We do not know even as a first approximate the mode of working of the body of any one member of the majority of the phyla of the animal kingdom. Until such is known, in at least a few individual species of each phylum, we shall not be in a position to understand the possibilities of adaptation which each fundamental type of morphology holds out and the real significance of the fitting of an animal to its environment.

The ecological relationships of animals to their environments present many aspects which are now capable of investigation by simple physiological experiment, and South Africa seems to me the country of all others which could provide the subjects for such an investigation.

Physiological work of the kind which I suggest, although it will show to what extent there are variations between races and species of animals which fit them specially for life under definite physical environments, will not in general elucidate those morphological differences which alone are recognisable in a museum, and have commonly been assumed to be of an adaptive nature. That these structural differences are adaptive even in the sense that, no matter in what circumstances they arose, they do now in fact fit each form especially to its circumstances, is for the most part pure assumption. I do not know a single case in which it has been shown that the differences which separate two races of a mammalian species from one another have the slightest adaptive significance.

There is no branch of zoology in which assumption has played a greater, or evidence a less, part than in the study of such presumed adaptations. The implication which lies behind any statement that such and such a structure is an adaptation is that under the existing environmental conditions an individual possessing it has a greater chance of survival than one which has not.

The extraordinary lack of evidence to show that the incidence of death under natural conditions is controlled by small differences of the kind which separate species from one another or, what is the same thing from an observational point of view, by physiological differences correlated with such structural features, renders it difficult to appeal to natural selection as the main or indeed an important factor in bringing about the evolutionary changes which we know to have occurred. It may be important, it may indeed be the principle which overrides all others; but at present its real existence as a phenomenon rests on an extremely slender basis.

The extreme difficulty of obtaining the necessary data for any quantitative estimation of the efficiency of natural selection makes it seem probable that this theory will be re-established, if it be so, by the collapse of alternative explanations which are more easily attacked by observation and experiment. If so, it will present a parallel to the theory of evolution itself, a theory universally accepted not because it can be proved by logically coherent evidence to be true but because the only alternative, special creation, is clearly incredible.

The alternative explanations which are put forward of the existence of the differences which separate species from species or one geographical race from another are in essence three: either the difference is regarded as adaptive and its initiation and perfectioning are attributed to a reaction of the animal which alters its structure in a favourable manner followed by an inheritance of the character so acquired; or, secondly, it is regarded as non-adaptive, or only accidentally of value, and held to have arisen by a change induced in the course of an individual development by the direct effect of some one or more environmental features, such change not necessarily being heritable in all cases. The third explanation is that the difference between one form and the other has arisen casually, isolation having enforced an inbreeding which led to the distribution of genes in different proportions in the two stocks.

The first alternative explanation suffers from the defect that the characters in question have not in general been shown to be adaptive, and that an inheritance of an acquired character of the kind required has not been shown to occur.

The second explanation, the direct influence of the environment, has the immense advantage that it is open to investigation by experimental methods, and suggests many attractive lines of work. Here again experiments have been few. The most successful is that on the induction of melanism in moths by Heslop Harrison and Garrett. By feeding caterpillars on food impregnated by salts of manganese or lead, these authors, in three independent series of experiments, obtained melanic individuals of a character which did not occur in the much larger numbers of controls fed on untreated food, nor under natural conditions in the district of origin of the parent individuals.

Harrison and Garrett attribute the melanism which appeared under these conditions to the direct effect of the metallic salts, either on the soma or, as is perhaps more probable, on the germ cells. They showed by a very adequate series of breeding experiments that the melanism which arose in this way is inherited as a simple Mendelian recessive.

It is obvious that such a direct environment effect, when taken in association with the completely established fact of the common occurrence of parallel or identical mutations in allied animals, provides a complete formal explanation of such facts as that the coat-colour of a race of a species of rodent from an arid region will in general be lighter in colour than that of a race from a more humid and therefore more thickly vegetated area. It is clear that such an explanation does not require that the coat-colour has any adaptive significance whatsoever: it is in complete contrast with the equally formally complete explanation by natural selection. But it has the advantage that it can be submitted to experimental confirmation.

The neo-Darwinian would explain this occurrence by assuming that the dark-coloured forms were less visible against the moist and therefore darker soil of the humid locality than lighter animals would be, and would thus escape the attacks of carnivores for a longer period. The light forms would escape notice under the bright illumination and glitter of an arid and especially a desert country. Such a view assumes without question that the colour of the two groups is heritable, though it makes no demands for any particular type of heredity.

The only experiments which have been made with geographical races of mammals are those which Sumner has carried on over many years. Sumner began his work by collecting considerable numbers of individuals of a certain species of the deer-footed mouse *Peromyscus* from localities in California which present extreme variations in rainfall and temperature. He showed that the mice from each locality varied, and that the distribution of the variates for each character formed a unimodal curve. He investigated by statistical methods the correlation between pairs of the characters with which he worked, showing that for many of them the correlation was small. He showed that the curves for different subspecies might overlap, so that no one individual could fairly represent its race.

Sumner also attempted to investigate the possibility of such environmental influences by direct experiment. He transplanted a small colony of mice into a very different environment, enclosing them in a small netted area and leaving them to breed. The offspring which appeared during the course of the experiment showed no tendency to approach the local races in their characters.

It may be accepted as a working hypothesis that the variable characters which separate one geographical race from another are produced under the influence of a number of genes, all independent, and all producing similar effects. As Prof. Karl Pearson pointed out in 1904, the effect of such multiple factors will be to produce an apparent blending inheritance ; a view now very generally accepted. It follows that, in certain cases at any rate, if a small group of individuals phenotypically similar, though genotypically different, differing from the norm of a population, be isolated and left to breed freely, they will, when considered as a population, tend to vary still more from the original mode in the population from which they sprang and that they will do so in the direction in which the original isolated group differed. Prof. Pearson has reached the same conclusion from his own very different point of view and has evidence that the expected result does actually occur.

If, then, we can conceive of circumstances which will bring about such isolation in such a way that the individuals so separated are determined by an environmental condition, we shall have an explanation of the divergence of local races which will account for the appearance in them of individuals which lie outside the range of variation actually observed in the small samples of the parent races which have been investigated.

There remains one type of adaptation which is perhaps of greater importance than those which we have been considering. Perhaps the most striking of all the phenomena of life is the power which all animals and plants possess of so regulating their functioning, and when necessary their morphology, that their life is continued in equilibrium with the conditions under which they find themselves.

How far such physiological adaptations are of the same nature as those internal morphological adaptations which alter the relative sizes of parts in ways determined by geometrical considerations of squares and cubes, and produce analogous modifications in other structural features, there is no evidence. What is certain, however, is that these, which are the fundamental things in evolution, lie open to experiment.

Thus the present position of zoology is unsatisfactory. We know as surely as we ever shall that evolution has occurred ; but we do not know how this evolution has been brought about. The data which we have accumulated are inadequate, not in quantity but in their character, to allow us to determine which, if any, of the proposed explanations is a *vera causa*. But it appears that the experimental method rightly used will in the end give us, if not the solution of our problem, at least the power of analysing it and isolating the various factors which enter into it.

The Relation of Organic Chemistry to Biology.[1]

By Prof. GEORGE BARGER, F.R.S.

SINCE, in the last resort, we are dependent on naturally occurring materials, which scarcely ever occur in a state of purity, it follows that the early chemists were even more concerned with separating one substance from another than many of us are to-day. Progress was at first limited to mineral substances capable of withstanding powerful reagents and a high temperature ; much of the old chemistry is concerned with the heavy metals. The substances formed in such large numbers by living beings are much less stable, and their isolation demands a special technique. It is significant that, in spite of their knowledge of the smelting of ores, of the manufacture of glass, and of many other arts, the ancients failed to distil alcohol. Later, the chemical investigation of organic material was apt to consist in destructive distillation, naturally adding little to knowledge. Only the more volatile and stable substances could be isolated in this fashion.

An important systematic advance was made by K. W. Scheele (1742–1786), whose contributions to organic chemistry are almost as important as his discovery of oxygen. Scheele was a pharmacist, and most of the early chemists were trained as such, or as physicians, from the iatro-chemical period onwards. This old connexion between chemistry and medicine was, however, scarcely a biological one. Joseph Black's work on fixed air and the mild alkalis indeed originated in medicine, from his M.D. dissertation, " De humore acido a cibis orto et magnesia alba", but the subsequent developments of Black's work were not biological in character. Again, although Berzelius was trained as a physician, his work had little connexion with biology.

The use of vegetable drugs, however, led pharmacists to examine the constituents of plants, and thus the foundations of descriptive biochemistry were laid. Scheele investigated a number of organic acids in the wet way. He obtained tartaric acid in 1769, and later benzoic acid by boiling gum benzoin with lime. He first prepared lactic acid (1780) from sour milk, and mucic acid by oxidation of milk sugar. When, soon afterwards, mucic acid was also obtained from gum tragacanth, it became evident that one and the same substance may be derived from both animal and vegetable sources. Oxalic acid was obtained from the acid potassium salt in *Oxalis acetosella*, and shown to be identical with an oxidation product of cane sugar. Scheele also obtained citric, malic, and even gallic acid by crystallisation from solution. Of more general biological interest is his discovery of uric acid, of glycerol, and of hydrocyanic acid ; the last (acidum berolinense) by heating potassium ferrocyanide with dilute sulphuric acid.

[1] From the presidential address to Section B (Chemistry) of the British Association, delivered at Cape Town on July 23.