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IRREVERSIBLE DIFFERENTIATION AND ORTHOGENESIS

THE publication in 1919 of the three noble volumes of posthumous works of the late Professor Whitman[1] redirects our attention to the problem of orthogenetic evolution. The evidence here presented may be regarded as demonstrative that in pigeons variations do not occur in all cases at random around fixed modes as unit characters in accordance with the laws of probability, but that they tend to appear in the course of phylogeny in an irreversible series.

Numerous other students of evolution have formulated similar conceptions under the names, orthogenesis, orthoplasy, directive evolution, etc., some of which are referred to by Whitman, and others are cited at length by Baldwin in his book on "Development and Evolution" (New York, 1902). Most of these statements leave much to be desired from the scientific standpoint and they frequently lead to the expressed or implied postulation of metaphysical factors.[2] Nägeli's principle of perfection is of this sort and has not been especially fruitful. Others, like Eimer,[3] though basing their conclusions on extensive critical observation, have allowed themselves to be swept along by controversial

1 "Orthogenetic Evolution in Pigeons." Posthumous Works of Charles Otis Whitman. Edited by Oscar Riddle. Published by the Carnegie Institution of Washington, 1919.

2 The term orthogenesis has been applied in a great variety of senses, some of them decidedly mystical. These are summarized by Vernon L. Kellogg in "Darwinism To-day," New York, 1907, pp. 274–288.

3 Eimer's Leyden address published by The Open Court Publishing Co., Chicago, 1898, under the title, "On Orthogenesis and the Impotence of Natural Selection in Species-Formation," gives a summary of his views with citation of the original sources of his data.

currents beyond the safe haven of calm and well-considered evaluation of all factors in the problem.

Competent naturalists of wide experience in many scientific fields are, however, continually bringing forth new confirmatory evidence that the direction of the evolutionary process is to some extent and in some way determined from within and that the course of differentiation of organic forms is not in its entirety directly and passively shaped by the environmental mold. That these internal factors are ultimately to be referred to the reaction between the living substance and its environment was clearly recognized by Eimer, as is shown by the following quotation:[4]

> In my view development can take place in only a few directions because the constitution, the material composition of the body, necessarily determines such directions and prevents indiscriminate modification. But through the agency of outward influences the constitution must gradually get changed. The organisms will thus acquire more and more physiological individuality and respond to outward influences more and more in a manner harmonizing with their specific individuality—and so new directions of development will be produced.

Eimer's further contention that this conception implies the unqualified acceptance of the inheritance of acquired characters has doubtless been an obstacle to the more general approval of his views. To this point we shall return.

As the currents of thought regarding the truth of evolution in general drifted more or less impotently in a sea of speculation until Lamarck, Darwin, DeVries and others confined it within scientifically definable banks by presenting plausible explanations of the possible mechanism of the process, so orthogenesis has remained an ill-defined and at times quasi-mystical hypothesis as long as we had no comprehensible account of the causative factors which may direct the course of future differentiation. It may be regarded as established that orthogenesis in some form is an evolutionary factor. But what of the method?

Child[5] has laid down some general principles which point the way in this inquiry. Undifferentiated tissues with active metabolism (termed tissues of the "young" type by Child) contrast sharply with the more stable and mature tissues whose protoplasm has assumed characteristic structural patterns in adaptation to specific functions (muscle, gland, etc.). The tissue patterns of the latter group not only maintain their individuality during the life of the organism, but their stability extends deeper into the hereditary organization of the species and their characteristic forms run true in successive generations. There is accordingly, as Child expresses it, a secular change in the character of protoplasmic organization in the direction of a fixation or stabilization of the more labile and metabolically active tissues of the embryonic or generalized type into more highly specialized and stable patterns. This process of evolution of form is, of course, concomitant with a differentiation and fixation of heritable behavior patterns.

The general physiological processes involved here have been analyzed by Child and the underlying physico-chemical apparatus has been experimentally studied in an illuminating series of researches on bio-electric phenomena and their inorganic analogies by R. S. Lillie.[6]

This process of progressive maturing of tissue in the course of evolution is not different in fundamental biological character from that seen in the course of ontogenetic development, and both are expressions of more efficient adjustment of the living substance to

[5] "Senescence and Rejuvenescence," Chicago, 1915.

[4] *Loc. cit.*, p. 22

[6] "Transmission of Activation in Passive Metals as a Model of the Protoplasmic or Nervous Type of Transmission," SCIENCE, N. S., Vol. 48, 1918, pp. 51–60. "Heredity from the Physico-chemical Point of View," *Biol. Bul.*, Vol. 34, 1918, pp. 65–90. "Nervous and Other Forms of Protoplasmic Transmission," *Sci. Mo.*, Vol. 8, 1919, pp. 456–474, 552–567. "Precipitation Structures Simulating Organic Growth. II. A Contribution to the Physico-chemical Analysis of Growth and Heredity," *Biol. Bul.*, Vol. 36, 1919, pp. 225–273.

the manifold diversities of the environment, that is, in the wide view they are adaptive. Natural selection may (or may not) act upon the products of this differentiation as they are formed. Inheritance of acquired characters in the ordinary sense of this expression is not implied here, though some recasting of current ideas of the individuality of the germ plasm and the nature of the mechanism of heredity is a necessary consequence of the recent studies in general protoplasmic physiology to which reference has been made.

Now this process of senescence of tissue is to a large extent reversible; that is, a specialized tissue may dedifferentiate and return to the embryonic type, as happens in the ordinary processes of reproduction, regeneration and the like. But this capacity for dedifferentiation is not universal, nor where it occurs is it always accomplished with equal facility. In general, specialized tissues return to the undifferentiated condition with greater difficulty than do the simpler and more generalized kinds and the capacity for form regulation diminishes *pari passu* with the increase in complexity of bodily organization. In higher organisms groups of general body cells are incapable of reproducing the whole body as in lower forms; in a salamander an entire limb can be regenerated, but in a man this is impossible; and differentiated nerve cells are incapable even of cell division. To this extent, tissue differentiation is irreversible.

This progressive stabilization of heritable patterns of organization is an essential factor in evolution, and to the extent that these patterns are irreversible the future course of evolution is predetermined. For, given a particular inherited structural pattern, variations will be distributed around this as a mode is accordance with a different frequency curve than would be shown if the inherited pattern were different; and the same applies to mutations..[7]

An aquatic species which has acquired adaptation to life on land has established new modes around which its variations and mutations are distributed. True, it may in time return to the water, though never in a higher animal by the process of dedifferentiation to the original aquatic form but only along lines of further differentiation derived from and congruous with its established terrestrial patterns.

Again, with the establishment of the ladder type of central nervous system as seen in annelid worms, a stable pattern was laid down with certain functional capacities. On the other hand, with the establishment of the tubular type of central nervous systems in early vertebrate ancestors, a different pattern was fabricated with its own characteristic correlated behavior. On the basis of each of these matured and stabilized tissue differentiations a wide variety of central nervous systems has been derived—from the annelid type the whole series of arthropods and from the protochordate type the whole series of vertebrates. But throughout each of these phyla the fundamental pattern has not been changed, nor have we any adequate evidence that one has ever been transformed into the other.

In other words, from the time when these two structural patterns were first established and stabilized, the process was irreversible; the tissues concerned have in this respect and to this extent passed from the "young" or labile state to the "mature" or rigidly determined form. The undifferentiated type antecedent to both of these phyla was labile in the sense that under appropriate conditions it could differentiate in either direction; but having passed over to either one of the differentiated forms, it has apparently lost its capacity to transform to the other type, either by dedifferentiation and remodelling of its pattern or by any other method. At any rate we have no convincing evidence that this has been done. In short, the whole future course of evolution of the vertebrate phylum was set in a different direction from that of the arthropods from the first appearance of a neural tube.

[7] Metcalf, M. M., "Adaptation through Natural Selection and Orthogenesis," *Am. Nat.*, Vol. 47, 1913, pp. 65–71.

The insects comprise the highest invertebrates and as a group they are remarkably efficient animals; but their extremely diverse specialization is spread out on a rather low plane and the behavior of each individual member of the group is tolerably rigidly limited to a narrow range of instinctive acts with small capacity for individual modifiability. The extreme plasticity of the group of ants as a whole, so graphically portrayed by Wheeler,[8] has been biologically determined through natural selection or otherwise by the adaptation of each of the diverse species and castes for a very special mode of life which must be followed through, with no considerable deviation. This is in sharp contrast with the plasticity of the higher mammals which rests rather on capacity for modifiability, docility and intelligent adaptation to new conditions of each individual animal.

Similarly, within the vertebrate phylum we find divergent modifications of the primary tubular pattern of the central nervous system, each of which, as soon as matured and stabilized in the inherited organization, favors subsequent differentiation in certain directions and precludes it in others, for this differentiation is irreversible.

The teleostean type of forebrain is quite unlike anything else in nature. It probably was early forecast in primitive ganoids with brains like those of the modern sturgeons, where there is no evagination of the cerebral hemispheres but instead local thickenings in the unevaginated walls of the rostral portion of the neural tube. Once this method of differentiation was established, there is no evidence that it ever gave rise to the type represented by Amphibia and all Amniota with hollow hemispheres. The teleosts, like the insects, are very efficient organisms and in the aggregate they adjust to a wide variety of conditions, but they are differentiated on a relatively low plane, the structural and behavior patterns of each species are rigid and narrowly circumscribed, and the group has given rise to none of the higher types.

In the primitive reptilian stock there was another divergence in pattern of forebrain evolution. One type developed masive basal nuclei in the cerebral hemispheres, as in modern saurians. This line of differentiation advanced to culminate in modern birds with basal nuclei (striatum complex) more massive than in any other animals and with very insignificant cerebral cortex. In correlation with this, the birds on the behavior side present the culmination of instinct, with intelligence of low order. A second reptilian type, starting with brain forms more like those of the modern turtles, followed a different line of differentiation and led up to the mammalian type with wide lateral ventricles and extensive superficial cerebral cortex. This type seems better adapted to develop into an adequate organ of intelligent behavior, and in this direction it appears not yet to have reached its limit.

In speaking of the influence of the arboreal habitat upon the evolutionary history of Primates, F. Wood Jones,[9] draws an interesting contrast between this phylum and the arboreal marsupials (Metatheria), in the following passage:

> These arboreal Metatherians have had all the educational advantages of a thoroughly arboreal life; nothing that we have pictured has failed to exert its influences upon them, and yet it is obvious that the advantage that they have taken of it has been slight. There are metatherian convergent mimics of Carnivora, Rodentia, Insectivora, and of most other Eutherian orders, but there is no metatherian convergent mimic of the eutherian Primates. It would not be unnatural, therefore, to assume that the full advantage could not be grasped by the metatherian animals, since the ground-plan of their brain would not permit it.

The argument continues that the absence of the corpus callosum in Metatheria gives the clew to this orthogenetic limitation.

From these and innumerable similar instances familiar to every comparative anatomist it may be argued that the process of differentiation, so far as this represents an irreversible process, is itself a natural cause of limitation of the future course of evolution

[8] "Ants," New York, 1913.

[9] "Arboreal Man," London, 1916.

within the boundaries set by the efficient working of the established pattern.

Looking at the animal kingdom from the behavioristic side, most animal activities are compounded of two factors: (1) innate and heritable factors (reflexes, instincts, and the like), and (2) acquired modifications of the inherited patterns (culminating in docility and intelligence). In some animal phyla the first component is dominant, in others the second. And the differentiation of an apparatus adequate for a highly refined and very elaborate instinctive behavior complex may preclude the development of the more labile modifiable types, as appears to be the case in insects, higher fishes, and to a less extent birds. The structural patterns serving the higher intelligent types of behavior have not been evolved from those lower brains exhibiting highly differentiated and stabilized inherited patterns correlated with complex instincts, but rather from more generalized forms which have remained more plastic (from the evolutionary standpoint) because less of their material has passed on into the mature form of tissue.

The higher forms retain their dominant position and continue advance in this direction because parallel with the elaboration of their stable, heritable nervous and instinctive patterns they retain sufficient labile nervous tissues of the "young" and plastic type to enable each individual to make his own adaptations to a great variety of environmental conditions and to profit by this experience.

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"It is not so much to know how to direct research men as it is to know where to find them."—*Old chemical proverb.*

AN inquiry which is received frequently by the administration of the Mellon Institute is, "Where do you obtain your research chemists?" It is a familiar truth that there is a serious scarcity of men of demonstrated research ability; and since, *ceteris paribus,* the institute adheres to the policy of starting new investigational work only as competent men are available, the question is, therefore, of scientific interest. It can not, however, be answered except with certain conditional stipulations. In the first place, there is a diversity of opinion as to the basic qualifications for research, and particularly for industrial research. Then, there is the requisite of considering the exact nature of the investigation and the definite type of researcher needed therefore. And, finally, there must be borne in mind the fact that the finding of every research man is attended with difficulty because it frequently involves the gift of prophecy on the part of the searcher—or, at least, the application of a proleptic study which is at present in an inchoate condition. The supply of men capable of working at high efficiency as scientific investigators has been, and probably always will be, well below the demand; and scientists having the requisites and spirit of the researcher are, indeed, difficult to find even by ones widely experienced in the direction of research. Perhaps the most effective instrument for the recognition of investigational keenness is the comparative method, but the study of its use is still in its infancy.

On account of the extraordinary importance of new ideas, particular emphasis should always be laid upon locating and supporting brilliant investigators. Such individuals can best be found in the universities, although it should be the ambition of every research director to attract, rather than to seek, qualified scientific investigators. The function of the university is to operate with the beneficent idea of increasing the sum of human knowledge, and among its most valuable products are those young men of initiative who will work for the exercise of the investigative instinct and the pleasure of overcoming difficulties. Dr. Robert Kennedy Duncan once said: