The Origin of Species as revealed by Vertebrate Palæontology.[1]

By Dr. HENRY FAIRFIELD OSBORN,
Senior Geologist, U.S. Geological Survey; Hon. Curator Vertebrate Palæontology, American Museum of Natural History; Research Professor of Zoology, Columbia University.

"Discussions 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. . . . The discontinuity of variation was recognised in abundance. Plenty of the Mendelian combinations would in nature pass the scrutiny of even an exacting systematist and be given 'specific rank.' In the light of such facts the origin of species was no doubt a similar phenomenon. . . . We cannot see how the differentiation into species came about. Variations of many kinds, often considerable, we daily witness, but no origin of species. . . . That particular and essential bit of the theory of evolution which is concerned with the origin and nature of *species* remains utterly mysterious." (William Bateson: Evolutionary Faith and Modern Doubts. Address in Toronto, December 28, 1921.)

IN the early part of the nineteenth century the geologists Hutton and Lyell, the masters of Darwin, overthrew the cataclysmic hypothesis of earth formation by the new uniformitarian doctrine in geology, "We must interpret the past by the present." Now is the time in biology to reverse this doctrine and demonstrate that we must *interpret the present by the past.* This we owe to the discovery of continuous genetic phyla of both invertebrate and vertebrate animals, in which the evolution of the germ-plasm can be continuously traced.

As distinguished from all observations in zoology, we deal in palæontology with secular evolution, *in which we observe the adaptive action and reaction of the heredity germ over long periods of time.* We also observe the secular action of natural selection (Darwin's selection factor), the secular direct reaction to environment (Buffon's factor), the secular adaptive action of habit (Lamarck's factor), the secular adaptive reaction to the living environment (Darwin's factor). As developed between 1893 and 1915 by Osborn, we must sharply separate Darwin's factor of selection, which has no energy content, and the above four energetic forces of evolution, namely, heredity, physical environment, living environment, and individual development or ontogeny.

Every organism develops through the normal interaction of these four forces; if either force is not normal the organism is not normal; if either force is progressive the organism will tend to be progressive; if either force is retrogressive the organism will tend to be retrogressive in the same manner. Whereas in the transmutation of chemical elements and evolution of form in all the inorganic universe we have to do only with the action, reaction, and interaction [2] of internal forces and external forces, in the transmutations of life we have to do with these *four* complexes of energy: first, the internal potential energy of heredity as observed in phylogeny; secondly, the internal energy of the developing organism as observed in ontogeny; thirdly, the external energy of the physical universe known as environment; fourthly, the rapidly multiplying energy of surrounding plant and animal organisms, known as the biota. From the beginning of life every typical organism is invariably developed under this quadruple principle, which is termed tetrakinesis in application to function, tetraplasy in application to form. Thus, whereas inorganic transmutation may be twofold in its elaborate complexes of energy, organic transmutation is invariably fourfold in its elaborate complexes of energy.

Herein lies the first distinction between inorganic and organic evolution. The second distinction is that before life appeared, the inorganic physico-chemico-mechanical content of our planet was exactly the same. Not a single combination of energy and matter in the entire planet was capable of resisting shock, of repairing waste, of combating disintegration, of co-ordinated resistance; consequently, the structural history of the inorganic planet was one of alternate construction and destruction. The third distinction is that while the evolution of life advances by physical, chemical, and mechanical methods which we may more or less definitely measure and observe, this is only a half-truth, because living mechanisms differ from lifeless mechanisms, no matter how perfect, in being more or less self-adapting, self-repairing, self-perfecting, self-regenerating, self-modifying, self-resourceful, self-experimental, self-creative. It is observed that these self-adaptive powers lie solely in the internal potential energy of heredity, while they may be evoked as reactions to changing physico-chemical environment, to ontogenetic experience, to the changing biota of animal and plant life. Organs, tissues, and cells that have lost connexion with the heredity germ-plasm wear out exactly like other machines.

Consequently, the prefix *bio* is essential; in living things we are dealing with bio-physical, bio-chemical, bio-mechanical phenomena. Life has a bio-physico-chemico-mechanical basis.

The primary relation of these four bio-physical, bio-chemical, bio-mechanical actions and reactions, all involving energy, to Darwin's non-energetic principle of natural selection may be illustrated in the annual migration of the golden plover, *Charadrius dominicus.* Numbers of this species winter in Hawaii, where the oceanic climate is singularly uniform the year around, with no violent changes of season. The inborn impulse to northern migration is chiefly a bio-chemical process; the inborn sense of direction that guides the bird northward over two thousand miles of open ocean is chiefly a bio-physical process; the flight is bio-mechanical so far as the heart, the circulation of the blood, the bones, and the muscles are concerned, but bio-chemical in its energy supply. Under the severe struggle for existence all atypical plover probably drop into the sea, but under bio-mechanical self-adaptation every plover that completes the flight to the nesting-place is improved thereby, and in this process the whole race is annually standardised. This crucial, dominant bio-physical, bio-chemical, bio-mechanical period of flight transfers the bird into the breeding grounds, where new principles of natural selection prevail, especially in all the bio-chemical activities of the plover.

In this plover story we illustrate two fundamental principles of biology: first, as the primordial part of the process, the tetraplastic principle of the animal

[1] Address delivered before the National Academy of Sciences, Washington, on April 28.

[2] From E. B. Wilson's "The Physical Basis of Life" we quote a few lines embodying our idea of *reaction*: "No conception of modern biology offers greater promise for the physico-chemical analysis of vital phenomena than that the cell is a colloidal system; and that what we call life is, in the words of Czapek, a complex of innumerable chemical reactions in the substance of this system." Also of *interaction*: "It has been proved that the individual unit often affects the production not merely of one character, but of many. The converse probability is shaping itself that the production of any single character requires the co-operation of several or many units, possibly of all. . . . Every unit may affect the whole organism and all the units may affect each character. . . . The whole system may be involved in the production of every character."

mechanism developed by Osborn between 1893 and 1918, that all typical organisms depend upon the typical action, reaction, and interaction of the four complexes of energy, physical, chemical, mechanical. Secondly, (*a*) Darwin's selection principle, whereby all organisms are constantly standardised in their adaptive actions, reactions, and interactions; (*b*) subsidiary to this, the Osborn-Baldwin-Morgan principle (1896–1898) of "coincident selection," whereby through heritable potentialities of self-improvement, self-adaptation, etc., every race of organisms is not only standardised but also constantly improved; (*c*) the negative of Darwin's principle, the "cessation of selection" or panmixia of Weismann, whereby there is a gradual recession of unused or less used organs from a dominant to a subsidiary position in the life of the organism, finally to retention only in the germinal stage; (*d*) the internal bio-mechanism of selection, the "intra-selection" of Roux, whereby every element in the developing organism also has to contribute its quota or decline.

While intensive observation by palæontology of successive genetic phyla of organisms demonstrates that the chief selection principle of Darwin is constantly operating in the rise and decline of all adaptive bio-mechanical organs, the subsidiary fortuitous selection hypothesis as originally conceived by Darwin leaves the greater part of the bio-mechanical evolution process entirely unaccounted for. While we palæontologists observe great currents of continuous bio-mechanical adaptation which are actually going on in the heredity germ-plasm, we find no evidence either of chance or of discontinuity in the whole domain of bio-mechanical evolution. The surface ripples of fortuity as observed in De Vriesian mutation and the occasional waves of heritage variation observed in botany, zoology, experimental embryology, and genetics do not blind us to the continuous adaptive bio-mechanical evolution of each organism, even to the minutest bio-mechanical detail in each organ.

This statement is borne out in a recapitulation of the chief bio-mechanical principles of adaptation formulated from the time of Aristotle and of Empedocles to the present time, five of which were first observed in zoology and confirmed in palæontology, the remaining four principles having been observed only in palæontology.

(*To be continued.*)

Periodicities and Predictions.

AN interesting paper by Prof. Axel F. Enström, Director of the Academy of Engineering Science, Stockholm, under the title "On Periodicities in Climatic and Economic Phenomena and their Co-variation," deals with the important question of extrapolating past climatic and economic data in order to predict future conditions. In his introduction the author claims that "an investigation along these lines of the coal prices and the general prices" published by him in 1913 has been justified by the prediction of an economic boom about 1918 and a depression with the bottom about 1922. But it is doubtful whether this success really affords a corroboration, for these events must have been mainly controlled by the termination of the War, and were forecasted by methods independent of such an upheaval.

It is rather surprising that the author "earnestly warns" his readers against the "absolutely unreliable" process of drawing a mean straight line through a graph of annual values and producing it; for the advantages and disadvantages of the method lie on the surface, and there are occasions when it may give useful information.

Prof. Enström points out that the ordinary plan of smoothing, say by 5 years, effects a bigger reduction in the amplitude of the shorter periods than it does in the longer: on the other hand, if we subtract each term of a series from the next the series of differences is free of secular change and the amplitudes of terms of short period grow by comparison with those of long period. So when he is examining the temperature of London in relation to a period of about 9 years, which he calls the ϕ period, he smooths with respect to periods of 2, 3, 5, 11, and 13 years, and takes differences three times: and in order further to bring out the ϕ component he subtracts from the resulting series that got by smoothing over 9 years; he then applies an elaborate correction (including a smoothing by 19 years) for the sake of the residual terms. As we should expect after so much selective treatment, the graph is strikingly cyclic, though there are irregularities; and the author's conclusion is that the ϕ period is "not a homogeneous sine-wave of constant wave length but possibly a compound wave": there is, however, no comparison of the amplitude with what would be given by a purely accidental set of data, and no Fourier analysis of the periods between 8 and 10 years. The question whether the period is compound is left unsolved.

In order to obtain a real basis for extrapolation in regard to the future, it seems clear that the series must be replaced by a number of harmonic terms, and extrapolation can only be made when it is shown that the series of harmonic terms gives a fair approximation to the original. The analysis of Prof. Enström appears rather complicated for the small amount of definite information that it provides regarding Fourier periods in the neighbourhood of 9 years.

A further departure is made in relation to "co-variation." After determining curves for the ϕ periods of two quantities in the manner already described, the correlation coefficient between these curves is obtained: as might be expected from the inevitable similarity, high coefficients are derived when the data of one curve are advanced or retarded so as to produce coincidence of phase: and obviously it is misleading to speak of these results, got by a process that in general removes most of the character from the original curves, as if they were derived direct from the originals themselves. Thus it appears very unlikely that the variations of the yield of wheat in France are to any serious extent controlled by the length of the world's railways or control them; but by working out the ϕ curves of these two quantities and moving the latter forward two years a coefficient of 0·82 is produced which Prof. Enström considers as "indicating a very high degree of correlation."

The working out of possible periods exercises great fascination on many minds, and trustworthy information regarding them is of decided value to science. But Beveridge's complete working out of the periodogram of wheat prices in western Europe led him to the conclusion that prophesying was not possible on the facts as he gave them; and Brunt's equally thorough investigation of Greenwich temperature led to a similar conclusion. Disappointment seems inevitable unless great care is exercised before domination by periods is announced, and we hope that the insight and industry of Prof. Enström will find further scope in their elucidation.