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FOR the physicist and chemist the term adaptation awakens but the barren echo of an idea. In biology it still retains a certain standing, though its significance has, in recent years, been rapidly contracting, as the influence of the conception for which it stands has waned. Many biologists are now of the opinion that their science would be better off entirely without it. They believe it has not only outlived its usefulness, but has become a source of confusion, if not, indeed, reaction.

Darwin's first task, in the "Origin of Species," was to demonstrate that species had not been independently created, but had descended, like varieties, from other species. But he was well aware that such a conclusion, even if well founded, would be unsatisfactory until it could be shown how the innumerable species inhabiting the world have been modified, so as to acquire that perfection of structure and coadaptation which justly excites our admiration.

To establish convincingly the doctrine of descent with modification as a theory of species, it was necessary for him to develop the theory of adaptation which we now know as natural selection.

The origin of adaptive variations gave him, at that time, little concern. Though keenly appreciative of the problem of variation which his studies in evolution presented, he dismissed it in the "Origin" with less than twenty−five pages of discussion. Such brevity is not surprising, since a more extended treatment would only have embarrassed the progress of the argument. In fact, his restraint in this direction enabled him, first, to avoid the difficulties into which Lamarck, with his bold attack on the problem of variation, had fallen; and second, by doing so, to deal the doctrine of Design a blow from which it has never recovered.

The latter was a service of well−nigh incalculable value to the young science of biology and, as it appeared, to modern civilization as well. But it has not been uncommon, from Aristotle's day to this, for the work of great men to suffer at the hands of less imaginative followers. Sweeping applications of Darwin's doctrine have been repeatedly made without due regard either for its original object or for the success with which that object was achieved. So I believe it to be no fault of Darwin that the growing indifference of European laboratories toward natural selection should find occasional expression in such a phrase as "the English disease." Disease, indeed, I believe we must in candor admit that devotion to it to be which blinds its devotees to those problems of more elementary importance than the problem of adaptation, which Darwin clearly saw but was born too soon to solve.

The problem of species has profoundly changed since 1859. For Darwin it was perforce a problem of adaptation. For the investigator of to−day it has become a part of the more inclusive problem of variation. Along with the logical results of natural selection he contemplates the biological processes of organic differentiation. He is no longer satisfied to assume the existence of those modifications that make selection possible. In his efforts to control them, the conception of adaptation as a result has been crowded from the center of his interest by the conception of adaptation as a process.

The survival of specially endowed organisms, the elimination of competing individuals not thus endowed, are facts that possess, in themselves, no immediate biological significance. Selection as such is not a biological process, whether it is accomplished automatically on the basis of protective coloration, or self−consciously by man. Separating sheep from goats may have a purely commercial interest, as when prunes and apples, gravel and bullets, are graded for the market. Such selection is, at bottom, a method of classification, serving the same general purpose as boxes in a post−office. Similarly, natural selection is but a name for the segregation and classification that take place automatically in the great struggle for existence in nature. The fact that it is a result rather than a process accounts, probably more than anything else, for its remarkable effect upon modern thought. It is non−energetic. It exerts no creative force. As a conception of passive mechanical segregation and survival, it was a most timely and potent substitute for the naive teleology involved in the idea of special creation.

As a theory of adaptation, then, natural selection is satisfactory only in so far as it accounts for the "preservation of favored races." It throws no light upon the origin of the variations with which races are favored. Since it is only as variations possess a certain utility for the organism that they become known as adaptations, the conception of adaptation is inevitably associated with the welfare of individuals or the survival of races. To disregard this association is to rob the conception of all meaning. Like health, it has no elementary physiological significance.

Our profound interest in the problem of survival is natural and practical and inevitable. But in spite of Darwin's great contribution toward a scientific analysis of the mechanism of organic evolution, and in spite of the marvelous recent progress of medicine along its many branches, the fact remains that so far as this interest in the problem of survival is dominant it must continue to hinder adequate analysis of the problem of adaptation. Indeed, it is in large measure due to such domination in the past that biology now lags so far behind the less personal sciences of physics and chemistry. For survival means the survival of an individual. And there is no doubt that the individual organism is the most conspicuous datum in the living world. The few who, neglectful of individuals and survivals, find their chief interest in living substance, its properties and processes, are promptly challenged by the many to find living substance save in the body of an organism. Thus, in a peculiarly significant sense, organisms are vital units. And since the individual organism shows a remarkable capacity to retain its identity under a wide range of conditions, adaptability or adjustability comes to be reckoned as the prime characteristic of life by all to whom the integrity of the individual organism is the fact of chief importance.

With the use of the words adaptability and adjustability, our discussion assumes a somewhat different aspect. Instead of contemplating further the mechanical selection of individuals on the basis of characters that, like the structure of "the woodpecker, with its feet, tail, beak and tongue, so admirably adapted to catch insects under the bark of trees," can not be attributed to the influence of the external conditions that render them useful, we are invited to consider immediate and plastic adjustments of the organism to the very conditions that call forth the response. For the fortuitous adjustments that tend to preserve those individuals or races that chance to possess them, are substituted, accordingly, the direct primary adjustments that tend to preserve the identity of the reacting organism. We turn thus from the RESULTS of the selection of favorable variations to the biological PROCESSES by which organisms become accommodated to their conditions of life.

At once the old questions arise. Are these processes fundamentally peculiar to the life of organisms? Does the capacity of the organism thus to adjust itself to its environment involve factors not found in the operations of inorganic nature? Our answers will be determined essentially by the nature of our interest in the organism whether we regard its existence as the END or merely an incidental EFFECT of its activities. The first alternative is compatible with thoroughgoing vitalism. The second, emphasizing the nature of the processes rather than their usefulness to the organism, relieves biology of the embarrassments of vitalistic speculation, and allies it at the same time more intimately than ever with physics and chemistry. This alliance promises so well for the analysis of adaptations, as to demand our serious attention.

Physiologically, the living organism may be thought of as a physico−chemical system of great complexity and peculiar composition which varies from organism to organism and from part to part. Life itself may be defined as a group of characteristic activities dependent upon the transformations in this system under appropriate conditions. According to this definition, life is determined not only by the physical and chemical attributes of the system, but by the fitness of its environment, which Henderson has recently done the important service of emphasizing.[1] Relatively trifling changes in the environment suffice to render it unfit, however, that is, to modify it beyond the limits of an organism's adaptability. The environmental limits are narrow, then, within which the transformations of the organic system can take place that are associated with adaptive reactions. The conditions within these limits are, further, peculiarly favorable for just such transformations in just such physico−chemical systems.

[1] "The Fitness of the Environment."

The essential characteristic of the adaptive reaction appears to be that the organism concerned responds to changing conditions without losing certain attributes of behavior by which we recognize organisms in general and by which that organism is recognized in particular. It exhibits stability in the midst of change; it retains its identity. But this stability, let us repeat, is the stability of a certain type of physico−chemical system, with respect to certain characters only, and exhibited under certain circumscribed conditions. In so far as the problem of adaptation is thus restricted in its application, it remains a question of standards, a taxonomic convenience, a problem of the organism by definition only, empty of fundamental significance.

It is to be expected that systems differing widely in composition and structure will differ in their responses to given conditions. This will be true whether the systems compared thus are organic, or inorganic, or representative of both groups. The compounds of carbon, of which living substance is so characteristically composed, exhibit properties and reactions that distinguish them at once in many respects from the compounds of lead or sulphur. They also differ widely among themselves; compare, in this connection, serum albumen, acetic acid, cane sugar, urea. No vitalistic factor is needed for the interpretation of divergencies of this kind. But there are many significant similarities between organisms and inorganic systems as well. These are so frequently overlooked that it will now be desirable to consider a few illustrative cases. For the sake of brevity, they have been selected as representative of but two types of adaptation commonly known under the names of ACCLIMATIZATION and REGULATION.

Let us first consider the case of organisms which become acclimatized by slow degrees to new conditions that, suddenly imposed, would produce fatal results. Hydra is an organism which becomes thus acclimatized finally to solutions of strychnine too strong to be endured at first. Outwardly it appears to suffer in the process no obvious modifications. Yet modifications of a physiological order take place, as is shown, first, by the necessary deliberation of the acclimatization, second, by the death of the organism if transferred abruptly back to its original environment.

In other forms the structural changes accompanying acclimatization may be far more conspicuous. For example, the aerial leaves of Limnophila heterophylla are dentate, while those grown under water are excessively divided. Again, the helmets and caudal spines of Hyalodaphnia vary greatly in length with the seasonal temperature.

In these and the large number of similar cases that might be cited, stability of the physiological system under changed conditions is only obtained by changes in the system itself which are often exhibited by striking structural modifications.

Compare with such phenomena of acclimatization the responses of sulphur, tin, liquid crystals and iron alloys to changes of temperature. The rhombic crystals that characterize sulphur at ordinary temperatures and pressures, give place to monoclinic crystals at 95.5 degrees C. Sulphur thus exists with two crystalline forms whose stability depends directly upon the temperature.

Similarly, tin exists under two stable forms, white and gray, the one above, the other below the transitional point, which is, in this case, 18 degrees C. At this temperature white tin is in a metastable condition, and transforms into the gray variety. The transformation goes on, then, at ordinary temperatures, but, fortunately for us as users of tin implements, very slowly. Its velocity can be increased, however, by lowering the temperature, on which, then, not only the transformation itself, but its rate depends.

In this connection may be mentioned cholesteryl acetate and benzoate and other substances which possess two crystalline phases, one of which is liquid, unlike other liquids, however, in being anisotropic. As in the preceding cases, these phases are expressions of equilibrium at different temperatures.

Especially instructive facts are afforded by the alloys of iron and carbon. Iron, or ferrite, exists under three forms: as alpha ferrite below 760 degrees, as beta ferrite between 760 degrees and 900 degrees, and as gamma ferrite above 900 degrees. Only the last is able to hold carbon in solid solution. The alloys of iron and carbon exist under several forms. Pearlite is a heterogeneous mixture containing 0.8 per cent. carbon. When heated to 670 degrees, it becomes homogeneous, an amount of carbon up to two per cent. dissolves in the iron, and hard steel or martensite is formed. In appearance, however, the two forms are so nearly identical as to be discriminated only by careful microscopical examination. Cementite is a definite compound of iron and carbon represented by the formula Fe C.

When cooled slowly below 670 degrees, martensite yields a heterogeneous mixture of pearlite and ferrite (or cementite, if the original mixture contained between 0.8 per cent. and two per cent. of carbon). Soft steels and wrought iron are thus obtained. When cooled rapidly, however, as in the tempering of steel, martensite remains a homogeneous solid solution, or hard steel.

One can not fail to notice the remarkable parallel between these facts and the behavior of Hydra in the presence of strychnine. In both cases new positions of stability are reached by modifying the original conditions of stability; and in both, the old positions of stability are regained only by returns to the original conditions of stability so gradual as to afford time sufficient for the necessary transformations in the systems themselves.

The forms which both organic and inorganic systems assume thus appear to be functions of the conditions in which they exist.

The fact that Hydra is able to regain a position of stability from which it had been displaced connects the behavior of this organism not only with the physical phenomena already cited, but still more intimately with the large class of chemical reactions which are similarly characterized by equilibrium and reversibility. Such reactions do not proceed to completion, which is probably always the case wherever the mixture of the systems under transformation is homogeneous, as in the case of solutions. They occur widely among carbon compounds. The following typical case will suffice to indicate their essential characteristics.

When ethyl alcohol and acetic acid are mixed, a reaction ensues which yields ethyl acetate and water. But ethyl acetate and water react together also, yielding ethyl alcohol and acetic acid. This second reaction, in a direction opposite to the first, proceeds in the beginning more slowly also. There comes a time, however, when the speeds of the two reactions are equal. A position of equilibrium or apparent rest is thus reached, which persists as long as the relative proportions of the component substances remain unchanged.

A great many reversible reactions are made possible by enzymes. In the presence of diastase, glucose yields glycogen and water, which, reacting together in the opposite direction, yield glucose again. In the presence of emulsin, amygdalin is decomposed into glucose, hydrocyanic acid and benzoic aldehyde, and reformed from them. Similarly in the presence of lipase, esters are reformed from alcohols and fatty acids, their decomposition products.

With the introduction of enzymes, certain complications ensue. Though it has been shown that lipase acts as a true catalyser, this may not hold for all, especially for proteolytic, enzymes. That reversible reactions actually occur in proteids, however, accompanied as they are in some cases at least by certain displacements of the position of equilibrium, there appears to be no question.[2]

[2] Robertson, Univ. Calif. Publ. Physiol., 3, 1909, p. 115.

These examples are but suggestions of the many reversible reactions that have now been observed among the compounds of carbon. That they have peculiar significance for the present discussion resides in the fact that living substance is composed of carbon compounds, so many and in such exceedingly complex relations as to present endless possibilities for shifting equilibria and the physical and chemical adjustments resulting therefrom.

With these facts in mind we may now turn from the consideration of acclimatization to a brief discussion of certain phenomena of regulation adaptive reactions that are especially conspicuous in the growth and development of organisms, but separated by no sharp dividing line from adaptive reactions of the other type.

When a fragment of an organism transforms, under appropriate conditions, into a typical individual, the process includes degenerative aa well as regenerative phases. There is always some simplification of the structures present, whose character and amount is determined by the degree of specialization which has been attained. The smaller the piece, within certain limits, and the younger physiologically, the more nearly does it return to embryonic conditions, a fact which can be studied admirably in the hydroid Corymorpha. In some cases the simplification is accomplished by abrupt sacrifice of highly specialized parts, as in Corymorpha, when in a process of simplification connected with acclimatization to aquarium conditions, the large tentacles of well−grown specimens fall away completely from their bases. In other hydroids (e. g., Campanularia) the tentacles may be completely absorbed into the body of the hydranth from which they originally sprang. Among tissue cells degenerative changes may be abrupt, as in the sacrifice of the highly specialized fibrillae in muscle cells; or they may be very gradual, as in the transformation of cells of one sort into another that occurs in the regeneration of tentacles in Tubularia.

An interesting case of absorption of parts came to my notice while studying the larvae of the pennatulid coral Renilla some fifteen years ago. As will be remembered, Renilla possesses eight tentacles with numerous processes pinnately arranged. During a period of enforced starvation, these pinnae were gradually absorbed, and the tentacles shortened, from tip to base. With the advent of food in the form of annelid eggs the reverse of these events took place. The tentacles lengthened and the pinnae reappeared, the larvae assuming their normal aspect.

It appears, then, that in some circumstances at least, the process of simplification may resemble very nearly, even in details, a reversal of the process of differentiation. That one is actually in every respect the reverse of the other is undoubtedly not true. This, however, is not to be wondered at. Mechanical inhibitions that are so conspicuous in some cases (e. g., Corymorpha) are to be expected to a certain degree in all. The regenerative process itself depends upon the cooperation of many physical and chemical factors, in many and complex physicochemical systems in varying conditions of equilibrium. And it is important to note that even the equilibrium reactions by which a single proteid in the presence of an enzyme, is made and unmade, do not appear always to follow identically the same path in opposite directions.[3]

[3] Robertson, vid. sup., p. 269.

Whatever their course in the instances cited and in many others, reversals in the processes of development do take place. In perhaps their simplest form these can be seen in egg cells. The development of a fragment of an egg as a complete whole involves reversals in the processes of differentiation of a very subtle order. The fusion of two eggs to one involves similar readjustments. Such phenomena have been held to be peculiar to living machines only. Yet it may be pointed out that there are counterparts of both in the behavior of so−called liquid crystals. When liquid crystals of paraazoxyzimtsaure−Athylester are divided, the parts are smaller in size, but otherwise identical with the parent crystal in form, structure and optical properties. The fusion of two crystals of ammonium oleate forming a single crystal of larger size has also been observed. Though changes in equilibrium that accompany such behavior of liquid crystals are undoubtedly very much simpler than the changes that accompany the regulatory processes exhibited by the living egg, the striking resemblance between the phenomena themselves tempts us not to magnify the difference.

Further temptation in the same direction is offered by the recent discovery[4] that the processes of development stimulated in the eggs of the sea urchin Arbacia by butyric acid or weak bases, and evidenced by the formation of the fertilization membrane, is reversible. When such eggs are treated with a weak solution of sodium cyanide or chloral hydrate, they return to the resting condition. Upon fertilization with spermatozoa, in normal sea water, they proceed again to develop.

[4] Loeb, Arch. f. Entw., 28, 1914, p. 277.

The facts that have now been briefly summarized have been selected to emphasize the growing intimacy between the biological and the inorganic sciences. No harm can conceivably come from it. On the contrary, there is every reason to be hopeful that the investigation of biological problems in the impersonal spirit that has long distinguished the maturer sciences of physics and chemistry will continue to develop a better control and fuller understanding of the processes in living organisms, of which the phenomena of variation in general, and of adaptation in particular, are but incidental effects.