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ARISTOGENESIS, THE CREATIVE PRINCIPLE IN THE ORIGIN OF SPECIES[1]

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As the title of his epoch-making work Darwin chose "The Origin of Species" (1859) because, as conceived by Linnaeus (1735), "species" was the ultimate unit of creation in the animal and plant world. *Nullae speciae novae* was the battle cry of the conservatives of pre-Darwin days, but what Darwin devoted his life to was the origin not of species but of adaptations, of which species are simply the by-products.

Mechanical adaptation was the oriflamme from Empedocles (495–435 B. C.), the father of the evolution idea, through Anaxagoras, Aeschylus, Aristotle and Plato, in forming what may be called the proto-Darwinian "chance hypothesis" as well as the proto-Lamarckian "inheritance of acquired adaption hypothesis." The progressive improvement or retrogressive degeneration of human and animal mechanisms were the guideposts to the use and disuse inheritance speculations from the naturalists of Greece and Rome to Erasmus Darwin and Lamarck, the formulator of the "Lamarckian hypothesis."

Osborn, too, for the past forty-three years a hunter of fossil titanotheres, of fossil mastodonts and elephants, concerned with the origin of the masterful horns of the titanotheres; in the elephants of the superb tusks, of the marvelous proboscis, of the supreme mechanical adaptation of the great grinders which grind uninterruptedly for over a century, loves to feel that in part at least he has answered Aristotle's question: "What then, hinders but that the parts in nature may also thus arise? For instance, that the

[1] Abstract of eleventh William T. Sedgwick Memorial Lecture, delivered at the Massachusetts Institute of Technology, Cambridge, Mass., at the meeting of the American Association for the Advancement of Science and the American Society of Naturalists, December 29, 1933.

teeth should arise from necessity, the front teeth sharp and adapted to divide the food, the grinders broad and adapted to breaking the food into pieces."

If any intellectual creed—for scientists have their creeds as well as theologians—may be slain by forty-three years of broad and intensive observation on the actual modes of the origin of species, it is the Empedoclean creed of "chance." Whatever may be true of the origin of the biophysical or biochemical adaptations of life, it is now positively demonstrated that nature never gambles or takes a "chance" mechanical adaptation in her origin of species.

In the recent language of the great physicist Bohr, organic mechanism is clearly distinguished from inorganic mechanism:

> On this view, the existence of life must be considered as an elementary fact that can not be explained, but must be taken as a starting point in biology, in a similar way as the quantum of action, which appears as an irrational element from the point of view of classical mechanical physics, taken together with the existence of the elementary particles, forms the foundation of atomic physics.

To borrow Bohr's metaphor, life is a "quantum" of adaptive action, reaction and interaction. Before life appeared on our planet not a single combination of energy and matter was capable of resisting shock, of repairing waste, of combatting disintegration, of coordinating reaction or resistance.

Is it not a significant fact that long prior to modern discoveries of liaison, correlating, interacting and coordinating processes in biophysics and biochemistry, naturalists like Hyatt, Cope and Osborn were applying mechanical and physical terminology to paleontological processes. Modern mechanics afford us, says Planck, the newest concepts of force, of acceleration, of retardation or of inertia, and of mass: "The main object of mechanics is to find the motion which results from a prescribed cause."

A synthesis of outstanding biochemical generalizations may be made from Hopkins' recent address on "Some Chemical Aspects of Life," as follows: Life's advent is the most significant event in the history of the universe; life obeys the second law of thermodynamics; in its energy flow it provides potential activities; of equal importance is organization; among its various means of trapping and transforming radiant energy are chlorophyll, autotrophic bacteria and purple bacteria.

Centering around biomechanical adaptations in the vertebrate class, including fishes, amphibians, reptiles, birds and mammals, are the definitions of species, genera, families and orders. Through intensive paleontologic research we have now perfectly clear concepts of what the formerly dry systematic terms "species," "genera," etc., mean. Paleontology revivifies these terms with principles of potentiality, of acceleration, of the coordinated significance of every process.

From the dawning comparative anatomy of Aristotle to the specific definitions of Linnæus, five locomotor types of quadrupeds have been recognized. Now for the first time, through very intensive alloiometric methods in the titanotheres, elephants and horses, we know how these highly divergent locomotor types evolve.

During the past forty-three years an opportunity quite without precedent in the whole history of biology has enabled us to replace more or less wild and random speculation and hypotheses of the past by observations, inductions, generalizations and principles soundly established in the titanotheres, verified, confirmed and extended in the proboscideans. For the first time in the 2,380 years of evolutionary speculation principles of phylogeny or animal descent become truly scientific when we can measure and number them in the sense of Francis Galton.

With the constant aid of William King Gregory we have applied the principles of measurement under the Greek term alloiometry, signifying the measurement of the always differential changes of proportion, with most significant new results on the widely contrasting heads, limbs, feet and teeth of the titanotheres and of the proboscideans. Alloiometrons may now be clearly defined, as follows:

> Alloiometrons are not governed or predetermined by germinal potentiality in certain lines of racial, specific, generic, family and ordinal descent. On the contrary, within species and even within races, for example the modern species of man *Homo sapiens*, diverse alloiometrons or more or less profound changes of proportion, are independently arising. Alloiometrons are relatively rapid in development, or temporal.

The limbs of both the giant titanotheres and elephants are in the slow-moving, weight-carrying graviportal type of quadruped with short feet. The alloiometrons of the titanothere limb segments are not so very dissimilar to those of the elephants, but both titanotheres and elephants present the widest possible contrasts to the alloiometrons of the cursorial equines, deer and antelope. *Equus* shares with all other swift-footed vertebrates the short thigh and arm bones and long lower limbs, while *Elephas* shares with all heavy slow-moving vertebrates the long thigh bone and the short lower limb. The elephantine alloiometrons (femur, 48.6 per cent.; tibia, 34.3 per cent.; pes, 17.1 per cent.) are similar to those of the giant dinosaur *Camarasaurus* Osborn, namely: femur, 48.6 per cent.; tibia, 33.7 per cent.; pes, 17.7 per cent. Close parallels with the equine alloiometrons are those of the swift-footed deer, antelope and gazelle.

The older testimony of comparative anatomy and embryology is enormously amplified by the testimony of paleontology, which is especially complete, on the ascending scale, in the speed ratios of the equines, *Eohippus* to *Equus,* over a period of thirty-five million years. The desert kiang reaches a maximum speed of thirty-five miles an hour; a few individuals attain forty miles an hour. As shown in the Gobi Desert observations of Andrews, the higher speed ratios are attained in the timid desert gazelle rather than in the desert kiang. We know the exact length ratios of the upper, middle and lower limb segments which correspond to these speeds. The desert gazelle (*Gazella subgutterosa*) is a light-bodied, slender-legged animal, reaching a maximum speed of sixty miles an hour for a short dash—perhaps a furlong; it can maintain its normal running speed of about forty miles an hour.

THE ORIGIN OF ADAPTATIONS BY ARISTOGENESIS

We now pass over the boundary of quantitative evolution expressed in alloiometrons into an entirely new and separate domain of research and generalization. Before the now venerable Society of Naturalists forty-three years ago the discovery of aristogenes was adumbrated in the concluding sentence of Osborn's paper, entitled "Are Acquired Variations Inherited?": "Disprove Lamarck's principle and we must assume that there is some third factor in Evolution of which we are now ignorant." This previously unknown factor proves to be aristogenesis; it was first known under the term "definite variation," (1890) then in 1908 as "rectigradation."

As contrasted with the origin of adaptations through alloiometrons, aristogenesis is a creative process from the geneplasm of entirely new germinal biomechanisms; the process is continuous, gradual, direct, definite in the direction of future adaptation. In contrast to alloiometrons which appear to be immediate and more or less temporal adaptive reactions to new habits, aristogenes are secular, appearing very slowly in the course of long periods of geologic time. Lines of ordinal, family, generic and specific descent may be distinguished by the potentiality of certain new geneplasmic aristogenes.

Two of the principles controlling aristogenes were first demonstrated in the origin of the bony horns of titanotheres, namely, that while potentiality and predisposition and predetermination give definite origins of the horn rudiments, these rudiments do not appear simultaneously in diverse lines of phylogenetic descent but in intervals of time widely separated geologically, perhaps by thousands or hundred thousands of years.

In the whole field of comparative anatomy and zoology no wider contrast could be afforded than the adaptive evolution and radiation of the titanotheres intensively studied in my Titanothere Monograph for the United States Geological Survey, and the adaptive evolution and radiation of the Proboscidea, now in preparation for the Memoirs of the American Museum of Natural History.

If the increase in living species of mammals is twenty-fold the increase in fossil species of titanotheres and proboscideans is one hundred fold. Of still more significance as regards the origin of adaptations is our knowledge of no less than forty-five lines of generic proboscidean ascent, in which the coordinate play of aristogenic and alloiometric origins can be followed in closely continuous phylogenetic order. The breaks between the surviving terminal twigs of the giant branching trees of proboscidean ascent disappear, and the first grand result is the replacement of all hypotheses of discontinuity or of breaks between species. Darwin's species stood apart like isolated mountain peaks, whereas to-day owing to our discoveries living species and subspecies are often comparable to mountain chains composed of lesser peaks completely connected by ridges known as intergradations. It is not the number of species and subspecies which is significant, but the facts as to habit and habitat which are recorded with them. Similarly, it is not the number of fossil species now known as compared with those of Darwin's time, but the linkage of families, genera, species, subspecies, and even of "ascending" and "descending mutations" reaching back over hundreds of thousands, if not millions, of years.

While the Proboscidea as a whole are under the broad principle I of adaptive radiation, the several organs evolve separately under principle II of particulate adaptive radiation. This is what actually happens in the forty-five separate lines of descent; we now know exactly how it happens, how adaptations and species originate; we do not know why it happens; before speculating as to the why and as to the nature of the inconceivably numerous chemico-physical modes of coordination let us concentrate on the three outstanding biomechanical centers, namely, the tusks, the proboscis and the grinding teeth.

Most extraordinary, however, is the shoveling function which evolved independently in four entirely distinct lines of descent, two outstanding examples of which are the Amebelodonts or "shovel-tuskers" of North America, all alike descended from the primitive shovel-tusker *Phiomia,* described by Andrews from the Oligocene Lake Moeris of Egypt; also the Platybelodonts or "flat-tuskers" independently discovered by Borissiak, Granger and R. C. Andrews in the Desert of the Gobi. The three known species of

Platybelodon exhibit a perfected pair of broadened chisels, reinforced within by dentinal tubules, kept sharp by polishing the lower surface on smooth rocks; this pair of lower incisors combines to form a shovel twelve inches broad, in form exactly like a coal shovel.

It has been assumed by all zoologists that all proboscideans evolved a proboscis and that ancestral proboscideans would show step by step the evolution of this remarkable organ. Accordingly, in all current literature and popular restorations the proboscis is shown in its variable stages; in our restorations three entirely distinct modes of naso-labial adaptation are displayed. After the most intensive research it appears that there are three widely distinct naso-labial adaptations; namely, (a) the broad hippopotamoid upper and lower lips of the Moeritheres; (b) the flat extended upper lip of the flat-tuskers (*Platybelodon*) and of the shovel-tuskers (*Amebelodon*); (c) the typical elephantine proboscis progressively extended until it reaches the ground and is capable of a great variety of functions.

In the aristogenesis of the twenty-six kinds of mastodonts it is the adaptations of the superior and inferior tusks combined with the manifold adaptations of the grinding teeth which give us two outstanding results; first, from the biomechanical standpoint, tusk and grinder adaptations absolutely confirm the principle of particulate adaptive radiation; second, these adaptations of the grinders and of the tusks combined afford a reliable means of determining both the habitat and the nature of the food supply which underlies the principle of adaptive radiation of these animals as a whole.

Despite these ingenious biomechanisms of all the 27 different kinds of dental adaptation, the Moeritheres, Deinotheres and Mastodonts signally failed during the progressive Eocene to Pliocene desiccation. In the northern hemisphere all adaptations failed, excepting three. Falconer's *Anancus* of East Anglia and Barbour's *Tetralophodon* of Nebraska alone survived into the Lower Pleistocene, while our classic mastodont, *Mastodon americanus,* alone survived into the dense humid forests of middle and eastern North America.

In the surviving elephantoid division the low transverse ridge-crest of the mastodont is perfected in the Upper Pliocene of the African ancestral elephants (*Archidiskodon*). The contrasts in the total length of the enamel foldings of the gigantic *Archidiskodon* (8,000 mm), of the gigantic *Parelephas* (10,000 mm), of the relatively small *Mammonteus* (6,000 mm) are coordinated with the relative intensities of their struggle for existence.

The proboscideans rank next to man in biological importance and far surpass the mechanically inferior man in demonstration of all the main principles of biomechanical aristogenesis and alloiometry. It is difficult to circumscribe aristogenesis and alloiometry within their respective originating and modifying spheres of action, but there are certain lines of proboscidean descent in which aristogenesis, for a long period of time, is the sole and dominating principle. In a definitely known period of geologic time an outstanding example of aristogenic origin from the geneplasm is witnessed in the Siwalik Hills of northern India during the flood-plain deposition. We witness here the aristogenic origin from the geneplasm in a definitely known period of geologic time, Oligocene to Miocene, of 24 new biomechanical units. Each of these aristogenes rises from the creative potentiality of the geneplasm, first as an inconspicuous rudiment, finally as a functional and useful cone or enamel folding.

The next principle of great significance in biomechanical evolution is that these new aristogenic primary cones arise only in the genera which are more or less closely affiliated by descent to the ancestral *Phiomia* of the Upper Oligocene of Egypt collected by Granger on the American Museum Expedition of 1907.

The rapidity of evolution of the aristogenic elements in the grinding teeth is now known to be entirely independent of the intensity of the selection principle of Darwin. During the relatively brief Plio-Pleistocene million and a half year period all the elephants were protected by the superb development of their incisive tusks; these tusks, together with the greatly superior mechanism of the grinding teeth, enabled the elephants to completely supersede or drive out the mastodont stocks and to replace the mastodonts in all parts of the world except Australia from which they were barred by impassable oceanic barriers, and South America, in which only a single species (*Parelephas cayennensis*) penetrated as far as French Guiana. It is also known that no species of elephant occupied the same geographic range as another species at any given period of geologic time; thus there was no competition between species. So far as we can judge, the elephants were the most dominant, resourceful, well-defended quadrupeds known at any time in the earth's history prior to the arrival of man. The independence of selection in aristogenic evolution is shown by the amazing rapidity with which the grinding teeth evolved, this evolution far outstripping that of the grinders of any of the contemporaneous rapidly breeding mammals. Whereas it is often very difficult to distinguish a swift-breeding Lower Pleistocene rodent from a modern rodent, the gap between the grinding teeth of the slow-breeding elephants in the same period of time is enormous.

Among Osborn's theoretic inductions is the following, that we are witnessing potentiality rather than predetermination. One definition of the term potential, *i.e.*, "Latent, undeveloped, but capable of developing and becoming effective; existing in the germ . . . ," while a purely physical term, appears to apply to the latency of the aristogenes both in the grinding teeth of the Proboscidea and in the horns of the titanotheres. The presence of this genedynamy or latent power in the germ, is attested by the entire history of the grinding teeth of the mammals extending back to the single coned pro-mammals of the Triassic time.

CONCLUSION

An interesting coincidence in the history of the evolution theory is that while William Bateson was working in Cambridge after his graduation (1882) from St. John's, under Weldon's direction he soon turned to the study of variation chiefly on the materials afforded in the Cambridge museums, and in the introductory pages to his well-known volume gave his preliminary conclusions: I. The forms of living things are various and, on the whole, are Discontinuous or Specific. II. The Specific forms, on the whole, fit the places they have to live in. How have these Discontinuous forms been brought into existence, and how is it they are thus adapted? This is the question the naturalist is to answer.

At the same time Osborn, studying in Cambridge (1879–1880) and Princeton (1881–1890), was also interested in the problem of variation, and in opening a discussion upon the Lamarckian principle before the American Society of Naturalists reached conclusions as to definite lines of blastogenic variation, as follows: "The conclusions we reach in this discussion must finally turn upon the existence of definite lines of blastogenic variation." Thus Osborn and Bateson laid out for themselves a program for future research based in Bateson's case on the concept of discontinuity between species, and in Osborn's case on the concept of the existence of definite lines of germinal variation still to be discovered.

The results of Bateson's research left him in a hopeless and agnostic mood. Osborn on the other hand is full of confidence.

Our knowledge of the chemical messengers which not only sustain the structural harmonies of the entire organism, but which hasten forward some processes and retard others, has advanced by leaps and bounds. We are still on the threshold of the biophysical messenger system, but the one fact that certain mammals are sensitive to slight changes in the barometric pressure of the atmosphere which heralds a coming storm is an indication of what we may anticipate in the physical sphere of action. The hard-won discoveries in aristogenesis which form the chief subject of the present address are entirely the outcome of the spirit of the "interpretation" of nature rather than the "anticipation" of nature, in the language of Bacon, the founder of inductive biology.

Nature is full of surprises; Nature seldom works according to the anticipations of man, even such semi-inductive anticipations as those of Charles Darwin and of Herbert Spencer. If, as we contend, the principle of Aristogenesis is firmly established by irrefutable paleontological evidence we are now in a new vantage point to attack the problem of the causes of biomechanical adaptations which have interested the mind and excited the imagination of man since the time of Empedocles. Let us summarize our present position for the direction of further research and experiment.

In biomechanical evolution there are two distinct processes. The one long known consists in the alloiometric modification of existing adaptations as in changes of proportion and of function. The other, discovered in course of researches on the phylogeny of the horses, titanotheres and proboscideans, consists in the gradual geneplasmic origin of new and distinct adaptations; it is to the latter originative and creative process that the term Aristogenesis is applied. Both processes become part of the hereditary equipment of the organism.

THE MECHANISM OF THE POLYMERIZATION AND DEPOLYMERIZATION OF OLEFINS[1]

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ALTHOUGH the polymerization of olefins is nearly as old as organic chemistry and in spite of the increasing industrial importance of this process, especially in connection with cracked gasoline, the theories which have been propounded to explain it have not been adequate. In most cases they have assumed types of changes which are entirely different from ordinary organic reactions. The theory presented in the present address is different from the preceding

[1] Abstract of an address by the retiring vice-president and chairman of Section C—Chemistry, American Association for the Advancement of Science, Boston, December 29, 1933.