SPECIAL ARTICLES

THE FOUR INSEPARABLE FACTORS OF EVOLUTION. THEORY OF THEIR DISTINCT AND COMBINED ACTION IN THE TRANSFORMATION OF THE TITANOTHERES, AN EXTINCT FAMILY OF HOOFED ANIMALS IN THE ORDER PERISSODACTYLA [1]

In a recent address entitled "Evolution as it appears to the Paleontologist" [2] I promised a fuller exposition of the law of the four inseparable factors.

During the past six years a very careful analysis of the modes and factors of evolution has been made in connection with my exhaustive study of the Perissodactyl family of Titanotheres, with the following result: all the processes and modes of evolution should be grouped under the *primary* processes of (1) heredity, (2) ontogeny, (3) environment, (4) selection. In this grouping heredity includes solely changes in the germ plasm. Ontogeny includes the somatic expression of heredity, somatic modification and adaptation, as well as the somatic environment of the germ plasm. Environment includes all nature external to the organism. Selection represents all competition, survival or elimination of individuals representing the combined product of heredity, ontogeny and environment. Variation is not included here because it is a *secondary* process.

A survey of the history of evolution theory shows successive waves of opinion or schools holding to the chief or more or less *separate* influence of these processes as factors; for example, environment (Buffon), ontogeny (Lamarck), selection (Darwin), heredity (the modern school). There is a very large element both of truth and of error in the tenets of each of these schools, because while the influence of each of these factors is undeniable, the exclusive influence of either of these factors is never found in nature, and can exist only in the mind of the observer.

The actual state of living nature is that of the *inseparable* and continuous action of these several factors as expressed in the following most fundamental biological law:

The life and evolution of organisms continuously center around the processes which we term heredity, ontogeny, environment, and selection; these have been inseparable and interacting from the beginning; a change introduced or initiated through any one of these factors causes a change in all.

Representing these processes respectively by the capital letters H, O, E, S, life and evolution may be represented by the formula:

$$H \times O \times E \times S.$$

This formula roughly expresses the intimate nexus which exists between all these processes, a nexus which is quite consistent with the fact that each has also its separate part in life and in evolution. The multiplication sign, $\times$, is to be interpreted in the active and passive sense of *influencing and influenced by.* As examples of what is meant by this formula we may cite such principles as the following: (1) that heredity is conditioned by ontogeny and environment; (2) that selection operates on the product of heredity, ontogeny and environment; (3) that ontogeny initiates many changes which are subsequently taken up by heredity; (4) that of the four processes involved in life and evolution heredity is by far the most conservative and stable, among other reasons because it is embodied in a form of matter (germ-plasm) least subject to changing external influences; that ontogeny, on the other hand, is the most unstable.

In contrast to the graphic representations of the original extreme hypothesis of Weismann, in which heredity is represented as a continuous current more or less isolated from ontogeny and environment there may be presented the following diagram.

This diagram brings out the real cause of the difficulties which arise, as illustrated below

[1] Abstract of paper read before the American Society of Zoologists, New Haven, Conn., December 26–28, 1907. This address was first delivered to Columbia students, November 3, 1905, and has been held two years for further consideration, before publication.

[2] Osborn, Henry Fairfield, "Evolution as it appears to the Paleontologist," Science, N. S., Vol. XXVI., No. 674, No. 29, 1907, pp. 744–749. Address before Seventh International Congress of Zoology, Section of Paleozoology, Boston, August, 1907.

(1–4), when we attempt to determine at what point in the chain of processes a new character is set in motion, in course of investigation of the initiation or origin of new characters.

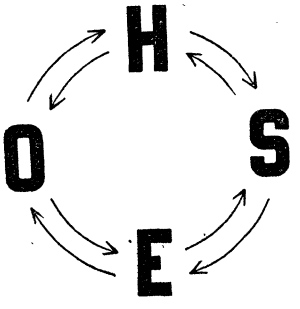

Diagram illustrating the reciprocal influences of heredity, ontogeny, environment and selection. Arrows *across* the circle would represent these relations still more completely.

1. For example, as concerns *heredity,* consider the slow "mutations of Waagen" or the rapid "mutations of De Vries." According to an *internal* theory the point of origin would be expressed by a formula presenting the theory that mutations originate in heredity, namely:

$$H^1 \, o \, E \, S .$$

The experiments of MacDougal[3] and others in the New York Botanical Gardens showing that mutations are sometimes set in motion *externally* or through environment, would be represented by the formula:

$$H^2 \, o \, E^1 \, S .$$

2. Similarly, as concerns *ontogeny,* the theory of the phenomena of "organic or coincident selection" might be represented by the following successive formulæ:

$H \, O^1 \, E \, S$ = first or ontogenetic phase.
$H^2 \, O^1 \, E \, S$ = second phase, or phase of coincidence of heredity with ontogeny.
$H^2 \, O^1 \, E \, S^3$ = third phase, in which coincident ontogenetic adaptations and hereditary predispositions are selected.

Here again the originating cause may be the environment, in which case the formula should be written E^1, O^2, H^3, S^4. This is a further example of the constant operation of the "inseparable law."

3. The initial influence of *environment* in the origin of new characters (or revival of ancestral characters) has been well illustrated recently in the interesting experiments of Beebe[4] in the New York Zoological Park, in which the eggs of the same mother bird (*Scardafella,* the scaly dove) were subjected to two extremes of environment, all other factors being excluded, with two types of plumage resulting. Here the formula is clearly:

$$H \, O^2 \, E^1 \, S .$$

4. Finally, as concerns *selection,* while it is admitted that this factor originates nothing, there are periods of intense struggle for existence when selection takes most active part in the perpetuation of certain characters and elimination of others and is thus indirectly initiative.

We are forced to the conclusion that all hypotheses which treat of these four processes as separable in a state of nature are unsound; that all methods of investigation which proceed on such assumption are unsound. At the same time investigation and experiment may proceed to test two working hypotheses: *First, that while inseparable from the others, each process may in certain conditions become an initiative or leading factor; second, that in complex organisms one factor may be initiative in one group of characters while another factor may at the same time be initiative in another group of characters, the inseparable action bringing about a continuously harmonious result.*

APPLICATION OF THIS LAW TO THE TITANOTHERES.—The hypothesis of the simultaneous operation of several factors on different groups of characters could only suggest itself to a paleontologist working upon a very complex organism in which an almost countless number of characters is simultaneously evolving. The analysis of these processes as applied to

[3] MacDougal, "Heredity and the Origin of Species," *The Monist,* January, 1906. Rept. Dept. Bot. Research (extract from fifth Year Book, Carnegie Inst., pp. 119–135), p. 129.

[4] Beebe, C. William, "Geographic Variation in Birds, with Especial Reference to the Effects of Humidity," *Zoologica,* N. Y. Zool. Soc., Sept. 25, 1907, pp. 1–41.

the evolution of the titanotheres is based on thousands of measurements, of the skull and teeth especially, and on comparisons of an exceptionally rich series of specimens in successive geological levels. So far as they have gone they appear to confirm the hypotheses of the separate and combined operation of the four factors on different classes of characters. A few illustrations only may be given of results which will be set forth very fully in the monograph.

1. Heredity appears to dominate the origin of new cuspules in the teeth because they arise in the form of rectigradations, that is, with a slow, definite, and continuous origin, in an adaptive direction and controlled by ancestral affinity. That is, the *same* results appear independently in descendants of the *same* ancestors.

2. Ontogeny rather than heredity appears to be in part an initial factor in fashioning the form of the cranium. We can not regard this as controlled by ancestral affinity, because descendants of the *same* ancestors give rise to *different* results, that is, to extremely divergent broad-skulled and extremely long-skulled forms.

3. Environment, besides its indirect action through heredity and ontogeny, seems to act broadly upon such change as the continuous increase of size, which independently favors the increase in size of the members of four series of titanotheres in contrast to a fifth which is dwarfed in size.

4. Selection (by our definition not an initiative factor), while generally operating on the whole sum of characters or the sum total of the organism, seems in this case to have operated especially on fluctuations in skull breadth or skull length respectively, in relation to the browsing or grazing habit; these congenital fluctuations being connected with ontogeny and organic selection.

The above is a very brief statement of the results of analysis of the evolution processes in general, and of the application of these processes to titanothere evolution in particular. It applies especially to the origin of new characters, with the clear appreciation of the end result that all such characters, or the potentiality of giving rise to them, finally become *germinal* or hereditary.

Henry Fairfield Osborn

QUOTATIONS

The Concilium Bibliographicum

We learn that at the recent meeting of the International Congress of Zoology held in Boston a committee was formed to raise an adequate endowment fund for the Concilium Bibliographicum. With the one exception of the final settlement of the question of nomenclature—if, indeed, such a settlement be possible—there is no step which the congress could have taken of such importance as this for zoologists in general, nor are there many which could have anything like its economic importance. The literature of zoology is at once the most extensive and the least accessible of all those of the natural sciences. It is estimated that the number of persons engaged in zoological investigations of one kind or another amounts to several thousands, while—to ignore altogether works published independently—there are more than 3,000 periodicals, written in over 20 different languages, which may contain matter of interest for the naturalist. Unfortunately, the difficulty of the situation is made greater by the refusal of most of these journals to limit the matter they publish to any one branch of zoology and also by the importance which claims of "priority" may give to articles that have appeared in the most obscure periodicals. Moreover, it is precisely those papers which, directly or indirectly, are of the greatest economic importance (whether to economic entomology, to the study of fisheries, or to parasitology) that are the hardest for the working zoologist to hear of and to obtain.

The Concilium Bibliographicum was founded in 1896 under the auspices of the International Congress of Zoology. Its offices are situated in Zurich and its staff of librarians and clerks is under the direction of Dr. H. H. Field. The work of the Concilium is to examine as many of the periodicals of the world as are accessible to it, to make abstracts of their contents, and to publish the results of its labors in the form of a card catalogue