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PALEONTOLOGY VERSUS GENETICS[1]

By Professor HENRY FAIRFIELD OSBORN

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AN interesting coincidence in the history of observation and speculation upon the nature and causes of evolution is found in the life studies of William Bateson and of the present author. In the years 1879 to 1882 Bateson was a student in the University of Cambridge. After an early zoological and embryological training he began an intensive study of variation as shown in recent osteological material, continued for a while in the biometric school and then became founder of the school of genetics. In the year 1879 the present author at the age of twenty-two was in Cambridge studying embryology under Balfour; he then took up studies in comparative anatomy and with Scott founded a new school of vertebrate paleontology.

[1] This article is an abstract of two addresses: "Bearing of Titanothere Researches on the Principles of Descent and Adaptive Radiation of the Mammals," American Philosophical Society, April 24, 1930; "Bearing of Titanothere Researches on the Principles of Mechanical Evolution," National Academy of Sciences, April 29, 1930.

William Bateson's theories and conclusions became increasingly negative; in 1893 he wrote: "If the study of variation can serve no other end it may make us remember that we are still at the beginning, that the complexity of the problem of specific difference is hardly less now than it was when Darwin first showed that natural history is a problem and no vain riddle."[2] In his presidential address of December 28, 1921, speaking as a geneticist, he made the following declaration:

> Discussion of evolution came to an end primarily because it was obvious that no progress was being made. We became geneticists in the conviction that there at least must evolutionary wisdom be found. When students of other sciences ask us what is now currently believed about the origin of species we have no clear answer to give. We can not see how the differentiation

[2] William Bateson, "Materials for the Study of Variation Treated with Especial Regard to Discontinuity in the Origin of Species," p. xii, London, 1894.

into species came about. Variation of many kinds, often considerable, we daily witness, but no origin of species. But that particular and essential bit of the theory of evolution which is concerned with the origin and nature of *species* remains utterly mysterious. The claims of natural selection as the chief factor in the determination of species have consequently been discredited. Our doubts are not as to the reality or truth of evolution, but as to the origin of *species,* a technical, almost domestic, problem.[3]

Osborn began paleontological studies in 1877 and more intensive research in the year 1890. On June 30, 1900, he succeeded Marsh as vertebrate paleontologist of the U. S. Geological Survey and at once began a most intensive geologic and biologic research on the evolution of the family of odd-toed ungulates known as Titanotheres from a name applied by Joseph Leidy to the jaw bone of *Menodus* discovered in 1846. The monograph on the Titanotheres covered twenty-nine years of research and exploration in New Mexico, Colorado, Utah, Wyoming, South Dakota, Montana, the Gobi Desert, Burma and the Balkans. The evolution of the Titanothere hereditary germ has accordingly been followed over a period estimated at ten million years from *Eotitanops* to *Brontops.* Comparison is made with the family tree of the odd-toed ungulates known as Perissodactyls showing the adaptive radiation of nine families and thirty-five subfamilies as compared with the Titanotheres which within a single family include twelve subfamilies, twenty-six genera and one hundred and six species, many of which are arrayed in close phylogenetic order.

This affords an unprecedented opportunity to contrast the zoological concept of Linnaeus of contemporaneous species with the modern paleontological concept of the origin and succession of species, subfamilies and families observed in close detail through long periods of time. Each minute part of many organs has been examined and precisely measured from its origin as it comes from the germ-plasm to its increasing importance into what may become an absolutely dominating character of the organism. This progression or retrogression is absolutely continuous and invariably definite and determinate rather than fortuitous. Characters rise and fall under twelve principles, three of which have been absolutely confirmed in the course of preparation of this monograph. The close analysis of thousands of separate characters gives us an entirely new concept of the origin of the "ascending mutations" of a genus. Inasmuch as every single one of the thousands of characters in the dental and skeletal mechanism is independently evolving, although constantly interrelated with all the other characters, a species is defined by one or more characters which reach a conspicuous stage either of progression or of retrogression. This is as true of paleontologic as of zoologic species, although in the latter case our definition is according to the eyes of Linnaeus and of Darwin, whereas in this paleontologic monograph we trace back to their origin the inconspicuous antecedents of each specific character.

It happens in the odd-toed ungulates such as horses, rhinoceroses and Titanotheres as well as in all other fossil mammals that conspicuous specific characters mostly include *allometrons* or changes of proportion, reduction or enlargement, and *rectigradations,* adaptively arising in new characters. Thus Leidy, Cope and Marsh independently divided Eocene horses by their successive rectigradations and allometrons.

In the Titanotheres, moreover, we enjoy the unparalleled opportunity of discovery that a genus consists not only of its visible generic characters but of invisible potential characters in the germ which may lie dormant for hundreds or thousands of years until they emerge. Moreover, each genus is characterized by different rates of velocities in the progression or retrogression of the thousands of characters which are embraced in its hereditary germ. For example, the horn and teeth rectigradations are hurried forward in one generic or subfamily phylum while they are closely guarded within the germ-plasm of another generic or subfamily line dwelling in the same geographic region. These origins of rectigradations are controlled by ancestral or potential heredity, whereas the origins of allometrons or changes of proportion respond directly to adaptive changes in environment.

The evolution of the Titanotheres has little to say about physical or chemical adaptations, but it gives us the most thorough and profound insight we have ever gained into mechanical adaptations. Altogether twelve principles are observed, the first nine of which are as follows: (1) principle of progression, development, of most useful mechanisms; (2) converse—retrogression, degeneration, of least useful mechanisms; (3) principle of compensation—gain of certain mechanisms compensated by loss of other parts; (4) principle of economy of mechanisms, related to principle of compensation; (5) principle of mechanical adaptation through ontogenetic or phylogenetic acceleration; (6) principle of mechanical adaptation through ontogenetic or phylogenetic retardation; (7) principle of mechanical autoadaptation of the individual, during ontogeny; (8) principle of coordination, correlation, coadaptation, of all the mechanical parts, ontogenetic and phylogenetic; (9) principle of organic selection of races which show highest powers of coincident mechanical autoadaptation and hereditary mechanical adaptation.

[3] William Bateson, "Evolutionary Faith and Modern Doubts," an address delivered on December 28, 1921, printed in SCIENCE, 55: 55–61, January 20, 1922.

Several of the above principles have been more or less fully known by anatomists, some of them reaching back of the time of Aristotle as treated in his "Physics" and in his "History of Animals." But the following three principles (10–12) are those which are first demonstrated in the Titanothere monograph although previously adumbrated in the author's earlier researches on the teeth of the Eocene primates and of the horses and rhinoceroses: (10) principle of allometrons, or adaptive changes of proportion in all the hard parts of mammals; (11) principle of rectigradations, or adaptive origins *versus* fortuitous or random origins of new characters; (12) principle of potential heredity, predetermination or emergence of rectigradations.

Whatever may be true as to fortuitous mutation and as to chance or random variation in chemical and physical adaptations, the mechanical evolution of the Titanotheres, a unique record of ten million years in the development of the Titanothere germ-plasm, shows absolute continuity in every single organ examined. There is not the slightest trace of discontinuity or of random origin.

Thus it may be claimed that the Titanothere monograph solves the chief principles involved in the origin of "ascending mutations," species, genera, subfamilies, etc., as displayed in the hard parts of mammals. There is a firm undeviating orthogenetic order in the entire animal mechanism. There is a phylogenetic continuity of germinal adaptation and reaction in response to secular changes of habit and of environment.

DUAL NATURE OF PHYSIOGRAPHY[1]

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IT may be held axiomatic that we live in a world which is active, dynamic and changing, in a world where energy is by nature more important, more universal, than matter. Causes arising from the flow of energy are elusive and difficult to formulate into natural laws; they seem to border too much upon the abstract. Effects impressed on matter are as a rule clearly visible and lend themselves to description, measurement and comparison. They are above all concrete. Therefore it is not wholly strange that physiography has developed to a great extent in the matter of description and interpretation of land forms.

However, physiography possesses a dual nature in causes and effects, in active forces and passive results. Geodynamics (even if necessarily modified by the word surficial) appears to be a good name for the study of those processes—active, dynamic, progressive—which are constantly at work molding the surface of the lithosphere. In contrast, geomorphology studies the physiographic products wrought by those same processes. Formal treatment of the subject, physiography, actually resolves the dual nature into two view-points, the one looking at the science in the light of activity, the other, of passivity. There remains the task of bringing out the contrasts between them.

GEODYNAMICS—THE ACTIVE PHASE

The so-called processes represent the forces at work, while the detailed surface features appear as the direct results; this is rather common knowledge. It is the attitude of approach and the method of treatment that may be radically new and different. In this case we refer to the dynamic view-point, which considers a stream to be the dominant factor in a fluvial environment, which accentuates the forces at work and represses the resultant products to mere incidents in the constant flow of energy. The stream, in fact, is the permanent, concrete reality of a situation. Geodynamics adopts the active view-point and seeks to analyze and understand intimately the physiographic processes, all the while cognizant of the fact that they are now and have been in the past at work on the land surfaces. This active phase of physiography contrasts vividly with the ordinary and purely passive study of earth form. The one is dominantly analytical and causative, the other descriptive and interpretative.

At first sight process and result depend vitally upon each other, since they are related as cause is to effect. They seem, indeed, to be inextricably interwoven—a slight variation in one either causes an equivalent change in the second or else is followed by a consistent response. These intimate relations may suggest of necessity a lack of reality in the dynamic view-point.

The absolute interdependence of process and product should not be assumed too strongly until another idea is considered. Let us imagine a comparatively resistant rock stratum forming a shoulder where it crops out on a valley wall. That stratum when first uncovered at the bottom of the valley no doubt influenced the rate of erosion and perhaps the exact position of the stream, but it did not alter or influence

[1] The work for this paper was carried on with funds made available by the research committee of the Graduate School of the Ohio State University