Fossils and Life.*

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I PROPOSE to consider the relations of palæontology to the other natural sciences, especially the biological; to discuss its particular contribution to biological thought; and to inquire whether its facts justify certain hypotheses frequently put forward in its name. If I subject those attractive speculations to cold analysis, it is from no want of admiration, or even sympathy, for in younger days I too have sported with Vitalism in the shade and been caught in the tangles of Transcendental hair.

The Differentia of Palaeontology.

Palæontology is often regarded as nothing more than the botany and zoology of the past. True, the general absence of any soft tissues and the obscured or fragmentary condition of those harder parts which alone are preserved make the studies of the palæontologist more difficult, and drive him to special methods. But the result is less complete; in short, an inferior and unattractive branch of biology. Let us relegate it to Section C!

Certainly the relation of palæontology to geology is obvious. It is a part of that general history of the earth which is geology. To the scientific interpreter of earth-history the importance of fossils lies, first, in their value as date-markers, and, secondly, in the light which they cast on barriers and currents, on seasonal and climatic variation. Conversely, the history of life has itself been influenced by geologic change. But all this is just as true of the present inhabitants of the globe as it is of their predecessors. It does not give the *differentia* of palæontology.

That which above all distinguishes palæontology, the study of ancient creatures, from neontology, the study of creatures now living, that which raises it above the mere description of extinct assemblages of life-forms, is the concept of Time. The bearing of this obvious statement will appear from one or two simple illustrations.

Effect of the Time-concept on Principles of Classification.

Adopting the well-tried metaphor, let us imagine the tree of life buried except for its topmost twigs beneath a sand-dune. The neontologist sees only the unburied twigs. He recognises certain rough groupings, and constructs a classification accordingly. From various hints he may shrewdly infer that some twigs come from one branch, some from another, but the relations of the branches to the main stem are matters of speculation, and when branches have become so interlaced that their twigs have long been subjected to the same external influences he will probably be led to incorrect conclusions. The palæontologist then comes, shovels away the sand, and by degrees exposes the true relations of branches and twigs. His work is not yet accomplished, and probably he never will reveal the root and lower part of the tree, but already he has corrected many natural, if not inevitable, errors of the neontologist.

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Effect of the Time-concept on Ideas of Relationship.

Etienne Geoffroy-Saint Hilaire was the first to compare the embryonic stages of certain animals with the adult stages of animals considered inferior. The idea grew until it was crystallised by the poetic imagination of Haeckel in his fundamental law of the reproduction of life, namely, that every creature tends in the course of its individual development to pass through stages similar to those passed through in the history of its race. This principle is of value if applied with the necessary safeguards. If it was ever brought into disrepute, it was owing to the reckless enthusiasm of some embryologists who unwarrantably extended the statement to all shapes and structures observed in the developing animal, such as those evoked by special conditions of larval existence, sometimes forgetting that every conceivable ancestor must at least have been capable of earning its own livelihood. Or, again, they compared the early stages of an individual with the adult structure of its contemporaries instead of with that of its predecessors in time.

Such errors were beautifully illustrated in those phylogenetic trees which, in the 'eighties, every dissector of a new or striking animal thought it his duty to plant at the end of his paper. The trees have withered because they were not rooted in the past.

A similar mistake was made by the palæontologist who, happening on a new fossil, blazoned it forth as a link between groups previously unconnected—and in too many cases unconnected still. This action, natural and even justifiable under the old purely descriptive system, became fallacious when descent was taken as the basis.

The so-called "generalised types," combining the features of two or three classes, and the "annectant types," supposed to unite lines of descent which had diverged many ages before, are conceptions still with us. But they are hopelessly inconsistent with any genealogy either proved or probable.

As bold suggestions calling for subsequent proof these speculations had their value, and they may be forgiven in the neontologist, if not in the palæontologist, if we regard them as erratic pioneer tracks blazed through a tangled forest. As our acquaintance with fossils enlarged, the general direction became clearer and certain paths were seen to be impossible. In 1881, addressing this Association at York, Huxley could say: "Fifty years hence, whoever undertakes to record the progress of palæontology will note the present time as the epoch in which the law of succession of the forms of the higher animals was determined by the observation of palæontological facts. He will point out that, just as Steno and as Cuvier were enabled from their knowledge of the empirical laws of co-existence of the parts of animals to conclude from a part to a whole, so the knowledge of the law of succession of forms empowered their successors to conclude, from one or two terms of such a succession, to the whole series, and thus to divine the existence of forms of life, of which, perhaps, no trace remains, at epochs of inconceivable remoteness in the past."

Descent not a Corollary of Succession.

Note that Huxley spoke of succession, not of descent. Succession undoubtedly was recognised, but the relation between the terms of the succession was little understood, and there was no proof of descent. Let us suppose all written records to be swept away and an attempt made to reconstruct English history from coins. We could set out our monarchs in true order, and we might suspect that the throne was hereditary; but if on that assumption we were to

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make James I. the son of Elizabeth—— Well, but that's just what palæontologists are constantly doing. The famous diagram of the evolution of the horse which Huxley used has had to be corrected in the light of fuller evidence. Palæotherium, which Huxley regarded as a direct ancestor of the horse, is now held to be only a collateral, as the last of the Tudors were collateral ancestors of the Stuarts. The later Anchitherium must be eliminated from the true line as a side-branch—a Young Pretender. Sometimes an apparent succession is due to immigration of a distant relative from some other region—"the glorious House of Hanover and Protestant Succession." It was, you will remember, by such migrations that Cuvier explained the renewal of life when a previous fauna had become extinct. He admitted succession, but not descent. If he rejected special creation, he did not accept evolution.

Descent, then, is not a corollary of succession; or, to broaden the statement, history is not the same as evolution. History is a succession of events. Evolution means that each event has sprung from the preceding one. Not that the preceding event was the active cause of its successor, but that it was a necessary condition of it. For the evolutionary biologist a species contains in itself and its environment the possibility of producing its successor. The words "its environment" are necessary, because a living organism cannot be conceived apart from its environment. They are important because they exclude from the idea of organic evolution the hypothesis that all subsequent forms were implicit in the primordial protoplast alone, and were manifested either through a series of degradations, as when thorium by successive disintegrations transmutes itself to lead, or through fresh developments due to the successive loss of inhibiting factors. I say "a species contains the possibility" rather than "the potentiality," because we cannot start by assuming any kind of innate power.

Huxley, then, forty years ago, claimed that palæontologists had proved an orderly succession. To-day we claim to have proved evolution by descent. But how do we prove it? The neontologist, for all his experimental breeding, has scarcely demonstrated the transmutation of a species. The palæontologist cannot assist at even a single birth. The evidence remains circumstantial.

Recapitulation as Proof of Descent.

Circumstantial evidence is convincing only if inexplicable on any other admissible theory. Such evidence is, I believe, afforded by palæontological instances of Haeckel's law, *i.e.* the recapitulation by an individual during its growth of stages attained by adults in the previous history of the race. You all know how this has been applied to the Ammonites; but any creature with a shell or skeleton that grows by successive additions and retains the earlier stages unaltered can be studied by this method. If we take a chronological series of apparently related species or mutations, a^1, a^2, a^3, a^4, and if in a^4 we find that the growth-stage immediately preceding the adult resembles the adult a^3, and that the next preceding stage resembles a^2, and so on; if this applies *mutatis mutandis* to the other species of the series; and if, further, the old age of each species foreshadows the adult character of its successor, then we are entitled to infer that the relation between the species is one of descent. Mistakes are liable to occur for various reasons, which we are learning to guard against. For example, the perennial desire of youth to attain a semblance of maturity leads often to the omission of some steps in the orderly process. But this and other eccentricities affect the earlier rather than the later stages, so that it is always possible to identify the immediate ancestor, if it can be found. An admirable example of the successful search for a father is provided by R. G. Carruthers in his paper on the evolution of *Zaphrentis delanouei*. Surely when we get a clear case of this kind we are entitled to use the word "proof," and to say that we have not merely observed the succession, but have proved the filiation.

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The "Line-upon-Line" Method of Palaeontology.

You will have observed that the precise methods of the modern palæontologist, on which this proof is based, are very different from the slap-dash conclusions of forty years ago. The discovery of Archæopteryx, for instance, was thought to prove the evolution of birds from reptiles. No doubt it rendered that conclusion extremely probable, especially if the major premise—that evolution *was* the method of Nature—were assumed. But the fact of evolution is precisely what men were then trying to prove. These jumpings from class to class or from era to era by aid of a few isolated stepping-stones were what Bacon calls anticipations, "hasty and premature," but "very effective, because as they are collected from a few instances, and mostly from those which are of familiar occurrence, they immediately dazzle the intellect and fill the imagination" ("Novum Organon," i., 28). No secure step was taken until the modern palæontologist began to affiliate mutation with mutation and species with species, working his way back, literally inch by inch, through a single small group of strata. Only thus could he base on the laboriously collected facts a single true interpretation; and to those who preferred the broad path of generality his interpretations seemed, as Bacon says they always "must seem, harsh and discordant—almost like mysteries of faith."

I have long believed that the only safe mode of advance in palæontology is that which Bacon counselled, namely, "uniformly and step by step." Was this not, indeed, the principle that guided Linnæus himself? Not until we have linked species into lineages can we group them into genera; not until we have unravelled the strands by which genus is connected with genus can we draw the limits of families; nor until that has been accomplished can we see how the lines of descent diverge or converge, so as to warrant the establishment of orders. Thus by degrees we reject the old slippery stepping-stones that so often toppled us into the stream, and foot by foot we build a secure bridge over the waters of ignorance.

The work is slow, for the material is not always to hand, but as we build we learn fresh principles and test our current hypotheses. To some of these I would now direct your attention.

Continuity in Development.

Let us look first at this question of continuity. Does an evolving line change by discontinuous steps (saltations), as when a man mounts a ladder; or does it change continuously, as when a wheel rolls uphill? The mere question of fact is extraordinarily difficult to determine. Considering the gaps in the geological record, one would have expected palæontologists to be the promulgators of the hypothesis of discontinuity. They are its chief opponents.

Again I must leave the facts and their interpretation, merely reminding you of such cases as the heart-urchins or Micrasters of the Chalk. Here, where we have a fairly continuous succession of many hundred feet of similar rock, we do find a slow and gradual change, such that no clean line can be drawn between one form and its successor.

Whatever may be the explanation, the facts do seem to warrant the statement that evolutionary change can be, and often is, continuous. I propose to speak of it as "transition."

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The Direction of Change.

Those who attempt to classify species now living frequently find that they may be arranged in a continuous series, in which each species differs from its neighbours by a little less or a little more; they find that the series corresponds with the geographical distribution of the species; and they find sometimes that the change affects particular genera or families or orders, and not similar assemblages subjected, apparently, to the same conditions. They infer from this that the series represents a genetic relation, that each successive species is the descendant of its preceding neighbour; and in some cases this inference is warranted by the evidence of recapitulation—a fact which further indicates that the change arises by addition or subtraction at the end of the individual life-cycle. For this appearance of successive differences we may here use the brief and non-committal term "seriation."

The comparison of the seriation of living species and genera to the seriation of a succession of extinct forms as revealed by fossils was first made by Cope, who in 1866 held the zoological regions of to-day to be related to one another "as the different subdivisions of a geologic period in time." This comparison is of great importance. Had we the seriations of living forms alone, we might often be in doubt as to the meaning of the phenomenon. In the first place, we might ascribe it purely to climatic and similar environmental influence, and we should be unable to prove genetic filiation between the species. Even if descent were assumed, we should not know which end of the series was ancestral, or even whether the starting-point might not be near the middle. But when the palæontologist can show the same, or even analogous, seriation in a time-succession, he indicates to the neontologist the solution of his problem.

Restricting ourselves to series in which descent may be considered as proved or highly probable, we find then a definite seriation—not merely transition, but transition in orderly sequence such as can be represented by a graphic curve of simple form. If there are gaps in the series as known to us, we can safely predict their discovery; and we can prolong the curve backwards or forwards so as to reveal the nature of ancestors or descendants.

Orthogenesis: Determinate Variation.

The regular, straightforward character of such seriation led Eimer to coin the term "orthogenesis" for the phenomenon as a whole. If this term be taken as purely descriptive, it serves well enough to denote certain facts. But orthogenesis, in the minds of most people, connotes the idea of necessity, of determinate variation, and of predetermined course. Now, just as you may have succession without evolution, so you may have seriation without determination or predetermination. Let us be clear as to the meaning of these terms. Variation is said to be determinate or "definite" when all the offspring vary in the same direction. All the changes are of the same kind, though they may differ in degree. For instance, all may consist in some addition, as a thickening of skeletal structures, an outgrowth of spines or horns; or all may consist in some loss, as the smaller size of outer digits, the diminution of tubercles, or the disappearance of feathers. A succession of such determinate variations for several generations produces seriation; and when the seriation is in a *plus* direction it is called progressive, when in a *minus* direction retrogressive. Now, it is clear that if a single individual or generation produces offspring with, say, *plus* variations differing in degree, then the new generation will display seriation. Instances of this are well known. You may draw from them what inferences you please, but you cannot actually prove that there is progression. Breeding experiments under natural conditions for a long series of years would be required for such proof. Here again the palæontologist can point to the records of the process throughout centuries or millennia, and can show that there have been undoubted progression and retrogression. I do not mean to assert that the examples of progressive and retrogressive series found among fossils are necessarily due to the seriation of determinate variations, but the instances of determinate variation known among the creatures now living show the palæontologist a method that may have helped to produce his series. Once more the observations of neontologist and palæontologist are mutually complementary.

Predetermination.

So much for determination; now for predetermination. This is a far more difficult problem, discussed when the fallen angels

> reasoned high
> Of providence, foreknowledge, will, and fate,
> Fixed fate, free will, foreknowledge absolute,
> And found no end in wandering mazes lost,

and it is likely to be discussed so long as a reasoning mind persists. For all that, it is a problem on which many palæontologists seem to have made up their minds. They agree (perhaps unwittingly) with Aristotle that "Nature produces those things which, being continuously moved by a certain principle inherent in themselves, arrive at a certain end." In other words, a race once started on a certain course will persist in that course, no matter how conditions may change, no matter how hurtful to the individual its own changes may be, progressive or retrogressive, uphill and downhill, straight as a Roman road, it will go on to that appointed end. Nor is it only palæontologists who think thus. Prof. Duerden has recently written: "The Nägelian idea that evolutionary changes have taken place as a result of some internal vitalistic force, acting altogether independently of external influences, and proceeding along definite lines, irrespective of adaptive considerations, seems to be gaining ground at the present time among biologists."

The idea is a taking one, but is it really warranted by the facts at our disposal? We have seen, I repeat, that succession does not imply evolution, and (granting evolution) I have claimed that seriation can occur without determinate variation and without predetermination. It is easy to see this in the case of inanimate objects subjected to a controlling force. The fossil-collector who passes his material through a series of sieves, picking out first the larger shells, then the smaller, and finally the microscopic Foraminifera, induces a seriation in size by an action which may be compared to the selective action of successive environments. There is, in this case, predetermination imposed by an external mind, but there is no determinate variation. You may see in the museum at Leicester a series beginning with the *via strata* of the Roman occupants of Britain, and passing through all stages of the tramway up to the engineered modern railroad. The unity and apparent inevitability of the series conjure up the vision of a world-mind consciously working to a foreseen end.

An occasional experiment along some other line has not been enough to obscure the general trend; indeed, the speedy scrapping of such failures only emphasises the idea of a determined plan. But closer consideration shows that the course of the development was guided simply by the laws of mechanics and economics and by the history of discovery in other branches of science. That alone was the nature of the determination, and predetermination there was none. From these instances we see that selection can, indeed must, produce just that evolution along definite lines which is the supposed feature of orthogenesis.

The arguments for orthogenesis are reduced to two: first, the difficulty of accounting for the incipient stages of new structures before they achieve selective value; and, secondly, the supposed cases of non-adaptive, or even—as one may term it—counter-adaptive, growth.

The earliest discernible stage of an entirely new character in an adaptive direction is called by H. F. Osborn a "rectigradation" (1907), and the term implies that the character will proceed to develop in a definite direction. Osborn gives as instances the first folding of the enamel in the teeth of the ancestral horses and the first slight elevation on the skull of the older Titanotheres, foreshadowing the large nose-horns of those strange Tertiary mammals. He contrasts rectigradations with the changes in shape and proportion of some pre-existing structure, and calls the latter "allometrons." Further, he claims that some predetermining law or similarity of potential governs the appearance of rectigradations, because they arise independently on the same part of the skull in different lineages at different periods of geological time.

Osborn maintains, then, that rectigradations are a result of the principle of determination, but this does not seem necessary. In the first place, the precise distinction between an allometron and a rectigradation fades away on closer scrutiny. When the rudiment of a cusp or a horn changes its form, the change is an allometron; the first swelling is a rectigradation. But both of these are changes in the form of a pre-existing structure; there is no fundamental difference between a bone with an equable curve and one with a slight irregularity of surface. Why may not the original modification be due to the same cause as the succeeding ones? The development of a horn in mammalia is probably a response to some rubbing or butting action which produces changes first in the hair and epidermis. One requires stronger evidence than has yet been adduced to suppose that in this case form precedes function. As Jaekel has insisted, skeletal formation follows the changes in the softer tissues as they respond to strains and stresses. In the evolution of the Echinoid skeleton any new structures that appear, such as auricles for the attachment of jaw-muscles and notches for the reception of external gills, have at their inception all the character of rectigradations, but it can scarcely be doubted that they followed the growth of their correlated soft parts, and that these latter were already subject to natural selection. But we may go further; in vertebrates, as in Echinoderms, the bony substance is interpenetrated with living matter, which renders it directly responsive to every mechanical force, and modifies it as required by deposition or resorption, so that the skeleton tends continually to a correlation of all its parts and an adaptation to outer needs.

The fact that similar structures are developed in the same positions in different stocks at different periods of time is paralleled in probably all classes of animals; Ammonites, Brachiopods, Polyozoa, Crinoids, and Sea-urchins present familiar instances. But do we want to make any mystery of it? The words "predisposition," "predetermining law," "similarity of potential," "inhibited potentiality," and "periodicity" all tend to obscure the simple statement that like causes acting on like material produce like effects. When other causes operate the result is different. Certainly such facts afford no evidence of predetermination in the sense that the development must take place willy-nilly. Quite the contrary; they suggest that it takes place only under the influence of the necessary causes.

The resemblance of the cuttle-fish eye to that of a vertebrate has been explained by the assumption that both creatures are descended, *longo intervallo* no doubt, from a common stock, and that the flesh or the germ of that stock had the internal impulse to produce this kind of eye some day when conditions should be favourable. It is not explained why many other eyed animals, which must also have descended from this remote stock, have developed eyes of a different kind. Nevertheless, I commend this hypothesis of Prof. Bergson to the advocates of predisposition. To my mind, it only shows that a philosopher may achieve distinction by a theory of evolution without a secure knowledge of biology.

When the same stock follows two quite different paths to the same goal it is impossible to speak of a predetermined course. [An instance of this was given.]

(*To be continued.*)

The Constitution of Cellulose.

IN an illuminating lecture delivered before the French Chemical Society on May 21, Prof. A. Pictet, of Geneva, described the results obtained by his pupils and himself on distilling cellulose at a low pressure, and showed how these can be interpreted so as to throw much new light on the constitution of this complicated substance.

When cotton cellulose is heated gradually in a distilling apparatus under a pressure of 10–15 mm. decomposition begins at 210° and an oil distils over equal in weight to 45 per cent. of the original cellulose, which soon solidifies, and consists of lævoglucosan. This is considered to be an anhydride derived from β-glucose, and to have the constitution

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CH(OH) . CH . OH
|        |
CH——O——CH
|        |
O—CH2 . CH . OH.
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Previous work has shown that cellulose furnishes on acetolysis a disaccharide, cellobiose, which probably contains an α-glucose and a β-glucose group. Also, with hydrobromic acid, cellulose gives bromomethylfurfurol. The origin of the latter, a hydrofuran nucleus containing two side-chains, the author terms the chitose grouping. Prof. Pictet therefore regards cellulose as containing two β-glucose groups, one chitose grouping, and probably an α-glucose group, represented thus:

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β | Ch
β | α?
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By acetolysis the α-glucose group and a β-glucose group together form cellobiose (50 per cent.), and in the decomposition with hydrobromic acid the chitose grouping furnishes bromomethylfurfurol (25 per cent.), the other three groups being converted into the black mass which is always formed in the reaction. Finally, on dry distillation under reduced pressure the β-glucose groupings split off to give lævoglucosan (50 per cent.),