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THE DILEMMA OF THE PALEONTOLOGIST

BY
E. C. CASE



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THIS paper discusses certain of the working principles of paleontology and shows that much of the work done upon fossils has been based on assumptions and on attempts to apply the laws of neobiology to organisms represented by only a fraction of their anatomy. It shows that many of the "laws" which were based on paleontological evidence and which have found their way into textbooks and manuals are now known to be invalid or highly questionable. It attempts to show how varying and conflicting are the conclusions that have been drawn from incomplete evidence. The troubled paleontologist is commonly unacquainted with recently proposed theories of evolution and is confused by the fact that much of the paleontologic evidence originally arrayed to prove evolution is now rejected as invalid. Things long accepted as basic evidence are now known to have been supported by untenable assumptions and abstractions. Unless these be made the paleontological record is incoherent, and

¹The manuscript of this paper was completed sometime before the appearance of Dr. W. K. Gregory's monumental two volume work, *Evolution Emerging*. The reader of that work will find there many illustrations of the problems which are only briefly mentioned in this paper.

if they are made the results are questionable. Especial emphasis has been given to the inadequacy of classic "laws" in order that the paleontologist may realize how unsatisfactory are the lines of evidence long accepted as guiding principles.

The dilemma of the paleontologist is that he is attempting with static and inadequate material to realize the life processes (physiology) of extinct organisms. His material is inadequate because each fossil specimen was a static end result of evolution at the time the organism died. Jepsen (1949, p. 491) said that evolution "was also built upon end products—adults—rather than upon genes, chromosomes and ontogenies." The material consists at best of only a part of the organism and much of this has been collected in a fragmentary condition.

Because a fossil is, or represents, only a part of the once living organism, it is obvious that only that part of it can be known from objective examination. The individual fossil only suggests broadly by its form the origin and development of the organism, whereas a living organism reveals its physiology as well as its morphology. A few genera or species are known from both the Pleistocene and the Recent, but their existence has been for so short a time that they give no evidence of evolutionary change under natural conditions (see *Siphonius*, referred to by Watson, 1949, p. 47).

The fossil offers no explanation of the machinery of evolution, but the material accumulated through geological time constitutes an enormous amount of evidence which may be arranged, rightly or wrongly, in evolutionary series. Dobzhansky (1950, p. 161, quoting Johansen) said that the living organism may reveal the cause of evolution, the fossil can show only the results. The earliest critical study of evolution made it evident that recourse must be made to paleontology to support or question the various theories proposed because of the element of time involved. As Osborn said (1926, p. 36): "Since 1859 there has been a host of over-worked explanations and hypotheses; the word 'variation' of Darwin has been a will-o'-the-wisp leading biologists into many morasses, with its many mutant terms 'variation,' 'selection,' 'mutation.'"

If the paleontologist is able to delimit the occurrence of a fossil² within the bounds of time, space, or conditions, he will almost certainly find suggestions of a past history and/or of a future development. These "suggestions" may be real or adventitious, but they do mark a stage in evolution and may mark the end of progress in one direction or the inception of a new path. It is essential that the paleontologist recognize these stages for, while such a segregation makes for clarity of some evidence, it may also introduce much possibility of error, since the investigator tends to attempt simplification by "lumping," or to increase complication by "splitting."

The method of evolution may be determined or inferred by the observation of living things and by experiment upon them; the fact of evolution can only be established by observation of chronologically arranged series of fossils showing stage-by-stage changes. It is a bit astonishing that so much that has been asserted concerning the biology of the fossil is found on careful examination to be based on assumption. In many cases this has been done consciously in full confidence that future discovery will justify it; in other cases the assumptions have been based on overconfidence.

The hints of history or futurity in a delimited fossil specimen are necessarily based on the similarity of structural characters, but this does not necessarily mean identity of origin; this is what Osborn had in mind when he said that series in a museum is by no means proof of series in nature. Many series that have been acclaimed as evidence have later been proven false by the recognition of convergence, divergence, polyphylety, or parallelism.

The sole criterion for the relationship of fossils is the form. Attempts to revivify the fossils by assumption and abstraction and to fit them into a conventional system based upon both physiology and morphology have proven so inconclusive that the suggestion has been made that it would be better to abandon such a forced classification and to devise a distinct one for fossils based on form alone (Huxley, 1942, pp. 401 and 408; McLaren and Sutherland, 1949;

²The term "a fossil" as here used may refer to a single specimen or, on occasion, to a group of specimens so closely similar as to indicate a distinct variety or species.

Bell, 1950). The magnitude and complexity of the task are so great that they have prevented any attempt to carry it out, despite many obvious advantages.

The burden of proof of evolution was early thrust upon paleontology. The record of attempts at its explanation by both scientists and philosophers has been repeatedly summarized. No explanation has been found fully acceptable, and many have been abandoned. Many suggested series running through millions of years were founded on the basis of similarity of structure, which was uncritically assumed to be proof of relationship. This was a fundamental error which has persisted through an immense amount of work and often in spite of ample proof of its erroneous character.

The maxim that "like produces like" has been shown to be erroneous in many instances (Jennings, 1930, pp. 12, 211, 219, 249), but before this was realized many phylogenies were proposed on the basis of similarity, and the procedure is still current with paleontologists who are unfamiliar with the presently accepted machinery of evolution.

A series of end results may be arranged in chronological order, apparently recording inheritance of characters and so phylogeny, but the same or a very similar series may be the result of many causes. This is especially true in cases in which the end results are complicated structures and in which only a part of the fossil is recovered.

Before the recognition of genetic processes the worker was faced by an enormous number of specimens from which he was at liberty to select those which, when placed in the proper relations, best fitted his chosen theory. By a judicious rejection of troublesome specimens, or emphasis upon helpful ones, seductive lines based on similarity of structure were visualized; there was no critical justification of phylogeny. Obviously, simulacra of lines of descent were easily produced and, equally obviously, somewhere, recognized or not, the true lines of descent must have existed; these were certainly far more devious than the straight lines of the conventional "family tree."

Organisms are constantly changing, either from generation to generation or from stage to stage of an evolutionary series. Each individual is a step in either a conservative or a more changeable series.

Each step will be in relation to its environment, advantageous or disadvantageous. The change may be so slight that it is undetectable by the paleontologist who is dealing solely with recovered parts of the organism. A vast number of changes will be detectable only after they are well established.

Of the almost innumerable forms which are constantly coming into being many disappear within a generation, others survive for generations, a few multiply rapidly. The success of any organism is measurable by the number of its descendants and the trends (traits of Dobzhansky) that it develops. Success is dependent on the ability of the new organism to find a niche in the environment favorable to its physiological needs; this may or may not be recorded for the paleontologist by morphological changes.

Dobzhansky (1950, p. 165) said that in organisms other than viruses the genotype is an integrated system of many kinds of genes. Estimates of the gene loci in higher organisms are of the order of thousands or tens of thousands, but these can only be inferred in the fossil, never identified as such.

Two things govern the evolution of life: one is dynamic, the constant occurrence of new forms; the other is static, the environment. The dynamic thing produces new forms, some of which are apparently devoid of any ancestral forms and many of which are the result of ancestral influences which have charted a tendency in some definite direction. Watson (1949, p. 52) said that the new things "... may have been brought about by natural selection retaining and directing changes made necessary [for instance] by a steadily increasing size of the animals during the evolutionary series." The static control is the environment; it is often spoken of as if it were an active force, but this is not true. The environment is only a set of conditions into which the new things are born to survive or perish. The expression "natural selection" has also been misused to imply action. Properly, it simply implies conditions in which the organism finds life or death.

In the early stages of the study of Mendelian inheritance it was practically a dogma that the environment could have no effect upon the evolution of new forms; these originated solely in the mutations

of the genes. Gradually, it has come to be realized that the environment has a great effect upon the mutating gene. The pendulum of opinion has swung so far that the statement is now made by Clements, Martin, and Long (1950) that environment is the controlling factor. In his review of their book, Reeder (1950) stated that Clements "finally came to believe that new forms could arise by the action of environmental factors alone." Reeder commented:

It has long been known that organisms show differential responses to varying environmental conditions. The authors of the volume conclude that adaptation is brought about by responses to direct physical factors and is expressed both in function and form. They further state that for all the species employed [in observation], there is no evidence that it arises through the selection of genetic strains or variations. They believe that it is possible to convert one Linnaean species into another by altering the environment.

Reeder did not accept the conclusion reached by Clements, Martin, and Long and cited works by Clausen, Keck, and Kelsey (Carnegie Institution of Washington, 1950) to the contrary. He said:

These authors conclude that natural selection determines the character of the plants that occupy a given environment, and that the ability of a plant to accommodate itself to a new environment is dependent upon its genetic constitution. They further state that, in their studies changes produced by the environment give no evidence of permanence, and although they may be quite spectacular, they never obscure the individuality of the plant.

Paleontology, dealing only with end results, can give no account of the action of the gene, but the paleontologist has always been aware of the possible integration of observed results with the action of the genes. Such an integration can only be explained by assumptions which bear the odium of the often quoted Scotch verdict "not proven."

A successful organism increases in number of individuals, and the adjustment to its environment becomes more definite; it is said to specialize. The term "adaptation" has been used by some workers but without change of meaning. Specialization may continue until a very small character or a very small factor of the environment determines its continuing success or causes its failure and disappearance. Certain phases of specialization have been regarded as degeneracy (Clarke, 1921), but are really evidence of more complete adjustment to the environment and, hence, to progress. The often

cited case of the cirriped, *Sacculina* (Parker and Haswell, 1897, Vol. 1, p. 535, Fig. 421, and p. 553), is far from degeneracy; it is rather a triumph of specialization. No worker is justified in assuming that a simplification of structure, or any abstraction of such a condition, is degeneration. If a trend toward sightlessness or an apodal condition is a trend toward success, then such a trend is far from degeneracy.

The paleontologist is constantly aware that his fossil has, in all probability, gone through a development similar to that of any living organism, and he is prone to use the terminology and principles of neobiology in a tentative way, as the most workable common language. His justification is his belief in the constancy, if not in the immutability, of the laws of life and the fact that his specimens as end results apparently fit into an evolving series.

Our knowledge of the fossil *per se*, obtained by purely objective examination, is confined to: (1) the form of the hard parts, mostly of adult individuals, rarely of immature stages, and more rarely of small items of the soft parts preserved as impressions; (2) its position in the geological column and hence, possibly, its position in a sequence of related forms, that is, its phylogeny; and (3) its geographical distribution.

As fossils are the relics of once living things there is a constant temptation to apply to them the laws of life (embryology, ontogeny, phylogeny, evolution) insofar as they affect the hard parts. The assumption that the laws of life are immutable has not gone unchallenged, as shown by the discussion of "emergent evolution" below.

Watson (1949, p. 45) has expressed much the same attitude toward the fossil. De Beers (1948, p. 181) said, "All workers on this subject would agree that their conclusions are based on 'Comparative Anatomy,' and would subscribe to the simple proposition that similarity of structure is indicative of a community of descent to the degree that such similarity is detailed and extensive."

The amount of fossil material properly collected and preserved is not yet sufficient to prove incontestably many of the assumptions that have been accepted as basal. Dobzhansky (1941, p. 6) said that since, by a conservative estimate, there are 1,500,000 species of plants and animals now in existence, there is no reason to believe that

the number was greatly different in any equal portion of post-Archaeozoic time. Edinger (1949, pp. 7 and 11) stated that we know the form of the brain in a "scarce half hundred of extinct reptiles" and that we do not "know the brains of as much as 1% of extinct mammalian genera. We know far less."

It must be constantly kept in mind that the fossil record is a matter of discrete occurrences which have in many instances been grouped together by interpretation of structure and by sequences in time; both, in most cases, forming a chain (phylogenies) with many weak links supported by assumptions and abstractions. This is a weakness only too often overlooked. Even the most nearly perfect phylogenetic series, as of the horse, elephant, camel, and ammonites, are subject to question.

In the great majority of cases the study of evolution has advanced by the formulation of a theory and then by an appeal to paleontology for evidence in proof, as it is the sole science that reveals the changes through time, which are evolution. In only one recognized process of evolution has the procedure been reversed. Objective study has shown that there is constantly present an apparent tendency to continuous evolution toward a definite end; this is orthogenesis. The observed facts have aroused a demand for an explanation by theory—an explanation which has not yet been vouchsafed, except as many biologists see in natural selection a condition that removes the less advantageous variations in an adaptive series and thereby renders the advantageous adaptations more evident through time.

From the form of some specimens, objectively considered, a more or less accurate and complete phylogeny can be constructed, but the physiological and mechanical activities can only be inferred by comparison with living things. Colbert (1949, p. 390) remarked that "the geneticist studies the mechanism of evolution while the paleontologist studies the results of evolution." Simpson (1944, p. xvi) said that "fossil animals cannot be brought into the laboratory for the experimental determination of their genetic constitution."

It is possible to understand the working of some simple machines from an inspection of them at rest, but this is not possible in an organism, for the mechanism is far too complicated and the motivation

far too obscure. Each fossil specimen was an end result of the machine at the time it came from the machine; beyond that succeeding generations may have been little or much changed. It is reasonable to suppose that the laws and forces of genetic evolution have prevailed through time in the evolution of all but the simplest forms of life, but with the cessation of dynamism in the machine (the death of the organism) there is no way in which the genetic activities of the organism can be traced. To apply genetic principles in explanation of paleontological events would be but to enter the field of possibilities and exploit any subjective preference held by the worker. Fortunately, most biologists and paleontologists have resisted the temptation to do this.

Simpson (1944, p. xvii) said:

The paleontologist is given only phenotypes, and attempts to relate these to genotypes have so far had little success. But here genetics can provide him with the essential facts. One cannot directly study heredity in fossils, but one can assume that some, if not all, of its mechanisms were the same as those revealed by recent organisms in the laboratory. One cannot identify any particular set of alleles in fossils, but one can recognize phenomena that are comparable with those caused by alleles under experimental conditions.

This is but to follow a plausible and preferred path based on an assumption. To trace a developing character in a phylogenetic series is not to recognize a genetic character, for a genetic character is the result of a single event, a mutation; undoubtedly, many workers in tracing such a development as size or the cusp of a tooth have not escaped the temptation to treat it as a genetic change.

The evidence furnished by fossils of the activities of the organism when alive is exclusively, or nearly so, circumstantial evidence. Such evidence is notably inconclusive, as has been repeatedly shown by the logic of the courts. Certain objects or certain sequent events may be taken as establishing the greater or lesser probability of other facts or events; any conclusion or verdict drawn from such evidence will always be subject to revision and will ever be a questionable link in proof. The fossil itself can not furnish better evidence. A series of specimens in a supposed phylogenetic line may be such as they appear or they may be unrelated items in a fortuitous juxtaposition.

The information gained from paleontology is limited because it

deals with only a small fraction of the organisms that have existed upon the earth and with only the preserved parts of these. It is comprehensive in that the phylogenetic series show actual change through time. Phylogenetic lines are demonstrable in some cases, but in most there are gaps which have to be filled by abstractions which are inescapably influenced by the subjective attitude of the worker. As Simpson (1944, p. 153) said:

It is doubtful whether an undeviating or even a relatively straight structural line can be traced from an archetypal protozoan to any real metazoan, an ancestral fish to any real tetrapod, a protolemur to any existing primate, and so forth. The major changes of direction are systematically poorly represented in the fossil record, a point already stressed, but there are numerous examples of changes and even of complete reversals in the direction of evolution of organisms on a minor scale or of single structures; for example, the secondary simplification of ammonites sutures, the reduction of the canines in the Felinae, or the dwarfing of certain races of elephants.

The morphological characters of extinct species are revealed or implied in their fossilized remains. It is very possible to arrange the items of a collection of related species, sequent in time, in many and various ways according to selected characters, just as any collection of inorganic material might be arranged according to size, color, weight, or otherwise; any arrangement would be largely dependent upon the bias of the arranger. Excellent examples of such a possibility occur in Huene's use of the structure of the vertebrae of tetrapods instead of the long-honored temporal region (Huene, 1948), and Steinman's arrangement of vertebrates according to form, as in his grouping together of all mammals with enlarged canine or incisor teeth (Steinman, 1908). Both of these attempts led to rather startling conclusions.

Paleontology has a dual significance: To the stratigrapher the fossils are of immense aid in determining the age and correlation of the beds in which they occur. To the paleobiologist the fossil "smells of mortality" and is subject to all the methods of biological investigation insofar as they are applicable to the preserved hard parts. This latter field is so large and so seductive that the enthusiastic and unwary paleobiologist may be, and has been, led to conclusions far beyond those warranted by the material at hand. There is con-

stant temptation to apply genetic principles to the explanation of phylogeny, but such explanations can only be specious and suggestive; only the result can be shown by the fossil, never the machinery.

Davis (1949, p. 77), speaking of the inadequacy of paleontology in proof of theories, wrote:

Adaptation can be studied to advantage only when the complex organism-environment interrelationship can be studied, even though from the evolutionary standpoint it is the morphological specialization of the organism that is of chief interest. The skeleton, recent or fossil, exhibits a part of the total *morphological change* of the organism, which in turn is only a part of the dynamic relationship that is adaptation. Evolution is measured in terms of morphological change, however, rather than in terms of dynamic relationships, and thus interest is ultimately in the agencies producing such changes. In the final analysis evolution is (except possibly on the very lowest levels) a shift in the direction or level of adaptation.

Davis (1949, pp. 87 and 88) went on to say:

Paleontology supplies factual data on the actual rates of change in the *skeleton* and the patterns of phyletic change in the skeleton. Because of the inherent limitations of paleontological data, however, it cannot perceive the factors producing such changes. Attempts to do so merely represent a superimposition of neobiological concepts on paleontological data.

Watson (1949, p. 60), after discussing the ways in which geographical races or subspecies have come into existence, said that "it seems evident that paleontology can very seldom, if ever, contribute much of importance to the matter."

Because the evidence for evolution from paleontology has been so commonly accepted without critical question it is worth while to review its nature and note how much of it is based on assumption and abstraction. The best way to do this is to discuss categorically certain of the principles and pitfalls.

FORESHORTENING OF GEOLOGICAL AND PALEONTOLOGICAL RECORD

The content of paleontology is the content of a history of life upon the earth. With the acceptance of evolution it became apparent that paleontology as a historical subject was the only source of evidence that organisms had changed with the passage of time. Such evidence could not be furnished by neobiology because the necessary time was far greater than the duration of many generations of

inquirers. Every piece of evidence of apparent change from form to form was avidly seized upon and cited in evidence, pro or con. Criticism soon showed that many of the supposed series were erroneous and that, at best, but few were known which showed the minute step-by-step changes that alone, it was thought, could prove evolution. The opponents of the theory seized upon the paucity of well-established series as a major argument against the universality of evolution. The reply of the evolutionist was "the imperfection of the geological record." As collections of fossils increased, the imperfection of the record partly decreased, but also partly increased as seemingly unfillable gaps became evident.

Scott (1919, p. 93), in a series of popular lectures, summarized the objections to the theory of evolution: (1) "The paleontological record, as we actually have it, is irreconcilable with the evolutionary conception, because of the many cases of the sudden and unheralded appearance of new kinds of organisms . . ." Scott answered, "This objection overlooks the phenomena of migration." And to this, one may add that discontinuous evolution has now been proven in living organisms and was, therefore, present in the once living. (2) "While the geneological series made out within certain families may be admitted as proving development within relatively small groups, the fossil record fails to connect the larger and more widely separated, thus indicating that evolution, while real enough, is of strictly limited possibilities." Scott's answer to this was that large gaps in the record have been filled by discovery and that there are obvious reasons why some will never be filled. The specimens from the earliest fossiliferous rocks show that the organisms were already well differentiated, and there is no hope of finding their ancestors.

Paleontology has the disabilities of a historical subject. The establishment of the sequence of events is its objective; the imperfection of its evidence is its failing. In human history the record becomes less and less clear as it recedes into the past, until events are recorded by dynasties or by a single name on an age-old pillar. Just so, the paleontological record is foreshortened by omissions, losses, misinterpretations. It is as if one were above the clouds which were pierced by occasional isolated peaks from which one is called upon

to interpret the landscape hidden below. Only those who have witnessed a mirage can appreciate how reality may be distorted; small objects may rise as shimmering towers, unrecognizable as the original. The paleontological record has similar distressing faults. H. G. Wells (1921) said: "One of the most difficult things for both the writer and the student of history is to sustain the sense of these time intervals and prevent these ages becoming shortened by perspective in his imagination." Gilluly (1949, p. 574) has discussed the same idea recently, using the term "geological perspective," and his account brings out clearly how the breaks in the record have been patched with assumptions. In the same article (p. 582) he has shown how the dating of geological events has been supported by similar assumptions: ". . . yet I will anticipate the details of my argument by stating that I believe our paleontological dating is nowhere nearly accurate enough to bracket orogenies within the narrow limits assumed by some workers."

Despite the distorted geological perspective and the foreshortened record, enough is certain to warrant the continued search. Enthusiasm for new revelations has caused fragmentary evidence to be arranged and rearranged to fit the idea of continuous, step-by-step evolution. This resulted in the ubiquitous phylogenetic trees which accompanied so many early papers but which have now largely disappeared except as expressions of the most general relations.

Foreshortening of the record is recognized by Ulrich (1911, pp. 495-501) in his statement that varieties and species of fossils did not originate in the shallow epicontinental seas, but that the new forms occurring in sequent zones originated in deep, permanent seas and appeared in the shallow seas by migration. It has been said (by Ulrich, I think) that no fossiliferous zone has been discovered that is thick enough, long-enduring enough, or fossiliferous enough to show varietal change in any species. (The word zone as here used connotes similarity of conditions throughout its extent.) Such new varieties or species as may be detectable in the place of their origin occur in thick formations representing millions of years.

LAW OF BRAIN GROWTH, CONTINUOUS SPECIALIZATION, OR
CONTINUOUS IMPROVEMENT

This is an instance in which paleontology has been used by specious argumentation to support an anthropomorphic conception. The law of brain growth was based by Marsh upon the endocranial casts of certain Tertiary mammals. He noted the relative increase in size and complexity of the brain when the casts were arranged in chronological sequence; the specimens were selected for the desired characters with no attention paid to taxonomic relations or to locality. Since the changes in the brain indicated an approach to the human brain, it has been called the law of continuous improvement.

There can be no law of continuous improvement, if by that is meant an approach to an idealized abstraction, such as that the human brain is the best brain in a predetermined course. Every series of variations, in whatever organisms, approaching a better adaptation to its environment is a specialization and an improvement. The terms "continuous specialization" or "continuous adaptation" connote adjustment to the environment and insofar indicate a real improvement. It would be difficult to maintain that the human brain with all its complexity is the best brain for the environment in which it functions. Witness the difficulty with which it adjusts itself to the conditions under which the human species lives, without self-destructive conflict.

In a similar way the term "degeneration" has been given a wrong meaning by anthropomorphic bias. Evolution is a constant adjustment to the environment by specialization (adaptation). This is true even in the most advanced state of parasitism. In such a trend the increasing dependence is an advance. The case of the cirriped *Sacculina* is an excellent example (Parker and Haswell, 1897). Cope (1896, p. 75) asserted that degeneracy is applicable to unit characters, not necessarily to the organism as a whole. It is known that units of structure, as the limbs of certain tetrapods, disappear by gradual wastage, but this is a case of correlated evolution; the animal, as a whole, is advancing in its adjustment to the environment by discarding certain no longer useful structures. Cope said:

In the phrase "from the simple to the complex" is implied an ascending scale of evolution. In the phrase "from the generalized to the specialized" we

may include both progressive and retrogressive evolution. Retrogressive or degenerative evolution has been a frequent phenomenon in the past, and scarcely an organism exists which does not display degeneracy in some detail of its structure. Progressive evolution has, however, not been prevented by the frequent occurrence of an opposite process; and, indeed, degeneration of parts, or types of life, have been necessary to the advance of other and better organs or forms.

Cope (1896, p. 86) also said: "The result of these investigations has been to prove that the evolution of the Vertebrata has proceeded not only on lines of acceleration, but also on lines of retardation. That is, that evolution has been not only progressive but at times retrogressive," and (1896, p. 75) "Degeneration is a fact of evolution as already remarked and its character is that of an extreme, which has been, like an over-perfection of structure, unfavorable to survival."

It is obvious that the process may be regarded as degeneracy or specialization, depending upon whether it is thought of in terms of unit characters or in terms of the organism as a whole. Clarke (1921) has given many instances of advanced specialization in fossil forms. He considers any departure from the normal as disease but this is obscure, for the normal condition of evolving organisms is constant change; any fixed normal in life is a pure abstraction. There is no degeneracy in a series following an established trend, no matter how simple or how elaborate the end product may be. In cases where whole parts, such as limbs, teeth, and body segments, are lost, the rudiments linger in decreasing importance. The rudiments might, as unit characters, be considered to be in a process of degeneration, but for the organism the loss is part of the process of specialization. Profit can be made on a falling market; loss or simplification to realize an end is as important in nature as in any humanly devised process.

Clarke (1921, p. 17) remarked of the goose barnacles: "These are most venerable degenerates of most adequate adjustment," and said (p. 18) that "with a thousand like cases, they speak only of extreme adaptation of their physiology to adjusted requirements." There is here a contradiction of terms, for so long as the animal survives in its environment and meets the stress of life by "adequate adjustment," it is progressing in its trend.

Specialization is of the same nature as "degeneracy" and can lead as readily to extinction. Simpson (1944, p. 143) said that "more specialized phyla tend to become extinct before the less specialized." Case (1915, p. 115) remarked that "perfect adaptation is a possible cause of extinction." Again, Simpson (1944, p. 176) spoke of "what Darlington calls 'lag,' failure of the genotype to produce mutation as rapidly as selection requires. Indeed, this is probably the most general cause of extinction." On the same page Simpson said of the extinction of *Smilodon* that "it was an environmental change, due to the scarcity and final disappearance of the prey for which the macherodonts were specialized that probably caused their extinction."

Simpson (1944, pp. 170-71) cited Swinnerton's work on *Gryphea* as an example of excessive specialization leading to extinction. On pages 62 and 63, Clarke (1921) made certain remarks about the goose barnacles that are quoted with the present author's suggestions of the real process: "Thus we seem to have traced back to pretty clear indications of its beginning this highly degenerate [highly specialized] crustacean, and in these early presentments see that the fixation which led to recreancy [high specialization] was for a purpose distinctly advantageous to ease of living [success in life]. . . ."

The law of continuous specialization can be inferred from apparent stages of its progress in living forms, as in the various degrees of loss of the limbs in certain tetrapods; it can be demonstrated only in long phylogenetic series, as that of the horse, the ammonites, and the echinoid *Micraster*.

LAW OF RECAPITULATION; BIOGENETIC LAW

This law was for long in good repute and was supported by both the paleontologists and the biologists. Increased information and critical study have greatly limited the scope and applicability of the law until at present it is believed to be usable only in a very broad sense or even rejected *in toto*. De Beer (1930, p. 109) has spoken confidently of the "dethronement [of] the theory of recapitulation."

Baer's conclusions, published in 1828, were based on the fact that he could not determine even the proper phyla of certain un-

labeled embryos, and Haeckel's (1866) formulation of the law of recapitulation, based on Baer's conclusions, became one of the commonplaces of every text on evolution.

Baer's observations were epitomized by him in four "laws" (here quoted from de Beer, 1930, pp. 4 and 5):

1. In development from the egg the general characters appear before the special characters.
2. From the more general characters the less general and finally the special characters are developed.
3. During its development an animal departs more and more from the form of other animals.
4. The young stages in the development of an animal are not like the adult stages of other animals lower down in the scale but are like the young stages of those animals.

Cope (1887 and 1896) pointed out that Dana and Agassiz had noted from taxonomic studies that new lines of evolution did not usually arise from highly specialized, progressive or retrogressive forms, but from the less specialized members of any group. This he called, in 1887 (p. 398), the "Doctrine of the Unspecialized," and in 1896 (p. 172), the "Law of the Unspecialized." A highly specialized organism is closely adapted to its environment and is often unable to readjust itself to any change, largely because the characters have already become adjusted and fixed, whereas a less highly specialized form could adjust itself by variation. In rare instances only do the highly specialized forms retain sufficient plasticity to embark on a new course. Thus, the amphibians did not arise from some well-adjusted fish but from a simple form capable of enduring in a new environment and originating a new line. This law is especially evident in paleontology where trends are traceable through time.

Haeckel's elaboration of Baer's conclusions overenthusiastically applied them to individual organisms. He stated as the law of recapitulation "that every animal in the course of its individual development tends to recapitulate the development of the race." In the fourth English edition of his *History of Creation* (1892, p. 355), Haeckel stated the law in somewhat different words: "Ontogenesis, or the development of the individual, is a short and quick repetition (recapitulation) of phylogenesis or the development of the tribe to which it belongs, determined by the laws of inheritance and adaptation."

There was enthusiastic acceptance of the law, but continued critical examination has shown that it could be substantiated in only a very general way. The paleontological evidence was incomplete, as only the hard parts were available, and the work of the embryologists brought out much that discredited the law. A few citations will show the uncertainty of its standing today. The first five authors quoted have rejected the law, the others have accepted it with more or less reservation.

Bateson (1894, p. 8) wrote:

But the claims of embryology did not stop here. In addition to the application of the general Theory of Descent, it has been sought to apply the facts of Embryology to solve particular questions of the descent of particular forms. It has been maintained that if it is true that the history of the individual repeats the history of the Species, we in the study of Development see not only that the various forms are related, but also the exact lines of Descent of particular forms. In this way embryology was to provide us with the history of evolution. . . . It will, I think, before long be admitted that in this attempt to extend the general proposition to particular questions of descent the embryological method has failed.

Streeter (1927) showed that the arrangement and transformations of the aortic arches, which have been repeatedly used as an example of the law of recapitulation, have been erroneously interpreted. He wrote (p. 405): "In short, embryonic blood vessels have no ground plan of their own, independent of the structures around them," and (p. 409) "To say that they [the aortic arches] are a transitory set of symmetrical and uniform tubes, a symbol of a phase in ancestral history, is no longer an adequate description of them." Furthermore (p. 409), he said:

With this better knowledge of the exact anatomy of the aortic arches it has become apparent that at no time does Rathke's embryonic type exist in the embryo—any more than the Owen's archetype vertebra. Apparently von Baer appreciated this, but his followers did not. They accepted irregular capillary vessels as vestiges of the arches, therefore virtually arches, and so constructed in their imagination an embryonic type, which at the best was only a compound of several stages.

Huxley (1942) did not discuss recapitulation at length but quoted Haldane (1932, p. 507) as speaking of "partial recapitula-

tion" and as discussing the evidence afforded by the Ammonites. Of the human species he (Haldane) said: "But many of its features recapitulate those of its adult ancestors."

Keith (1949, p. 193) described the condition of a foetal chimpanzee within a month of its term, which is preserved in the Museum of the Royal College of Surgeons in London.

In the final month of development the chimpanzee foetus becomes clad with hair, and is born a hairy animal. . . . If the law of recapitulation represented the whole truth, then we should have to suppose that the chimpanzee comes of a hairless human-like ancestry which later put on a hairy dress. Such is an impossible interpretation, for hairyness is one of the most ancient of mammalian characters, and all the records of the rocks are against it. The foetal chimpanzee, in its hairless stage, is not repeating an old or ancestral feature, but is exhibiting a new one. The stages passed through by a developing animal are not only retrospective; they are also prospective. In the development of the body new characters are interpolated with the old.

De Beer (1930, p. 9) showed that Agassiz, Keibel, Mehnert, and Garstang, among others, have pointed out "that the order in which characters appeared in phylogeny is not always faithfully reproduced in ontogeny."

De Beer (1930, p. 56) said:

Nearly all the cases mentioned in this chapter [Chap. VII] have been adduced to prove the theory of recapitulation, and it has been my task to show that they do not prove it. What they do prove is embryonic similarity and repetition of characters in *corresponding* stages of the ontogenies of ancestor and descendant, which reveals the affinity between different animals, but supplies no evidence as to what the adult ancestral form was like.

De Beer (1948, p. 181) said:

Other authors are still caught in the coils of the theory of Recapitulation. They hold that the young stages of ontogeny of a descendant represent the past adult stages of ancestors in the evolutionary history. They are thereby led to the adoption of several far-reaching corollaries, such as the principles that evolutionary novelties can only be incorporated into a phylogenetic line at the adult stage, and that a character which appears early in the ontogeny of the descendant must have been evolved early in its phylogeny. This unfortunate theory, unsound in its premises, illogical in its deductions, and disastrous in its results, is now generally recognized as the imposter which it is. Perhaps the best demonstration of the absurdities to which the theory of recapitulation leads is that provided by Gregory when he wrote "If the biogenetic law were

universally valid it would seem legitimate to infer that the adult common ancestor of man and the apes was a peculiar hermaphroditic animal, that it subsisted exclusively upon its mother's milk and that at an earlier phylogenetic period the adult ancestor was attached to its parent by an umbilical cord."

On page 184 of the same article (1948), de Beer said:

On the other hand, the adult stage of the descendant can sometimes resemble the youthful stage of its ancestors, the mode of evolution having taken the form of prolongation of the ontogeny and retention in the adult descendant of characters that were youthful in the ancestor. This is paedomorphosis.

Clarke (1921, p. 16) said: "Their ontogeny, or individual history, here as often, reflect[s] the successive phases of development through which their entire race has come." Smith-Woodward (1923, p. 30) is quoted by de Beer (1930, p. 8) as saying that speaking as a paleontologist he is "convinced that whenever he is able to trace lineage he finds evidence of the recapitulation of ancestral characters in each life history." Russell (1930, p. 8) said recapitulation "does take place, and it must be reckoned with as a general feature of development." On page 9 he added: "But recapitulation remains all the same an important characteristic of development and as such requires explanation."

Wells and others (1931, p. 366), speaking of Baer's conclusions, said: ". . . that animals resemble each other more and more the further back we pursued them in development," and concluded, "This law in general holds good; and this resemblance of embryos and larvae is a very striking fact, very difficult to explain save on evolutionary lines." The same authors, (p. 373) said: "Recapitulation occurs like something done under a powerful and unavoidable inertia of tradition, like something deep in the nature of the living creatures," and on pages 368-69 they said: "Tens of thousands of animals do recapitulate the past during development. . . . But it is a general and not a complete recapitulation. . . . Because of that recurrent urge each individual animal repeats within its individual cycle of life those uneffaced tendencies from the remote past of its race." In this last quotation there is a hint of the mnemonic theories proposed by the philosophers rather than the biologists.

LAW OF IRREVERSIBILITY OF EVOLUTION: DOLLO'S LAW

This law is not compatible with the law of recapitulation. De Beer (1948, p. 181) said that those who believe in the law of irreversibility hold:

That evolutionary trends, once established in the phylogeny, commit the type to a peculiar morphogenetic policy from which there is no retreat. The effects of this view are negative and exclusive, in that they lead its protagonists to assert the impossibility of derivation of one type from another if the latter possess a character which the former lacks. Possession of such a character disqualifying the holder from participation in a pedigree, is called Specialization. The Neanderthaloid type possesses large brow ridges which modern man lacks; believers in irrevocability are therefore bound to exclude Neanderthal man from the ancestry of modern man.

Irreversibility has been used by many to mean that a structure which has lost something of its original function and form cannot return to that function and form. In certain dinosaurs, the animal which has adopted a bipedal gait and reduction of the forelimbs cannot return to a quadrupedal gait and large forelimbs, but it has been shown that the Ceratopsidae with small forelimbs had returned to a quadrupedal gait and at the time of their extinction were enlarging the forelimbs.

Hyatt has shown that a similar loss and partial regain of a character took place in certain ammonites, as evidenced by changing degrees of involution of the whorls and the details of ornamentation.

According to Lull (1929, p. 249), the law of irreversibility "says that an organ once lost can never be regained and that a specialized form can never again become generalized."

Romer (1949, p. 112) has shown that these and other examples are not true to the meaning of the law as expressed by Dollo, who admitted that an animal "may change the general course of its evolution and return, for example, to a former mode of life long since abandoned; but in doing this it does not revert precisely to its former structure." All traces of its progress are not completely lost. Romer (p. 109-10) said:

The phrase "irreversibility of evolution" is an imposing one, but is obviously absurd in broad interpretation and contradictory if stated in terms of organs. It is today difficult to understand how any great degree of adherence to this

"doctrine" came about. Adherence to this creed has made it difficult to develop reasonable phylogenies for various groups for which there is an abundance of fossil material, and it has been responsible in many cases for the supposition that successive representatives of a group have not descended one from another, but that the known types are a series of side branches from an unknown main line of "unspecialized" forms. . . . But evolution is definitely known to be reversible. Recent forms alone give strong evidence to that effect, and the paleontological evidence is conclusive. Dwarfism of elephants and hippopotami, etc. in the Mediterranean region [is] definitely not a retention of a primitive diminutive size but [is] to be considered as a secondary dwarfism.

ORTHOGENESIS

Orthogenesis is the evolution of forms in a direct line toward some seemingly definite end. Lull (1929, p. 151) said: "Orthogenesis is the assumption that variations, and hence evolutionary changes, occur along certain definite lines impelled by laws of which we know not the cause." Simpson (1944, p. 158) said: "An isolated purely linear pattern is not typical of orthogenesis, or if orthogenesis be defined as involving such a pattern, the Equidae are definitely not orthogenetic." On pages 163-64 he said:

This general picture of horse evolution is very different from most current ideas of orthogenesis. It may be agreed that there are rectilinear elements involved, but they are certainly less widespread and less persistent than is usually asserted for this classical example of orthogenesis. They are thoroughly consistent with orthoselection, which indeed seems the most reasonable explanation of these trends in the horses. They are flatly inconsistent with the idea of any inherent rectilinearity, predetermined trend or solely preadaptive control. . . . A dispassionate survey of many of the phenomena of orthogenesis, so-called, strongly suggests that much of the rectilinearity of evolution is a product rather of the tendency of the minds of scientists to move in straight lines than of a tendency for nature to do so.

Orthogenesis is the single obvious case, so far as the author knows, in which observed facts have demanded an explanation by theory rather than a theory has demanded factual evidence in support. Unhappily, biologists have been unable to furnish such a theory or to agree among themselves on any approach to a satisfactory theory. The mechanists believe that from the abundance of variations natural selection conserves those best fitted to the environment and must in time develop a recognizable adapted series. The paleobiologists en-

counter such series and are ever conscious of the need for a causal explanation which will avoid any directive vitalistic principles.

Constant effort to formulate an explanation has resulted in a long list of terms, many of them suggested by authors who had only a new name when they believed that they were offering a new idea. Such terms as momentum in variation (Loomis, 1905), rectigradation, unknown factor in evolution, aristogenesis, trend, entelechy, teleology, heterogony have been offered. The foreshortened record of paleontology is not adequate in either quantity or quality of material to carry conviction. Only in a few series are the specimens sufficiently numerous and the time occupied sufficiently short to permit probability that an orthogenetic series is present. The few probable series lend support to less evident series and strengthen the temptation to fill the gaps by abstractions. It has long been known that the end result is logically the same whether it be due to natural selection of random variations or to directed evolution.

It has been stated that discussions of orthogenesis have been descriptions of the process, not explanations. One rather takes exception to Colbert's (1949, p. 130) critical remarks concerning the attitude of the paleontologists toward orthogenesis. He said:

Orthogenesis is a concept dear to the heart of many paleontologists. In fact, since the days of the early students of evolution, support for orthogenesis as a valid evolutionary principle has been stronger in the field of paleontology than in any of the other scientific disciplines concerned with evolutionary studies. This is not to be wondered at, when one considers how frequently the paleontologist has before him sequential series of fossils that show definite evolutionary trends through geologic time. It is not surprising that the paleontologist has been impressed by such trends, to such a degree that he has evoked the concept of orthogenesis or straight line evolution to explain them.

As shown above, the paleontologist has never "invoked the concept of orthogenesis" as an explanation; he has constantly presented the evidence for direct evolution and has as consistently demanded an explanation, a workable theory, which would have no vitalistic element. He is still demanding such a theory. Colbert's (1949, p. 134) list of evolutionary events which he considers to constitute orthogenesis is an obvious sample of a description; it is not an explanation.

The following quotations illustrate the confusion of opinions. Huxley (1942, p. 31) said:

The paleontologist confronted with his continuous and long range trends, is prone to misunderstand the implications of a discontinuous theory of change such as mutations, and to invoke orthogenesis or Lamarckism as explanatory agencies. Since there are more rare than abundant species, the biogeographer will have to discount the fact that he is dealing mainly with a process irrelevant to the major trends of evolution regarded as a long range process; while the ecologist and the pure physiologist, appalled by the complexity of the phenomena which they study, are apt to give up the quest for any evolutionary explanation at all.

Huxley (1942, p. 465) said:

Most biologists also look askance at orthogenesis, in its strict sense, as implying an inevitable grinding out of results, predetermined by some internal germinal clockwork. This is too much akin to vitalism and mysticism for their liking; it removes evolution out of the field of analysable phenomena; and it, too, goes contrary to Ockham's razor in introducing a new and unexplained mechanism when known agencies would suffice. Furthermore, as R. A. Fisher has cogently pointed out, the implications of orthogenesis, like those of Lamarckism, run directly counter to the observed fact that the great majority of mutations are deleterious. In any event, as we shall see in a later chapter (p. 506), the cases in which a true orthogenetic hypothesis is demanded in preference to a selectionist one are very few, and even in these few it may turn out that it is our ignorance which is responsible for the lack of alternative explanations. As set forth elsewhere (p. 516), numerous cases exist where evolutionary potentiality is restricted; but these are quite distinct from orthogenesis in the strict sense of a primary directive agency in evolution.

Huxley (1942, p. 509) also said:

However, we must provisionally face an explanation in terms of orthogenesis—i.e., of evolution predetermined to proceed within certain narrow limits, irrespective of selective disadvantage except where this leads to total extinction. It should be noted that, even if the existence of orthogenesis in this cause be confirmed, it appears to be a rare and exceptional phenomenon, and that we have no inkling of any mechanism by which it may be brought about. It is a description, not an explanation. Indeed its existence runs counter to fundamental selectionist principles.

Huxley's attitude seems to be rather more that of a propagandist than an enquirer.

Wells and others (1931, p. 432) cited as a common attitude the view that there is a "sort of inner drive, an innate destiny of the species." De Beer (1930, p. 33) spoke of "this incorrigible tendency"

(of the titanotheres) to produce larger and larger horns by continuous variations in the same direction. Wells and others (1931, p. 433) said of Bateson that he "developed an increasing disability to satisfy himself that any progressive variation could occur."

It must be stressed that apparent orthogenesis is a repeatedly observed occurrence still demanding explanation. Some biologists prefer the dubious explanation that the seemingly direct evolution is a secondary effect of natural selection; other biologists accept the observed series but are unable to formulate an explanation that is not tinged with the vitalism which they reject. The various imagined processes, each with minor differences, perhaps, and identified by new-coined terms are, as has been said, descriptions of action rather than explanations.

Romer (1949, p. 107) said of orthogenesis: "Currently, however, paleontological interest in this doctrine is on the wane. There are probably few instances of long-continued phyletic lines which are unbranched and do not change their direction. In many groups which were thought to follow an orthogenetic pattern, fuller knowledge of fossils shows that branching does occur." Romer gives instances from the line of fossil horses, so long considered as a type example of orthogenesis, which show branching and discontinuity. The rhinoceroses, according to Wood, "show no trunk whatever for their tree, but rather a straggling bushy effect." Romer's conclusion is that orthogenetic phenomena are much less common than has been supposed and such as occur may be explained by orthoselection; the last term simply meaning that natural selection has eliminated the variations least in line and emphasized those most alike.

It is evident that the lines seized upon by the earlier evolutionists and hailed as conclusive evidence have not stood the test of criticism. Romer (1949, p. 108) said in a footnote: "Specific identification in fossil horses is a very dubious matter." According to Romer (1949, p. 109), a very general tendency in orthogenetic lines is increase in size, but in the fossil-horse line "there has been, it is sure, a persistent reservoir of smaller forms lying along the main branches of the evolutionary tree from which, in age after age, phyletic lines of larger forms have continually arisen."

Watson (1949, p. 49) said: "This orthogenesis is sometimes supposed to have been brought about by some mechanism inherent in the animal which would ensure that changes proceeded, as it were, automatically with time, and that they proceeded in a definite direction. This conception, which is not by any means impossible, demands very serious consideration and criticism." In the same paper (p. 53) he said that "it is very important to try to find any example of an orthogenetic change which cannot be accounted for in terms of natural selection."

Watson (1949, p. 60) said that "subspecies or variations may be due to segregation of small changes or to nutritional effects." On page 61 of the same article he wrote:

If I am right in the conclusions I have drawn as to the evolution of this group [the labyrinthodonts] we have exhibited in it a new phenomenon, the existence of structural changes which proceed with time brought about not by any environmental influences (adaptations in the ordinary sense) but dependent upon some internal quality common to all members of the group, which survives from its introduction to its disappearance.

It must be admitted that Watson in this statement treads on very thin ice in his approach to a nonmechanistic explanation of evolution.

Jepsen (1949) has given a detailed discussion of orthogenesis, but a conclusive explanation is still wanting.

EVOLUTION DEPENDS UPON THE CONSTANCY AND FREQUENCY OF VARIATION

This theory has attracted the attention of the philosopher as well as the scientist. In attempts at explanation the philosopher has made up for his lack of factual knowledge by a wealth of assumption and abstraction in support of his belief in an all-compelling cause for which a large number of names have been given, such as the *Élan Vital* of Bergson, the *Life Force* of Shaw, and the *Bildungstriebe* of Goethe. Biologists have learned that new varieties are constantly occurring in enormous numbers and paleontologists have discovered that this is true as far back in time as recognizable life has been found.

It is here that the paleobiologists and the neobiologists must accept different evidence. The paleobiologist has only the end result,

the existence of an enormous number of individually different fossils for whose existence he has only the phenotype in proof. These phenotypes may be arranged in such sequence of time and form as appeals to the worker. The paleobiologist, however, cannot escape the conviction that the fossil in his hands was governed during its life by much the same laws and principles as govern living things and must, so far as possible, be interpreted according to such laws and principles. A few examples of possible interpretations are given below.

No matter what theory of evolution may be examined, it is evident that, with the exception of a few long-enduring forms (whose apparent peculiarities may be due more to our ignorance than to actualities), there has been a constant pressure of reaction between organisms and their environment (of which other organisms are a part). This pressure is manifested by some variation in the individual descendant organism. The variation may be of any kind whatsoever, physical or physiological, and may be directly observable or only indicated by some later departure from an expected course. One thing seems certain; variation is an individual reaction of a single organism and not a mass reaction of any group of organisms which may be called for convenience a subspecies or a population, although the conservative tendency of heredity may induce a seeming direction of variation which could suggest to a predisposed mind a trend through time.

With the practically infinite possibilities of variation and environment there is no possibility of a rigid law, or laws, of evolution. Criticism of every theory leads to the recognition of a fringe of unexplainable occurrences, and any attempt to reduce or eliminate this fringe by comparable averages only leads to further assumptions. This lawlessness has been noted by every student of evolution, be he a paleobiologist or a neobiologist, and occasionally a voice is raised in protest. Scott (1919, p. 377) said: "Living tissue is always groping about in search of improvement." Holmes (1948, p. 328) said: "In fact, the whole picture of the world of life is such as to indicate that the forces which have guided the course of its evolution have ever operated in an opportunist fashion." De Beer (1930, p. 30) said: "It is therefore possible to imagine that a certain amount of 'clandes-

tine' evolution of qualitative novelties may take place in the young stages of development while the adult stages are peacefully undergoing quantitative changes." De Beer (1948, p. 184) said: "It was also shown by de Beer that paedomorphosis allows for the possibility of evolution from the point of view of the paleontologists taking place 'clandestinely.'"

In common with others Simpson has encountered the embarrassing lack of rigidity in the laws (if such there be) governing evolution. Troubled by such vagaries he has attempted to illustrate them and shepherd the errant incidents under a new terminology.

A few short quotations from Chapter XII, "The Opportunism of Evolution," of Simpson's *The Meaning of Evolution* (1949) will show the meaning of "opportunism" as used by him:

[P. 160] Over and over again in the study of the history of life it appears that what can happen does happen. There is little suggestion that what occurs *must* occur, that it was fated or that it follows some fixed plan, except simply as the expansion of life follows the opportunities that are presented. In this sense, an outstanding characteristic of evolution is its opportunism. "Opportunism" is, to be sure, a somewhat dangerous word to use in this discussion. It may carry a suggestion of conscious action or of prescience in exploitation of the potentialities of the situation.

After some defense, he said:

The word is only a convenient label for these tendencies in evolution: that what can happen usually does happen; changes occur as they may and not as would be hypothetically best; and the course of evolution follows opportunity rather than plan. . . . What can happen is always limited and often quite strictly limited. Boundless opportunity for evolution has never existed.

[P. 164] Evolution works on the materials at hand: the groups of organisms as they exist at any given time and the mutations that happen to arise in them. The materials are the results of earlier adaptations plus random additions and the orienting factor in change is adaptation to new opportunities.

[P. 165] Take, for instance, the expectation of multiple solutions of adaptational problems. These exist for almost any such problem that you can name and they account for much of the swarming diversity of life.

[P. 167] There are two aspects of opportunism: to seize such diverse opportunities as occur, and when a single opportunity or need occurs, to meet it with what is available, even if this is not the best possible.

Speaking of adaptive radiations Simpson (p. 178) said:

That such phenomena represent opportunism and not plan or purposes in evolution is attested by the fact that such independent radiations produce ani-

mals similar in ways of life but not the same in structure, indeed sometimes remarkably different. . . . [P. 185] This review of some of the opportunistic elements in evolution reinforces the evidence, seen also in discussing oriented evolution, that evolution is neither wholly orderly nor wholly disorderly. It certainly has no grand and uniform plan, nor any steady progression toward a discernible goal. On the other hand, it shows continued trends and a neat interlocking of the various sorts of organisms so that they interact systematically and fill out the possible ways of life, many of which they have themselves, by merely coming into being, created. The history of life is an odd blend of the directed and the random, the systematic and the unsystematic.

[P. 185] Apparent opportunities are not always exploited and gaps are not invariably soon filled. The rule that all of life's opportunities tend to be followed up also has exceptions.

The culmination of his state of mind is found on page 121:

Perhaps at the end the strongest effect left by the record of life will be one of an odd randomness in it, a sense that it is dominated by a sort of insensate opportunism.

The following illustration is along the same line and may aid in clarifying the idea. World War II brought into common usage an expression "blitzkrieg," which is only partly understood by many who employ it. Lynn Montross in his *War through the Ages* (1946, p. 787, 2d ed.) cited Mikesche as explaining that the term "blitzkrieg" (lightning war) was applied in description of the constantly changing zigzag course of the assaults resembling the conventional pattern of the thunderbolt, as well as the speed of the assault:

The important thing to remember about blitzkrieg is its combination of a lateral with a forward movement, giving the effect of a fast-moving machine which grinds while it slices. The direction of the three break-through attacks [such as in Poland] is not necessarily straight ahead—more often they slant off on an angle which follows the path of least resistance, and as these spearheads make their rapid thrusts, other and lesser attacks are aimed at one side or the other to widen the gap.

In order to better understand the analogy let it be supposed that a well-equipped and organized army enters a resistant region. The army depends in part upon the rapidity of its movement but also upon its ability to take advantage of every favorable opportunity. A carefully prepared plan of action has been worked out, but provision has been made for change of direction, for weight of armor, and for method of attack. The army starts on its pre-

arranged course but receives information from its intelligence of a weakly protected area, or of a concentration of troops or supply. Immediately, a proper force is diverted to capture men or material. Perhaps the officer in charge of the diverted column hears of still other desirable objectives; his orders permit him to make further diversion or to send out smaller groups to seize the new objectives. In this way the original planned line of advance is followed, but the actual course may become very different by reason of the diversions, which give the forked lightning effect.

If one considers any group of organisms at any one time or place, he finds that there are innumerable variations, all capable in larger or smaller degree of advancing in several different directions and surrounded by conditions (environment) that will aid or obstruct such advance; any shift in the fauna or flora constitutes new environment, for the old definition of environment as "the sum of the contacts of an organism with the external world organic or inorganic" still holds good. Osborn (1905, p. 148) said that "environment includes all nature external to the organism."

Each variant is in contact with an enormous number of environmental possibilities, far more than are realized or than can be appreciated by the crude senses of man. It is very possible that some factor in the 10th decimal place of value, as one might place it, may determine the success or failure of a variation. Any group of forms, such as those with the development of any of the types of adaptive radiation, is advancing in a definite line, but the line may split or flourish or decline as the "blitzkrieg" of evolution develops. There is the pressure of endless variation seizing on every possibility of the environment, and it must be kept in mind that each variation alters the environment for competing forms in some degree. The action of a species rich in varieties occurring in the midst of an abundance of environmental possibilities is easily likened to a well-equipped army entering a new territory. The species itself is the main army with an already established trend toward some definite end. The multitude of new varieties enter new environments, each to work out its fate. It is in some especially active reaction of adaptation and environment that Simpson's "quantum evolution" would

show many new varieties. Simpson (1949*a*, p. 224) said: "The increased rate of evolution takes place in a period during which the group is not in adaptive equilibrium but is in a relatively unstable transition from one (usually slowly shifting) equilibrium to another, a transition for which I have proposed the term evolutionary quantum step." In other words, the increased rate takes place during an active interval of the blitzkrieg of evolution, as when in localities or time intervals there is an unusual dominance of a species or variety; when a plant, or animal, "takes" an area.

In paleontology, where only form can be considered and where material is inadequate, one is apt to be misled by a foreshortened view and is prone to supply lacking steps by abstractions which must necessarily be subjective, to some extent at least. Phylogenetic trees are drawn with straight connecting lines because such diagrams are simple and convincing, but it is far more probable that the direction of each line is constantly changing and that the true line of descent was as angulate as the pictured paths of portions of a blitzkrieg army, or many times more angulate since the development of a species in nature takes an immensely greater time than the life of any army.

Some speculative writers insist that the reactions of an organism "as a whole" must be different from the reactions of a unit character, but this cannot be considered in paleontology because only a small portion of the organism is known. It would be possible to personify a single Cretaceous oyster and to recount its environment, its history, and its trends from the supposititious characters suggested by its hard parts, but by emphasis on another set of characters shown on the same shell a totally different account could be written, or a dozen of them, all equally fabulous and all the result of the ingenious speculations of the authors. It must also be remembered that the physiological varieties which have no expression in form are probably equal in potency and number to those which do have visible change.

It is now known from experiment that extraneous conditions and substances in the environment do alter heritable genetic characters; natural physiological variations probably have a similar effect. Paleontology cannot reveal physiological species; speculation in this field can only be suggestive.

Sonneborn (1949, p. 529) gave a list of some agents that have been shown to affect the gene. He said:

Less than twenty-five years ago, there was thought to be no way by which environmental conditions could bring about hereditary changes in organisms. Since that time, more and more environmental agents capable of inducing hereditary changes have been discovered: first, temperature and x-rays; then other ionizing radiations and ultraviolet light; more recently, chemicals such as colchicine, mustard gas, and formalin. These agents alter the chromosomes in both body cells and germ cells, but only the effect produced on the germ cells, or cells from which they are derived, are inherited in sexual reproduction.

Unquestionably other agents potent through time have affected the gene.

Dobzhansky (1950, p. 161) said:

It is well known that the course of development is influenced by the environment. Therefore the outcome of development at any stage is a function of both the heredity of the developing individual and the environment in which the process has taken place. Heredity does not determine traits; it determines, according to the somewhat awkward expression proposed by the Danish biologist Raunkiaer, the "norm of reaction" of the organism to the environment.

Dobzhansky (1941, pp. 17-18) said:

Figuratively speaking every genotype exerts a pressure on the environment, tending to take possession of all available space. Conversely, the environment exerts a constant pressure on the genotypes of the organisms residing in it, tending to modify them in various ways. . . . Nevertheless genotypic changes do occur in which the environment plays at least the role of a trigger mechanism. More important still, any genotype is the result of age-long processes of evolutionary development, in which the environment through natural selection has been a force of paramount importance. The structure of the genotype and hence the kind of changes it is capable of producing are in the last analysis environmentally determined. The "determining environment" is however not merely the one prevailing at the moment, but rather it is the sum of the historical environments to which the organism has been exposed in phylogeny.

Muller (1949, p. 433) said: "We have seen that the direction and speed of evolution will be determined largely by selection pressure, that is, by the molding factors of the outer environment acting in relation to the possibilities of the organism for further change in advantageous directions." It is largely the appalling intricacy of genetic relations and actions shown in Muller's summary (1949, p. 241) and Simpson's (1944, p. 163) discussion of trends that have impressed the paleontologist with the hypothetical character of any

attempt to recognize genetic characters in the fossil, although he willingly admits that the organism represented by the fossil must have been governed by the laws of genetics.

ENVIRONMENT

Simpson's definition of environment (1944, p. 188) is that it "includes not only the physical conditions, average and variant, of the organism's geographic surroundings, but also all existing foods, competitors, and enemies, all forms of life affecting the given organism in any way whatever, other members of the same group, and even the organism itself, considered as an element in the total situation in which it exists. Clearly, no two animals ever have precisely the same environment and no one environment ever remains the same from one instant to another." This is more detailed but not more inclusive than the definitions given by Osborn and Case. It is unnecessary to emphasize the complexity of the environment so defined, but it requires much effort to realize it. So much had been written of the environment and so many conclusions have been drawn by authors who have considered only a few of the more obvious factors that the value of much of their work must be challenged.

According to Dobzhansky (1941, p. 16), Johansen has formulated two concepts that are fundamental, the phenotype and the genotype:

The phenotype is what we measure and describe in our direct observations and experiments, the organism's structures and functions. . . . The genotype is the genetic constitution, the sum total of the hereditary factors received by the organism from its ancestors. The genotype of an individual cannot be perceived directly; one can infer its properties only by examining the individual's pedigree, or progeny, or both. The relation between the genotype and the phenotype is a dynamic one, since the former determines the reactions of the organism to its environment. A phenotype is always the resultant of the interactions between a genotype and an environment.

Only the phenotype is veritable to the paleontologist, but he is constantly tempted by the possibilities resulting from the inference and assumption to speculate upon the nature of the genotype; such speculation may result in brilliant and seductive theories but has no real basis.

Specifically, each variation introduces new factors into the environment of closely related forms as it introduces new conditions or responds differently to established conditions. Such alterations of conditions may be so slight as to be imperceptible to us and still be determinant in the course of evolution. Dobzhansky (1941, p. 271) cites Moenkhaus's experiments in which the pH content of the water effected distortion in the fish *Fundulus*. Other even apparently less significant factors have produced important effects in experimental work. Simpson (1944, p. 96) said: "In large populations very minute selective advantage may be effective in determining the direction of evolution."

Isolation of an organism is freedom from the effect of the environment. It may be partial or complete, relatively rapid or slowly progressive through long time. The interrelation of the organism and the environment is so intricate that workers may well be "appalled by the complexity of the phenomena which they study, and are apt to give up the quest for any evolutionary explanation at all." (Huxley, 1942, p. 31).

Isolation may be due to physiological variation, as an achieved immunity to disease; it may be due to geographical conditions; it may be due to acquired size, possession of armor or weapons; agility or cunning, and so forth. The increase in numbers of an isolated species or variety often results in weak strains, in overspecialization, and in early extinction. Paleontology records numerous instances in which increase in population by isolation has been halted by some unknown destructive factor.

There is evidence that during geologically long periods of time there have been environmental conditions over large areas differing radically from those prevailing today. Typical, among others, are:

1. Conditions resulting from the dominantly igneous and metamorphic forces of pre-Cambrian time. The geological record is here so foreshortened that about all that paleontology can decipher is that life began in the Archeozoic, and that by the Proterozoic it was well advanced and widely distributed.

2. The time of distribution of enormous quantities of iron oxide in the Great Lakes region, Venezuela, Labrador, and Brazil. There

is no direct evidence of life in the iron ore beds and no certainty of the equivalence of fossiliferous beds assigned to the same time interval.

3. The long periods of low relief of the land and wide spread of shallow, epicontinental seas during the Paleozoic. This was the most continuous and nearly uniform environment, both in time and space, that has endured upon the earth; a far more uniform environment than that of the Tertiary or Recent. To the fossils of this time the principles of neobiology can most nearly be applied.

4. The periods of excessive desiccation in which were deposited large quantities of evaporates, such as halite, sylvite, and calcium sulphate in its various forms, frequently in association with terrestrial debris. The paleontology of such deposits suggests peculiar conditions frequently demanding a high degree of specialization in the fauna and flora. Du Toit (1948, p. 113) wrote of the Red Beds of the Molteno of South Africa:

As regards the climatic implications there is conflict of opinion, the Red Beds being interpreted by some as semi-arid and by others as semi-tropical deposits—views difficult to reconcile. Perhaps some of this has been due to the natural tendency to interpret too closely in terms of the present the physiological conditions of the remote past. It must be recognized that while deltas, deserts, peneplains, and geosynclines of vast dimensions have with justification been deduced for the past it is not easy to find comparable examples of such features on the Earth today.

5. The several relatively short periods of continental glaciation, in and after which there was an environment much as exists today.

Each of these is but an example of what was going on in a lesser degree in a multitude of localities. In some cases paleontology gives a partial record of the effect of the environment; all give opportunity for endless speculation.

DISCONTINUOUS EVOLUTION

Discontinuous evolution is now a recognized process. When the post-Darwinian examination of the method of evolution was begun, it was held that evolution was accomplished by a continuous series of small steps. Any sudden breaks in the series, or any sudden appearance of new forms, were explained away as due to imperfections of

the geological record. Increase in knowledge revealed the occurrence of sudden and unheralded changes which came to be called saltations or mutations, the terms having reference mainly to physical changes, but being applicable to physiological changes when recognizable. The development of genetics gave a new meaning to the term "mutation" and gave proof that sudden changes (discontinuous evolution) do take place and are partly explainable. Phylogenetic series of continuous small changes are no longer indispensable proof of evolution to the paleontologist.

Dobzhansky (1941, p. 7), however, said that the theory of evolution asserts that "the discontinuous variation observed at our time level—the gaps now existing between clusters of forms—have arisen gradually, so that if we could assemble all the individuals which have ever inhabited the earth, a fairly continuous array of forms would emerge."

Osborn (1905, p. 236) said: "that saltation is a constant phenomenon in nature, *vera causa* of evolution, no one can longer deny." On page 232 he said: "The whole tendency of paleontological discovery is to resolve what are apparently saltations or discontinuities into processes of continuous change," but this does not deny saltation from an unknown cause. Osborn (1912, p. 186) said: "It is true that the evidence for continuity in the *heredity* of characters is as convincing as that for discontinuity in the *genesis* of characters is debatable."

Schindewolf (1936), cited by Davis (1949, p. 74), "noted that the morphological discontinuities correspond to the observed discontinuities in the fossil record, which he accepted as representing abrupt transitions from one major type to another, rather than as deficiencies of record."

Dobzhansky (1941, p. 343) said:

The fossil record indicates that the tempo of evolution within a phyletic line is not uniform in time; periods of an explosive proliferation of new forms are succeeded by a more gradual development. A circumstance that is most irksome to a student of phylogenetic histories is that major evolutionary advances, the first appearance of new families, orders, and classes, seem to occur suddenly, with few or no intermediates between the new groups and their putative ancestors being preserved as fossils. The "missing links" are, indeed,

seldom found. Schindelwolf (1936), in his brilliant and provocative discussion of the bearing of paleontological findings on theories of evolution, stresses this sudden emergence of the radically new organic forms and infers that evolution takes place in part by what seems to correspond to Goldschmidt's systematic mutations. The facts at hand can, however, be accounted for without recourse to Goldschmidt's assumptions.

Osborn (1912, p. 207) quoted from Johansen: "All degrees of continuity between phenotypes may be found but real genetic transmission must be distinguished from the transitions which we find in museums."

Mayr (1949, p. 296) said that to the paleontologist:

The work on living species shows that speciation is a very gradual process and that sudden changes are exceedingly rare. Hence it becomes apparent that the so-called "mutations" in the paleontological record are not genetic events. Rather, as Rensch (1933) and others have pointed out, "mutational" breaks in phylogenetic lineages must be interpreted as biogeographical events (shifts in population). . . . The splitting of one population into two seems to be possible only in spatial segregation. However, in the paleontological literature numerous cases are reported of lineages that forked at a single locality in successive strata into two or more species, as, for example, the Steinheim snails. It is highly desirable that paleontologists should reinvestigate such cases with the best modern stratigraphic and biometric methods. A confirmation of the older findings would be a powerful endorsement of the hypothesis of sympatric [co-extensive distribution] speciation.

EMERGENT EVOLUTION

The interpretation of fossils has been very largely based on the assumption that the laws of life are immutable and have been so since life began. According to this assumption the Lyellian dictum voiced for the inorganic world, that the present is the key to the past, is applicable to the organic world as well. But its validity has been challenged by a group of biologists who discuss what they call "emergent evolution." Jennings (1930, p. 360) has reviewed the matter and given a statement of its principles. Emergent evolution "holds that evolution is creative; that in its operation essentially new things and new methods of action emerge, not calculable or predictable from what has gone before." Jennings' idea of mechanistic evolution is that the life of the past was governed by exactly the same "masses, motions and arrangements" as exist now. By the prin-

principles of emergent evolution the past and future may have been, or may become, governed by different laws, and it cannot be assumed that all fossils may be interpreted by "laws" now in force. To quote further from Jennings (1930):

[Page 364] As we look deeply into the past history of the world, it appears that there was a time when sensation, feelings, ideas, and the like, did not occur; for the conditions required for their occurrence did not exist. The possibility, indeed the great probability, must be reckoned with, that such things developed from a preexisting situation in which they did not occur. A great class of things, in that event, arose, emerged, in the process of evolution—things that could not have been predicted by computations based on what existed before this class of things arose. Changes of this kind are what is meant by emergent evolution.

[Page 369] Thus the emergent evolutionist holds that in the course of evolution there have emerged things that are new, of a different kind from any thing that has gone before; and that are not predictable from a knowledge of the preexisting things, from a knowledge of the preexisting particles, their arrangements and motions. And at the same time the methods of movement of the particles change, so that the later motions and arrangements are no longer predictable from knowledge of previous motions and arrangements. New laws of motion, new methods of action, have appeared, as new arrangements of particles occur, and peculiar mental states arise. And this is continuing as evolution proceeds, at present as in the past.

If these ideas prevail the assumed integrity of continuous step-by-step evolution is no longer tenable. If the laws of life were not and are not immutable, the interpretation of response to the environment can no longer be believed to follow a constant pattern, and phylogeny is open to constant question. It is probable, but as yet unconfirmed, that such changes as emergent evolution suggests are major changes developed through long time; smaller changes through shorter time may still serve as suggestive and valuable incidents to be tested.

Hooton (1943, p. 481) said that the lemurs "possessed the most precious of animal endowments, adaptability. This adaptability is essentially the faculty of grasping an environmental opportunity and following, not the line of least resistance but that of greatest opportunity." On page 483 he said: "The really progressive animal must if possible adapt environment to itself and not become too malleable to its influence. It must maintain its organic independence, it must

possess a certain initiative whereby it picks and chooses, and when choice is narrowed to its extreme disadvantage it needs to move on in search of better things." Hooton's "adaptability" has a very different meaning from the adaptation equivalent to specialization. It means the possession of a power of choice in responding to an altered environment. It is a most cogent example of the "essentially new thing" predicted by the believers in emergent evolution. It indicates the occurrence in a group of organisms of a common new character described by Jennings as "not calculable or predictable from what has gone before." Hooton spoke of his "adaptability" as an endowment, the action of an external force; Jennings said that the believer in emergent evolution regards evolution itself as creative, the action of an internal force. Both imply the presence of a force of which nothing is known. Hooton's "adaptability" fits very closely Jennings' requirements for an emergent character; it must have had its beginning in the first mammals, or the mammal-like reptiles, of the Triassic and been well advanced in the Paleocene.

Simpson (1949, Chap. XIX) in discussing the origin of moral and ethical characters in man described very clearly the development of a new thing, a step forward in emergent evolution, foreshadowed by Hooton's "adaptability."

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