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FOSSILS AND LIFE[1]

THE DIFFERENTIA OF PALEONTOLOGY

LIKE botany and zoology, paleontology describes the external and internal form and structure of animals and plants; and on this description it bases, first, a systematic classification of its material; secondly, those broader inductions of comparative anatomy which constitute morphology, or the science of form. Arising out of these studies are the questions of relation—real or apparent kinship, lines of descent, the how and the why of evolution—the answers to which reflect their light back on our morphological and classificatory systems. By a different approach we map the geological distribution of genera and species, thus helping to elucidate changes of land and sea, and so barring out one hypothesis of racial descent or unlocking the door to another. Again, we study collective faunas and floras, unravelling the interplay of their component animals and plants, or inferring from each assemblage the climatic and other physical agents that favored, selected, and delimited it.

All this, it may be said, is 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 paleontologist 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 paleontology to geology is obvious. It is a part of that general history of the earth which is geology. And it is an essential part even of physical geology, for without life not merely would our series of strata have lacked the coal measures, the

[1] From the address of the president of the Geological Section of the British Association for the Advancement of Science, Cardiff, 1920.

mountain limestones, the chalks, and the siliceous earths, but the changes of land and sea would have been far other. To the scientific interpreter of earth-history, the importance of fossils lies first in their value as date-markers; 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 paleontology.

That which above all distinguishes paleontology—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. Not the quasi-absolute time of the clock, or rather of the sun; not various unrelated durations; but an orderly and related succession, coextensive, in theory at least, with the whole history of life on this planet. 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 recognizes 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 paleontologist 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.

I could easily occupy the rest of this hour by discussing the profound changes wrought by this conception on our classification. It is not that orders and classes hitherto unknown have been discovered, not that some erroneous allocations have been corrected, but the whole basis of our system is being shifted. So long as we were dealing with a horizontal section across the tree of life—that is to say, with an assemblage of approximately contemporaneous forms—or even with a number of such horizontal sections, so long were we confined to simple description. Any attempt to frame a causal connection was bound to be speculative. Certain relations of structure, as of cloven hoofs with horns and with a ruminant stomach, were observed, but, as Cuvier himself insisted, the laws based on such facts were purely empirical. Huxley, then, was justified in maintaining, as he did in 1863 and for long after, that a zoological classification could be based with profit on "purely structural considerations" alone. "Every group in that [kind of] classification is such in virtue of certain structural characters, which are not only common to the members of that group, but distinguish it from all others; and the statement of these constitutes the definition of the group." In such a classification the groups or categories—from species and genera up to phyla—are the expressions of an arbitrary intellectual decision. From Linnæus downwards botanists and zoologists have sought for a classification that should be not arbitrary but natural, though what they meant by "natural" neither Linnæus nor his successors either could or would say. Not, that is, until the doctrine of descent was firmly established, and even now its application remains impracticable, except in those cases where sufficient proof of genetic connection has been furnished —as it has been mainly by paleontology. In many cases we now perceive the causal connection; and we recognize that our groupings, so far as they follow the blood-red clue, are not arbitrary but tables of natural affinity.

Fresh difficulties, however, arise. Consider the branching of a tree. It is easy to distinguish the twigs and the branches each from each, but where are we to draw the line along each ascending stem? To convey the new conception of change in time we must introduce a new set of systematic categories, called grades or series, keeping our old categories of families, orders, and the like for the vertical divisions between the branches. Thus, many crinoids with pinnulate arms arose from others in which the arms were non-pinnulate. We can not place them in an order by themselves, because the ancestors belonged to two or three orders. We must keep them in the same orders as their respective ancestors, but distinguish a grade Pinnata from a grade Impinnata.

This sounds fairly simple, and for the larger groups so it is. But when we consider the genus, we are met with the difficulty that many of our existing genera represent grades of structure affecting a number of species, and several of those species can be traced back through previous grades. This has long been recognized, but I take a modern instance from H. F. Osborn's "Equidæ":[2]

> The line between such species as *Miohippus* (*Mesohippus*) *meteulophus* and *M. brachystylus* of the Leptauchenia zone and *M.* (*Mesohippus*) *intermedius* of the Protoceras zone is purely arbitrary. It is obvious that members of more than one phylum [*i. e.*, lineage] are passing from one genus into the next, and *Mesohippus meteulophus* and *M. brachystylus* may with equal consistency be referred to *Miohippus*.

The problem is reduced to its simplest elements in the following scheme:

a	*b*	*c*	*d*	*e*	*f*	Italics.
a	b	c	d	e	f	Lower-case Romans.
A	B	C	D	E	F	Capital Romans.
α	β	γ	δ	ϵ	ϕ	Greek.

Our genera are equivalent to the forms of letters: Italics, Roman, Greek, and so forth. The successive species are the letters themselves. Are we to make each species a genus? Or would it not be better to confess that here, as in the case of many larger groups, our basis of classification is wrong? For the paleontologist, at any rate, the lineage α, A, a, *a*, is the all-important concept. Between these forms he finds every gradation; but between *a* and *b* he perceives no connection.

In the old classification the vertical divisions either were arbitrary, or were gaps due to ignorance. We are gradually substituting a classification in which the vertical divisions are based on knowledge, and the horizontal divisions, though in some degree arbitrary, often coincide with relatively sudden or physiologically important changes of form.

This brings us to the last point of contrast. Our definitions can no longer have the rigid character emphasized by Huxley. They are no longer purely descriptive. When it devolved on me to draw up a definition of the great Echinoderma, a definition that should include all the fossils, I found that scarcely a character given in the text-books could certainly be predicated of every member of the group. The answer to the question, "What is an Echinoderm?" (and you may substitute Mollusc, or Vertebrate, or what name you please) has to be of this nature: An Echinoderm is an animal descended from an ancestor possessed of such-and-such characters differentiating it from other animal forms, and it still retains the imprint of that ancestor, though modified and obscured in various ways according to the class, order, family, and genus to which it belongs. The definitions given by Professor Charles Schuchert in his classification of the Brachiopoda[3] represent an interesting attempt to put these principles into practise. The Family Porambonitidæ, for instance, is thus defined:

> Derived (out of Syntrophiidæ), progressive, semirostrate Pentamerids, with the deltidia and chilidia vanishing more and more in time. Spondylia and cruralia present, but the former tends to thicken and unite with the ventral valve.

The old form of diagnosis was *per genus et differentiam.* The new form is *per proavum et modificationem.*

Even the conception of our fundamental

2 1918, *Mem. Amer. Mus. N. H.*, N. S., II., 51.

3 1913, Eastman's "Zittel."

unit, the species, is insecure owing to the discovery of gradual changes. But this is a difficulty which the paleontologist shares with the neontologist.

Let us consider another way in which the time-concept has affected biology.

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. Through the more precise observations of Von Baer, Louis Agassiz, and others, the idea grew until it was crystallized 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. Often, too, the searcher into the embryology of creatures now living was forced to study some form that really was highly specialized, such as the unstalked Crinoid *Antedon,* and he made matters worse by comparing its larvæ with forms far too remote in time. Allman, for instance, thought he saw in the developing *Antedon* a Cystid stage, and so the Cystids were regarded as the ancestors of the Crinoids; but we now find that stage more closely paralleled in some Crinoids of Carboniferous and Permian age, and we realize that the Cystid structure is quite different.

Such errors were due to the ignoring of time relations or to lack of acquaintance with extinct forms, and 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 paleontologist 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. In those days one heard much of generalized types, especially among the older fossils; animals were supposed to combine the features of two or three classes. This mode of thought is not quite extinct, for in the last American edition of Zittel's "Paleontology" *Stephanocrinus* is still spoken of as a Crinoid related to the Blastoids, if not also to the Cystids. Let it be clear that these so-called "generalized" or "annectant" types are not regarded by their expositors as ancestral. Of course, a genus existing at a certain period may give rise to two different genera of a succeeding period, as possibly the Devonian *Cœlocrinus* evolved into *Agaricocrinus,* with concave base, and into *Dorycrinus,* with convex base, both Carboniferous genera. But, to exemplify the kind of statement here criticized, perhaps I may quote from another distinguished writer of the present century:

> The new genus is a truly annectant form uniting the Melocrinidæ and the Platycrinidæ.

Now the genus in question appeared, so far as we know, rather late in the Lower Carboniferous, whereas both Platycrinidæ and Melocrinidæ were already established in Middle Silurian time. How is it possible that the far later form should unite these two ancient families? Even a *mésalliance* is inconceivable. In a word, to describe any such forms as "annectant" is not merely to misinterpret structure but to ignore time.

As bold suggestions calling for subsequent proof these speculations had their value, and they may be forgiven in the neontologist, if not in the paleontologist, 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 paleontology 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 paleontological facts. He will point out that, just as Steno and as Cuvier were enabled from their knowledge of the empirical laws of coexistence 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 recognized, 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 make James I. the son of Elizabeth—well, but that's just what paleontologists are constantly doing. The famous diagram of the Evolution of the Horse which Huxley used in his American lectures has had to be corrected in the light of the fuller evidence recently tabulated in a handsome volume by Professor H. F. Osborn and his coadjutors. *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 can not 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 can not start by assuming any kind of innate power.

Huxley, then, forty years ago, claimed that paleontologists 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 paleontologist can not 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 paleontological 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 creatures 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. Here we have to remember that the ancestor may not have lived in the same locality, and that therefore a single cliff-section does not always provide a complete or simple series. 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*.[4] 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.

It has, indeed, been objected to the theory of recapitulation that the stages of individual growth are an inevitable consequence of an animal's gradual development from the embryo to the adult, and therefore prove nothing. Even now there are those who maintain that the continuity of the germ-plasm is inconsistent with any true recapitulation. Let us try to see what this means. Take any evolutionary series, and consider the germ-plasm at any early stage in it. The germ, it is claimed, contains the factors which produce the adult characters of that stage. Now proceed to the next stage of evolution. The germ has either altered or it has not. If it has not altered, the new adult characters are due to something outside the germ, to factors which may be in the environment but are not in the germ. In this case the animal must be driven by the inherited factors to reproduce the ancestral form; the modifications due to other factors will come in on the top of this, and if they come in gradually and in the later stages of growth, then there will be recapitulation. There does not seem to be any difficulty here. You may deny the term "character" to these modifications, and you may say that they are not really inherited, that they will disappear entirely if the environment reverts to its original condition. Such language, however, does not alter the fact, and when we pass to subsequent stages of evolution and find the process repeated, and the recapitulation becoming longer, then you will be hard put to it to imagine that the new environment produces first the effects of the old and then its own particular effect.

Even if we do suppose that the successive changes in, say, an ammonite as it passes from youth to age are adaptations to successive environments, this must mean that there is a recapitulation of environment. It is an explanation of structural recapitulation, but the fact remains. There is no difficulty in supposing an individual to pass through the same succession of environments as were encountered in the past history of its race. Every common frog is an instance. The phenomenon is of the same nature as the devious route followed in their migrations by certain birds, a route only to be explained as the repetition of past history. There are, however, many cases, especially among sedentary organisms, which can not readily be explained in this way.

Let us then examine the other alternative and suppose that every evolutionary change is due to a change in the germ—how produced we need not now inquire. Then, presumably, it is claimed that at each stage of evolution the animal will grow from the egg to the adult

4 1910, *Quart. Jour. Geol. Soc.*, LXVI., 523.

along a direct path. For present purposes we ignore purely larval modifications, and admit that the claim appears reasonable. The trouble is that it does not harmonize with facts. The progress from youth to age is not always a simple advance. The creature seems to go out of its way to drag in a growth-stage that is out of the straight road, and can be explained only by the fact that it is inherited from an ancestor. Thus, large ammonites of the *Xipheroceras planicosta* group, beginning smooth, pass through a ribbed stage, which may be omitted, through unituberculate and bituberculate stages, back to ribbed and smooth again. The anal plate of the larval *Antedon,* which ends its course and finally disappears above the limits of the cup, begins life in that lower position which the similar plate occupied in most of the older crinoids.

Here, then, is a difficulty. It can be overcome in two ways. A view held by many is that there are two kinds of characters: first, those that arise from changes in the germ, and appear as sudden or discontinuous variations; second, those that are due to external (*i. e.,* non-germinal) factors. It seems a corollary of this view that the external characters should so affect the germ-plasm as ultimately to produce in it the appropriate factors. This is inheritance of acquired characters. The other way out of the difficulty is to suppose that all characters other than fluctuations or temporary modifications are germinal; that changes are due solely to changes in the constitution of the germ; and that, although a new character may not manifest itself till the creature has reached old age, nevertheless it was inherent in the germ and latent through the earlier growth-stages. This second hypothesis involves two further difficulties. It is not easy to formulate a mechanism by which a change in the constitution of the germ shall produce a character of which no trace can be detected until old age sets in; such a character, for instance, as the tuberculation of the last-formed portion of an ammonite shell. Again, it is generally maintained that characters due to this change of germinal factors, however minute they may be, make a sudden appearance. They are said to be discontinuous. They act as integral units. Now the characters we are trying to explain seem to us paleontologists to appear very gradually, both in the individual and in the race. Their beginnings are small, scarcely perceptible; they increase gradually in size or strength; and gradually they appear at earlier and earlier stages in the life-cycle. It appears least difficult to suppose that characters of this kind are not initiated in the germ, and that they, if no others, may be subject to recapitulation. It may not yet be possible to visualize the whole process by which such characters are gradually established, or to refer the phenomena of recapitulation back to more fundamental principles. But the phenomena are there, and if any hypothesis is opposed to them so much the worse for the hypothesis. However they be explained, the instances of recapitulation afford convincing proof of descent, and so of genetic evolution.

THE "LINE UPON LINE" METHOD OF PALEONTOLOGY

You will have observed that the precise methods of the modern paleontologist, 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 premiss—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."[5] No secure step was taken until the modern paleontologists began to affiliate mutation with mutation and species with species, working his

[5] *Nov. Org.,* I., 28.

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."

It is impossible to read these words without thinking of one "naturæ minister et interpres," whose genius was the first in this country to appreciate and apply to paleontology the Novum Organon. Devoting his whole life to abstruse research, he has persevered with this method in the face of distrust and has produced a series of brilliant studies which, whatever their defects, have illuminated the problems of stratigraphy and gone far to revolutionize systematic paleontology. Many are the workers of to-day who acknowledge a master in Sydney Savory Buckman.

I have long believed that the only safe mode of advance in paleontology is that which Bacon counselled and Buckman has practised, namely, "uniformly and step by step." Was this not indeed the principle that guided Linnæus himself? Not till we have linked species into lineages, can we group them into genera; not till we have unravelled the strands by which genus is connected with genus can we draw the limits of families. Not till 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.

Francis Arthur Bather

ATLANTIC AND PACIFIC SALMON

History repeats itself with monotonous regularity and the most patent facts of scientific knowledge apparently make no impression on the people at large even where their own interests are vitally concerned. They try over and over the same experiment and after the clearly foretold results have been secured they lament the unfortunate consequences. Not only that but an expenditure of money to improve the situation is often rendered useless by action which passes without adequate protest from those most immediately interested.

In former centuries the Atlantic salmon ran yearly in the rivers of the New England coast in such numbers as to excite the amazement of our forefathers. They thought the supply inexhaustible but in 1798 a dam was erected on the Connecticut River and the results are thus described by Jordan and Evermann.

> The salmon was at one time very abundant in the Connecticut, and it probably occurred in the Housatonic and Hudson. . . . The circumstances of their extermination in the Connecticut are well known, and the same story, with names and dates changed, serves equally well for other rivers.
>
> In 1798 a corporation known as the Upper Locks and Canal Company built a dam 16 feet high at Millers River, 100 miles from the mouth of the Connecticut. For two or three years fish were seen in great abundance below the dam, and for perhaps ten years they continued to appear, vainly striving to reach their spawning grounds; but soon the work of extermination was complete. When, in 1872, a solitary salmon made its appearance, the Saybrook fishermen did not know what it was.

The experiment has been tried in many other places and each time the result has been the same. We have heard much in recent years about the dangers confronting the Pacific salmon which furnishes so important a part of the food supply of this country and of other parts of the world. Scientific men have called attention to the serious dangers which ill-considered promotion and careless destruction of spawning grounds have brought to bear on the supply of this splendid fish.

In response to these warnings President Roosevelt appointed a commission for the investigation of problems connected with the Pacific salmon and its fisheries and Congress has continued the work of studying the situation and of aiding the fish to maintain its position by the establishment and development of hatcheries. One of the oldest and most prominent is at Baird, California. It is accordingly