26 May 1961, Volume 133, Number 3465 SCIENCE

CURRENT PROBLEMS IN RESEARCH

Some Problems of Vertebrate Paleontology

The study of fossil vertebrates elucidates the general principles of evolutionary biology.

George Gaylord Simpson

Paleontologists sometimes argue among themselves over whether they really are, or should be, geologists or biologists. The discussion is usually futile and sometimes absurd. Paleontology is characterized, but is not fully defined, by having its own objective subject matter: fossils. Fossils occur in rocks, and they are organisms. Their extended study necessarily overlaps widely into both of the broader (or more miscellaneous) sciences of geology and biology. Without really departing from his own science, a paleontologist may even find himself engaged in work that does not directly involve any fossils and that is quite strictly geological (for example, sedimentation) or biological (for example, genetics).

Traditionally, invertebrate paleontologists have been more geologically, and vertebrate paleontologists more biologically, oriented. The tradition arose because invertebrate paleontology, both commercial and academic, has always had an important role as a service branch of geology, supplying most of the correlations needed for stratigraphy and for historical geology in general. Vertebrate paleontology has had few commercial applications, and it has tended to attract students who were interested in studying organisms as such more than in rendering a practical service to geologists. That tradition still has an evident influence on the two fields, but the distinction is now breaking down. Both invertebrate and vertebrate paleontology are becoming broader, and paleontologists in both fields are becoming more diverse in approaches, methods, and aims.

In view of the great and still increasing spread of subject matter, a major problem of vertebrate paleontology is that of manpower. There simply are not enough vertebrate paleontologists, or enough positions for them, for adequate and consistent cultivation of the whole subject. Definition is difficult and may even be invidious, but if by "vertebrate paleontologist" we mean someone who has vertebrate paleontology as his primary field and who is working continuously in it at an independent, professional research level, there are only about 65 vertebrate paleontologists in North America and perhaps as many more in all the rest of the world (*1*). They are, however, backed up by a corps of technical personnel who do little independent research themselves but who greatly promote such research. It is further true that a significant proportion of the important research in vertebrate paleontology is done by people who are not primarily professionals in this subject but who work in it occasionally or marginally. The total number of people now making some contribution to the science runs well into the hundreds. Nevertheless, it is an unfortunate fact that some brilliant new possibilities opening up in the field of vertebrate paleontology are not being followed up simply because there are not enough specialists to work on all of them.

The most basic essentials for continued progress in vertebrate paleontology are still the same as the earliest activities, and will continue to be so as far as can be seen into the future. Involved here are the flow of new discoveries and data from the field, laboratory preparation of specimens, and study of their morphology and taxonomy. Much the greatest part of current effort is devoted to these classical but continuously necessary activities. There are still new fossil fields to be discovered. Renewed collecting in known fields, often by campaigns over many years, is necessary to make more nearly adequate collections and to provide field data up to modern standards, which are far more rigorous than the standards of even a few years ago. Laboratory preparation is still a bottleneck, one of the reasons why vertebrate paleontology is often a slow science. Decades may necessarily elapse between beginning a large project with field work and ending it with final publication of the results. In addition, almost all the basic taxonomy of a generation or more ago now requires revision in the light not only of new materials but also of new principles and standards. (This does not mean that the earlier work was wasted; the new principles and standards arose from it, and many of its data are as useful as ever.)

It is precisely here, in its most basic activities, that vertebrate paleontology has many of its most striking recent discoveries, and improvements in techniques and approaches, and also has its continuing problems. It must be stressed again that here is not only the great bulk of work in vertebrate paleontology but also the most fundamental aspect of that work. It is further to be emphasized that much of the current progress and many of the most pressing prob-

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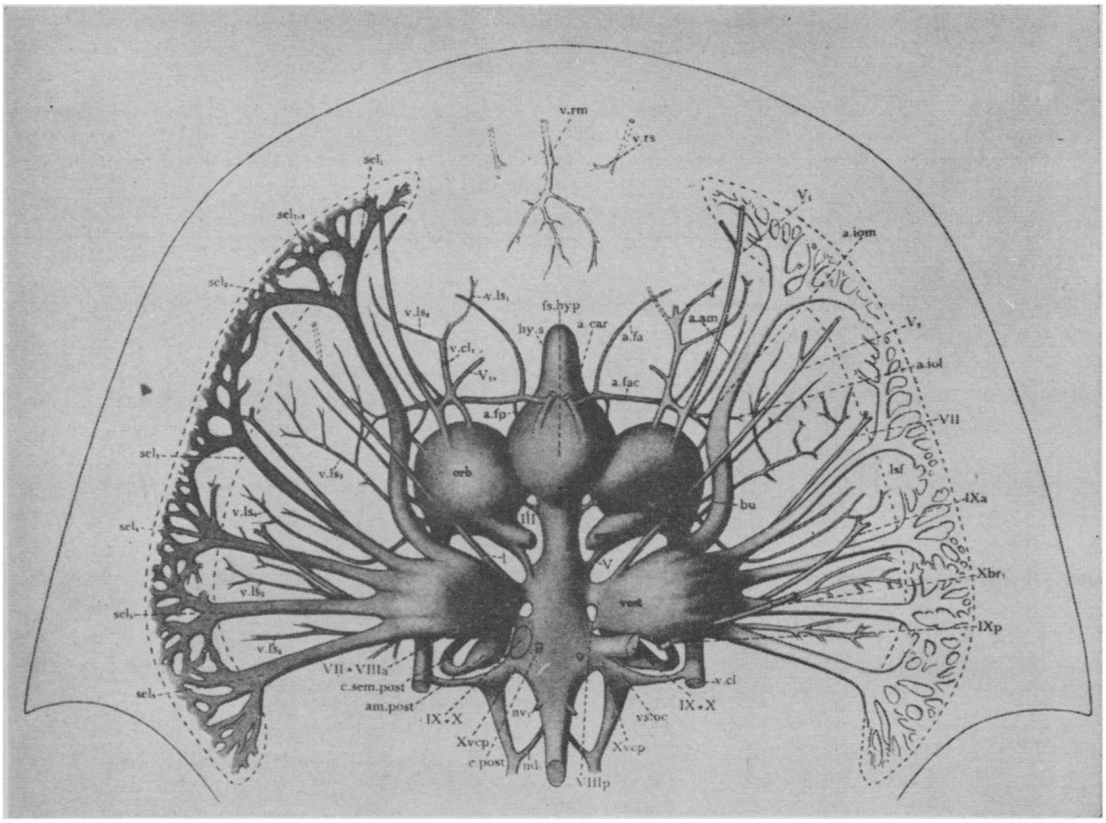

Fig. 1. Detailed endocranial anatomy of an ancient fossil vertebrate, *Kiaeraspis auchenaspidoides*, a jawless fish from the late Silurian of Spitsbergen. [After E. A. Stensiö]

lems are on the geological side of the subject, in sedimentation, stratigraphy, correlation, chronology, and related topics. Nevertheless, and solely because of limitations of space, those parts of the subject are treated only incidentally in the following discussion. My purpose here is to consider problems of broader and more theoretical biological interpretation that arise after the basic data, taxonomic and geologic, are in hand. Even within that more limited scope, the treatment can be only a sampling and an exemplification of a few problems and in no sense a review of the field (*2*). Some aspects of morphology and systematics, closely related to the basic data, are considered briefly before certain interpretive problems more removed from that level are treated.

Morphology

Even in its 18th-century beginnings, vertebrate paleontology was never confined to collection, preparation, description, and classification. It is, however, especially characteristic of the work done in recent years—the 1940's and 1950's—that there has been a great irruption of new ideas, new goals of interpretation, renewed efforts toward theorizing in broader ways and at more generalized levels. At present there seems to be some reaction against that tendency, and a certain ambivalence has arisen in the profession. This is not a clear-cut dichotomy into an *école des faits* and an *école des idées* but only a difference in the points of view of those who would lay greater stress on one or the other of what are, after all, mutually dependent and equally necessary aspects of the same whole. There is the need, on one hand, for more detailed, complete, and accurate anatomical observation, description, and illustration (*3*), but also, on the other, for generalization and theoretical formulation that alone can make such data meaningful.

On the observational side, vertebrate comparative anatomy, not only of fossil but also of recent animals, has become largely the province of vertebrate paleontology. It is indicative that outstanding textbooks in that field are those by Romer, a vertebrate paleontologist. All vertebrate paleontologists have perforce been anatomists, but a modern school of morphology has arisen largely through the efforts of Watson in England, Gregory in the United States, and Stensiö in Sweden and has been carried on especially by their respective students. To take a single school as an example, Stensiö and his students have investigated the anatomy of many early vertebrates in almost incredible detail and have produced reconstructions that often incidentally have striking esthetic values (*4*) (see Fig. 1). The methods involve not only delicate macroscopic preparation but also thin sections, serial sections, and plastic reconstructions. Study of all fossil species in equal detail is neither desirable nor possible, but application of this approach to at least some characteristic members of all major groups is an eventual necessity, and a beginning has barely been made. As regards later vertebrates, Whitmore's study of some Oligocene artiodactyl skulls is not quite, but unfortunately almost, unique (*5*).

The most ardent advocates of descriptive anatomy for its own sake do not deny the need for some generalizing principles. In this respect there are two schools. A small group consisting mainly of Naef, Kälin, and their students, notably Zangerl in the United States, has approached comparative anatomy as a self-contained subject with its own principles independent of those of any other biological discipline (*6*). For them, generalization is by abstraction of a "Morphotypus," which is essentially the archetype of the pre-evolutionary typological idealistic morphologists or *Naturphilosophen* exemplified by Goethe. For the great majority of vertebrate paleontological morphologists, however, the central principle is now that of evolutionary homology—derivation of structures from a common ancestry and their modification in the course of phylogenetic descent.

From the latter point of view, greatest interest attaches to major transformations that are involved also in important problems of systematics and of evolutionary theory. The fish-amphibian transformation is being studied especially by Jarvik, in the laboratories under Stensiö's direction (*4*), and also by Westoll, Romer, and others. As another example, the reptile-mammal transition, outlined in a general way long since, is now under new attack in greater phylogenetic and morphogenetic detail by, among many others, Brink and Crompton in South Africa; Watson, Parrington, and Westoll in England; and Romer, Patterson, and Olson in the United States (*7*). This transition was a main subject of a colloqium in Oxford, England, in 1960. Another classical problem now under renewed attack concerns the evolutionary morphogenesis of mammalian molar teeth. One of the triumphs of paleontological morphology of the late 19th and early 20th centuries was the discovery by Cope and Osborn that therian (that is, both marsupial and placental) molar dentitions all went through a common stage now called tribosphenic. The origin of the tribosphenic dentition, however, is still quite uncertain, but it is being studied with new evidence from Mesozoic mammals and mammal-like reptiles. That was a main subject of another international meeting in 1960, organized by Vandebroek in Brussels (*8*).

Classic approaches to morphology, even when evolutionary in principle, deal typically with individual structures in a somewhat static way. Newer, more dynamic approaches are now also being followed. One of these approaches, already with a rather large literature and applications of well-developed methodology to a great variety of vertebrate groups, deals with ontogenetic structural changes, especially as influenced by relative growth (*9*). Another, which seems at least equally promising but still presents serious unsolved methodological problems, has to do with covariation, correlation, and association of anatomical character complexes within populations and among groups of related forms (*10*). Studies of the more classic sort are still of prime importance and not to be disparaged, but the most striking progress in morphological principles will probably be in these newer fields in the near future, and in work relating morphology to the biology of the individual (*11*).

Systematics

As early as the 18th century fossil vertebrates were being classified according to the same system as Recent animals, and of course this still is and always must be a basic and principal activity in this science, perhaps the most basic of all. Since Linnaeus and Cuvier, in addition to innumerable more superficial changes of form and content, there have been two deep revolutions in the principles of systematics. Vertebrate paleontology has been influenced by and has contributed to both. First was the change from special creation to evolution as an explanation for the diversity of life, and hence to the order in nature which makes classification possible. Second, more subtle and harder to grasp but equally fundamental, was the change from classification in which categories were defined by typological abstractions of constant characters and individuals were the members of taxa to classification with phylogenetically defined categories and with varying populations as the members of taxa. In the latter revolution, not yet complete, vertebrate paleontologists have been both leaders and laggards. Some were pioneers in using the conceptually statistical, sample-population approach to taxa and in using phylogenetic categories, and others still do not adopt either of those concepts (*12*).

The problems of obtaining adequate, unbiased samples and, alternatively, of making proper allowances and corrections for inadequacies and biases are particularly acute in paleontological systematics. Almost all vertebrate paleontologists have become aware of those special problems, most of which have been identified and listed, but there are still few specific and concrete studies. Two examples of the kind of studies that are pertinent here may be cited. Olson has presented a model theoretical and practical study of size distributions in samples of growing animals (*13*). Shotwell has attempted to separate members of proximal and distant communities in quarry accumulations by calculating the number of bones recovered per individual (*14*). It is irrelevant, for our purposes, that Shotwell's method may prove to have restricted applicability (*15*). Ideas of that sort and their testing, both by theoretical models and by particular actual occurrences, are badly needed if we are to make adequate evaluations of the fossil record and place generalizations about it on a sounder basis.

Changes in the concept of species and in the interpretation of samples in recent years have been so profound that practically no "species" of fossil vertebrates described more than 20 years ago, and not all of those described since then, can now be taken at face value as properly defined and biologically significant species of natural populations. Fortunately, that situation is changing now, and biologically sound specific descriptions are so numerous in recent work as hardly to need exemplification. One consequence of the previous situation has been that most sound paleontological studies of systematics, and of the evolutionary processes that underlie systematics, have hitherto necessarily been above the species level. Knowledge of structure and processes within species, or between closely related species, has come mostly from recent animals and has lacked a significant time dimension. It is, however, now clear that such studies can be based on some fossil groups with particularly favorable sampling conditions, and this indicates a whole field of important problems to which vertebrate paleontology may soon be expected to make more significant contributions.

As regards the systematics of higher categories, the situation in vertebrate paleontology has long been more favorable. Most of our theoretical understanding of the nature of such categories and of how the corresponding taxa have evolved has been provided by vertebrate paleontology, and this is one of its most active current fields of research. Moreover, in most groups of vertebrates (teleost fishes and birds are the outstanding exceptions) actual classification at high-categorical levels is now based primarily on paleontological data. Many of the important current problems in this field arise from increasing evidence of some degree of polyphyly and parallel evolution at high levels—evidence which makes the delimitation of, for instance, the classes Amphibia, Reptilia, and especially Mammalia increasingly difficult and disputed (*16*) (see Fig. 2). Among the many examples of similar problems in systematics at successively lower levels

(*17*), mention may be made of work on the separation of the orders Insectivora and Primates (or the dismemberment of those orders); on recognition of suborders of the order Rodentia, which probably does not have natural suborders (*18*); and on redefinition of genera and phyletic lines in the supposedly well-known horse family (*19*). The examples are all among mammals, but others of the kind occur in every vertebrate class.

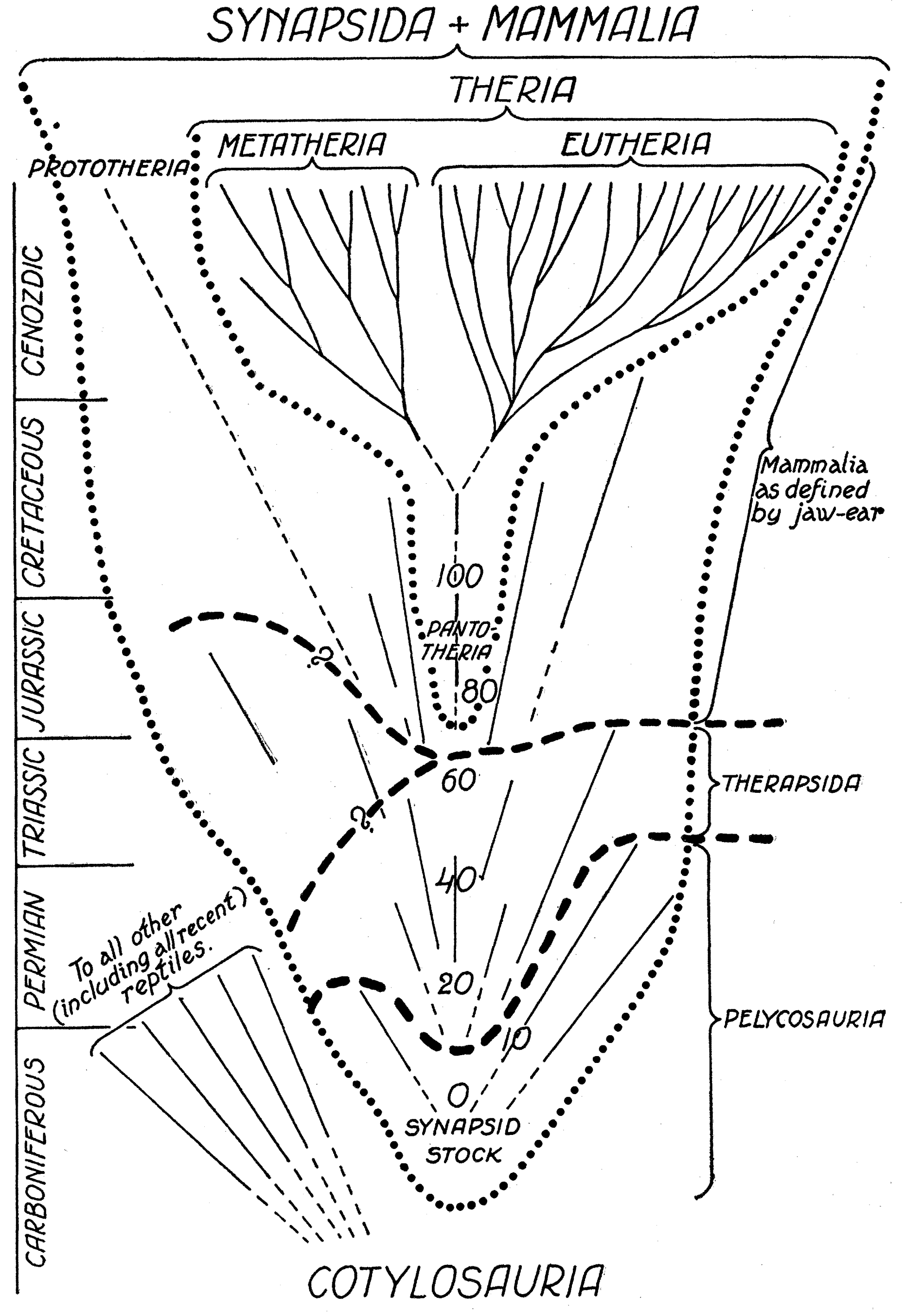

Fig. 2. A problem in phylogeny and systematics: relationships of the Mammalia to their ancestry are shown schematically. The light lines represent the general pattern (but not the detail) of phylogeny as now known. Heavy dashed lines separate successive taxa as now usually recognized. Numerals are estimates of degree of advance (in percent) from fully reptilian to fully mammalian basic characteristics.

Functional Biology of Individuals and of Species

Vertebrate paleontologists have always attempted to draw inferences about general functional characteristics of prehistoric animals—how they moved, what they ate, and the like. Such inferences were based almost entirely (and necessarily, as it seemed) on analogies with similar, living animals. They tended to become mere fantasies when referring to structures for which there are no such analogies—for example, the dorsal fins of some Permian pelycosaurs, the "hoods" of some duck-billed dinosaurs, or the claws of the phylogenetically ungulate chalicotheres. Such analogical, and often more subjective and anecdotal than scientifically inductive, studies reached their height in the *"Palaeobiologie"* of Abel, half a century ago. After Abel, analogies, quite properly, were still sought, but for some years the field seemed to have little further potential for the production of new ideas or of more rigorous methods.

Here we are in the midst of a definite revival. Problems are being more broadly conceived but more strictly defined, and better methods are being devised to solve them. In part, the current approach involves greater precision and better analogical evidence in application to the same kinds of problems as those attacked earlier in a looser way. This is the approach in reconstructions and functional analysis of musculature [for example, of ceratopsians, by Haas (*20*), following earlier work by Lull and others] or in interpretation of limb function from trackways [for example, in amphibians, by Peabody (*21*), also following and improving on earlier work by many hands]. In other instances, earlier intuitive judgments have been replaced by quantitative experimental data derived from working models—for example, in studies of early reptilian auditory function, by Hotton (*22*).

Similar use of models has already been made in studies of a variety of functional problems (for example, of locomotion in early fishes and in pterodactyls), and the method is capable of much further extension. It has the advantage not only of giving quantitative results but also of being applicable to structures without close analogs in living animals. In some instances study by means of mathematical, rather than physical, models and analyses has the same advantages. For example, the problem of the pelycosaur dorsal fin, mentioned above, seems essentially solved by Romer's demonstration that the regression relationship of fin area to body volume is appropriate to the functioning of the fin as a temperature-regulating mechanism (*23*) (see Fig. 3).

Those successful attacks on old problems by new methods are supplemented in an even more interesting way by the formulation and at least partial solution of quite new problems, either over-

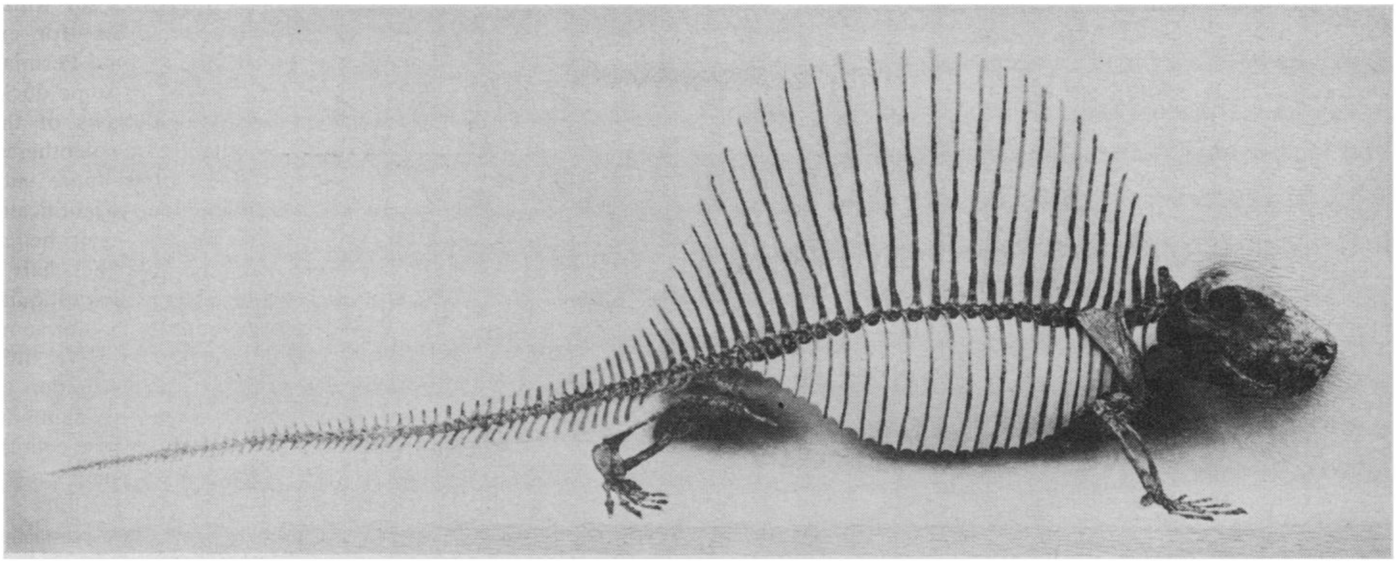

Fig. 3. A paleobiological problem: the Permian reptile *Dimetrodon*, with a large dorsal fin of long-disputed function, now interpreted as a heat-regulating device. [Museum of Comparative Zoölogy, Harvard University]

looked previously or believed insoluble on the basis of fossil materials. An important example is the biological consideration not only of single structures but of whole organ systems as developmental and correlational fields. Butler pioneered in that approach some time since (*24*), and it is being carried further not only by Butler but also by others, notably Kurtén (*25*) (see Fig. 4). Kurtén, who is particularly ingenious in quantitative biological approaches to paleontology, has also developed life tables, survivorship curves, and age pyramids for fossil populations (*25*).

Such studies of structures and of populations broaden the interpretive capacity of paleontology by bringing in functional and dynamic aspects previously amenable to profitable study only among living animals. They have, however, still greater potential importance because they can bring an extended time dimension to such studies and thus supply an evolutionary basis not attainable from study of recent animals alone. That potential is barely beginning to be realized in the present pioneering phase, but the possibilities are certainly great.

Faunas, Ecology, and Biogeography

A next step in deepening and broadening the contributions of vertebrate paleontology to general biology is the consideration not only of individuals and of specific populations but also of whole faunas. This, again, is not a new field but goes back in a tentative and subjective way to the very beginnings of the science. In retrospect, it is seen to have had a turning point and to have begun to enter a new era with the work of W. D. Matthew in the first three decades of this century. Since then, and at a pace that is still accelerating, problems outlined or exemplified by Matthew have been attacked by more varied, more rigorous, and in good part more quantitative methods, and new kinds of problems in the same general field have been formulated.

Here the ideal is the functional study of whole biotas, plants, invertebrates, and vertebrates in relation to their environments, to earlier and later biotas, and to the contemporaneous biotas of other areas. Needless to say, this ideal has not been and in fact cannot be fully achieved; not even a recent biota has been fully described, still less functionally interpreted, in accordance with the ideal. Nevertheless, it is being approached in numerous and varied, necessarily more restricted and somewhat piecemeal, studies. Data for this kind of study come from all the fields that have been previously mentioned, and from still others. Here the geological basis, which I do not have space to consider, becomes particularly important—especially sedimentation, geochronology, correlation, and stratigraphy, including microstratigraphy, in which faunal associations are tied in very precisely, down to millimeters in some instances, with successive stratigraphic levels. Sampling problems, already briefly mentioned, are here acute, and there is great need for better understanding of the factors that act between the living fauna and the preservation of part of it in fossil state, as well as factors involved in the formation of fossil deposits in general. Study of such factors has been called "biostratonomy" by Weigelt and "taphonomy" by Efremov, although it may be a little premature to designate as distinct sciences fields in which, unfortunately, there is as yet little concrete accomplishment.

Basic biological data on this subject are the taxa present in a given fossil association and their relative abundance. The present tendency and need is to narrow specifications to the point where a fossil association may, perhaps with minor exceptions, be taken as representative of a single ecological community. M. C. McKenna, among others, has recently exemplified the graphic and tabular presentation of such data, his examples being strictly localized mammalian faunules within a broader regional fauna of early Eocene age (*26*). A next step involves inference about the ecological characteristics of the various taxa and thence about the ecological structure of the community. The community characteristics are related in turn to the environmental situation, and in favorable instances community differences can be related to ecological environmental distributions on a local or microgeographic basis. A brilliant example at this level has been provided by Olson, who in a sequence of Permian vertebrate faunas not only has demonstrated the microgeographic distribution of ecological types correlated with sedimentary facies (Figs. 5

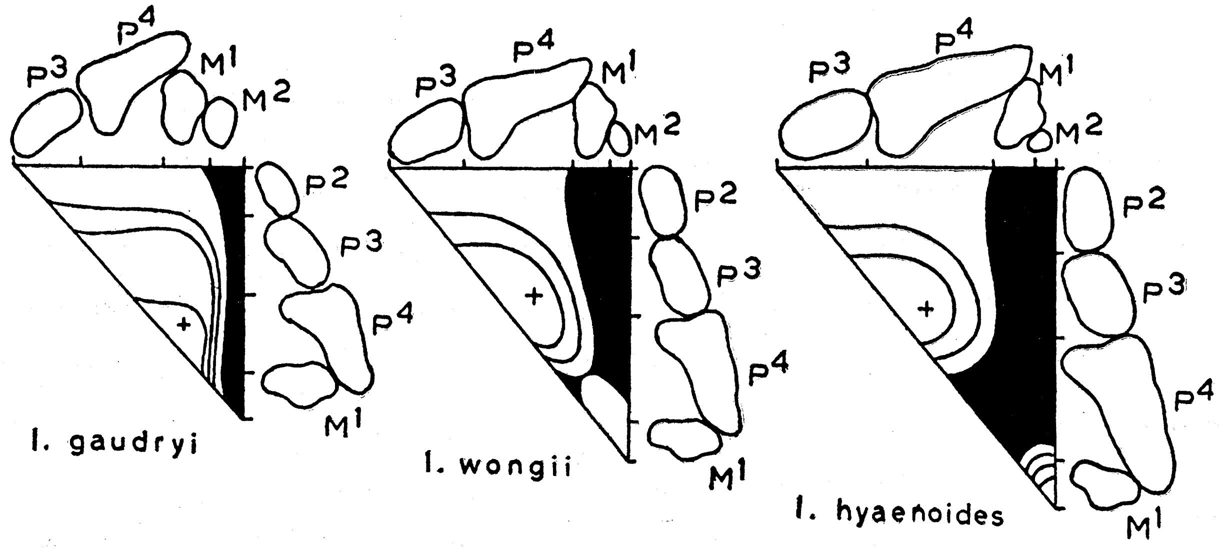

Fig. 4. Correlation fields in the dentitions of fossil mammals: upper-cheek teeth of three species of the Pliocene hyena *Ictitherium*. The triangular fields indicate the correlation between teeth diagrammatically indicated vertically above and horizontally to the right. For the black areas the coefficient of correlation z is less than .50. The contours represent higher values, in steps of .10. [After B. Kurtén]

and 6) but also has followed ecological and evolutionary changes through a sequence of environments over considerable periods of time (*27*).

Biogeographical study at the next higher level, in which more strictly historical-evolutionary elements are in interplay with ecological factors, concerns the distributions of evolving species and faunas over larger areas, up to continental size. Of special interest here is the evolutionary origin and geographic emplacement of recent biotas within the various biotic regions of the world. There have been many studies at this level for particular groups of plants and animals, but mostly on the basis of living organisms only. Without some control by directly historical—that is, paleontological—evidence, such conclusions must be viewed with strong reservations. For mammals, especially, and particularly for those of Europe and North America, there is already an enormous accumulation of late Cenozoic specimens and data, but almost all of them have still to be analyzed adequately from this point of view. There is here a particularly large number of fascinating problems soluble by materials at hand or readily obtainable and only awaiting students with the ability, interest, and time to work on them.

There are, to be sure, many published papers on geographic shifts of particular species and genera, and a few concerned with more extensive faunal associations, especially during late Cenozoic climatic changes. An example is the recent demonstration by Hibbard of the southern movement of some warm-climate vertebrates in the United States as climates became cooler in the late Cenozoic (*28*). For the most part, however, the scattered studies so far made lack both generality and precision. An example of a broader approach is Shotwell's study of morphological change, geographic distribution, and correlation with distributional changes in vegetation for two related families of rodents from late Eocene to Recent in the western United States (*29*). Here, as usual, the available data still are not wholly adequate, but this may be viewed as a sort of pilot study that indicates a profitable direction for future research.

Study on a still broader scale is that of the historical development of whole regional and continental faunas and of relationships among them. Darwin was already impressed by this subject as a young man when he collected fossil mammals in South America on the voyage of the *Beagle*, and in fact it was one of the two principal lines of evidence that converted him to belief in evolution. (The other was the differentiation and the evident affinities of birds in the Galápagos Islands.) Matthew devoted more detailed attention to the subject, and he has successors who have followed in his footsteps and have, with constantly improved data, gone well beyond him. The main outlines of Cenozoic and mostly mammalian faunal evolution are now well established for Europe, North America, and South America, and Eurasian–North American and North American–South American faunal relationships and interchanges are also fairly well understood (*30*). Of course, even for these best-known sequences, innumerable details remain to be filled in, and the degree of precision is seriously limited by the still unsatisfactory status of intercontinental correlation. Elsewhere, great blocks of evidence are still lacking or are extremely inadequate—for example, for the whole Tertiary in Australia, the early Tertiary in Africa, and the early Paleocene throughout the world except for the Rocky Mountain region of the United States.

Currently accepted general principles of historical biogeography and its (rather few) special methods, such as the quantification of faunal resemblances (*31*), are derived largely from paleomammalogy in the tradition of Darwin and Matthew. This is evident, for instance, in a fine recent treatise on the historical biogeography of nonmarine vertebrates, which happens to have been written not by a vertebrate paleontologist or a mammalogist but by an entomologist, Darlington (*32*). Such studies, departing from a geological basis at one end, also have repercussions in geology at the other end. For example, mammalian migrations and faunal relationships practically rule out any real possibility that significant continental drift has occurred during the Cenozoic.

Evolution

It is an extraordinary but explicable fact that evolution was not discovered by vertebrate paleontologists; the rather complex explanation hinges on the inadequacy of data before 1859 and on the philosophy and prestige of Cuvier, the first professional vertebrate paleontologist. After publication of *The Origin of Species,* vertebrate paleontologists rapidly became evolutionists, and in the late 19th and early 20th centuries they developed three principal roles in this respect. First, they supplied clinching evidence of the truth of evolution. Second, along with the invertebrate paleontologists and the paleobotanists, they undertook to trace the actual history of evolving organisms. Third, they proposed various theories and so-called laws of evolution.

The truth of evolution has been adequately established long since, and although every paleontological discovery adds to the proof, the paleontologist's role in that connection is no longer important. Tracing the history of organisms is still a central purpose of paleontologists, who are now advancing more rapidly than ever but are still not even in full sight of this goal. The many problems and gaps in that field are not under consideration in this brief review. The third role is now more important than ever before, but its nature has changed radically in the last 20 years (*33*).

An eminent vertebrate paleontologist, Lehman, recently declared: "*On ne crois plus guère aux lois de l'évolution*" (*3*). He was not, of course, raising doubts about the fact of evolution but expressing disillusionment with some of the theoretical preoccupations of his predecessors and recommending stricter concentration on morphology. Early evolutionary vertebrate paleontologists were much concerned with developing generalizations, which they often incorrectly called "laws," on the basis of what they knew of the fossil record. Some of these generalizations have proved to be incorrect; others have had to be more or less profoundly modified; and a few have been validated as generalizations open to exception. Orthogenesis, which was not really first proposed by vertebrate paleontologists but was accepted by many of them and is still often considered a paleontological "law," is in the first category. As defined in the most usual of its many and sometimes conflicting definitions, it flatly is not true; lineages are not impelled by some internal or supernal force to keep on evolving indefinitely in the same direction (*33*). "Dollo's law" of the irreversibility of evolution is an example in the second category. It was partly wrong as Dollo himself stated it, but it reflected a correct generalization now embraced in the broader statement of evolutionary irrevocability: organisms do not, as a rule, wholly return to any ancestral condition nor yet wholly lose effects of any ancestral condition (*33*). Examples in the third category are "Cope's law," that individuals in evolving lineages tend to become larger as time goes on (*34*), or "Williston's

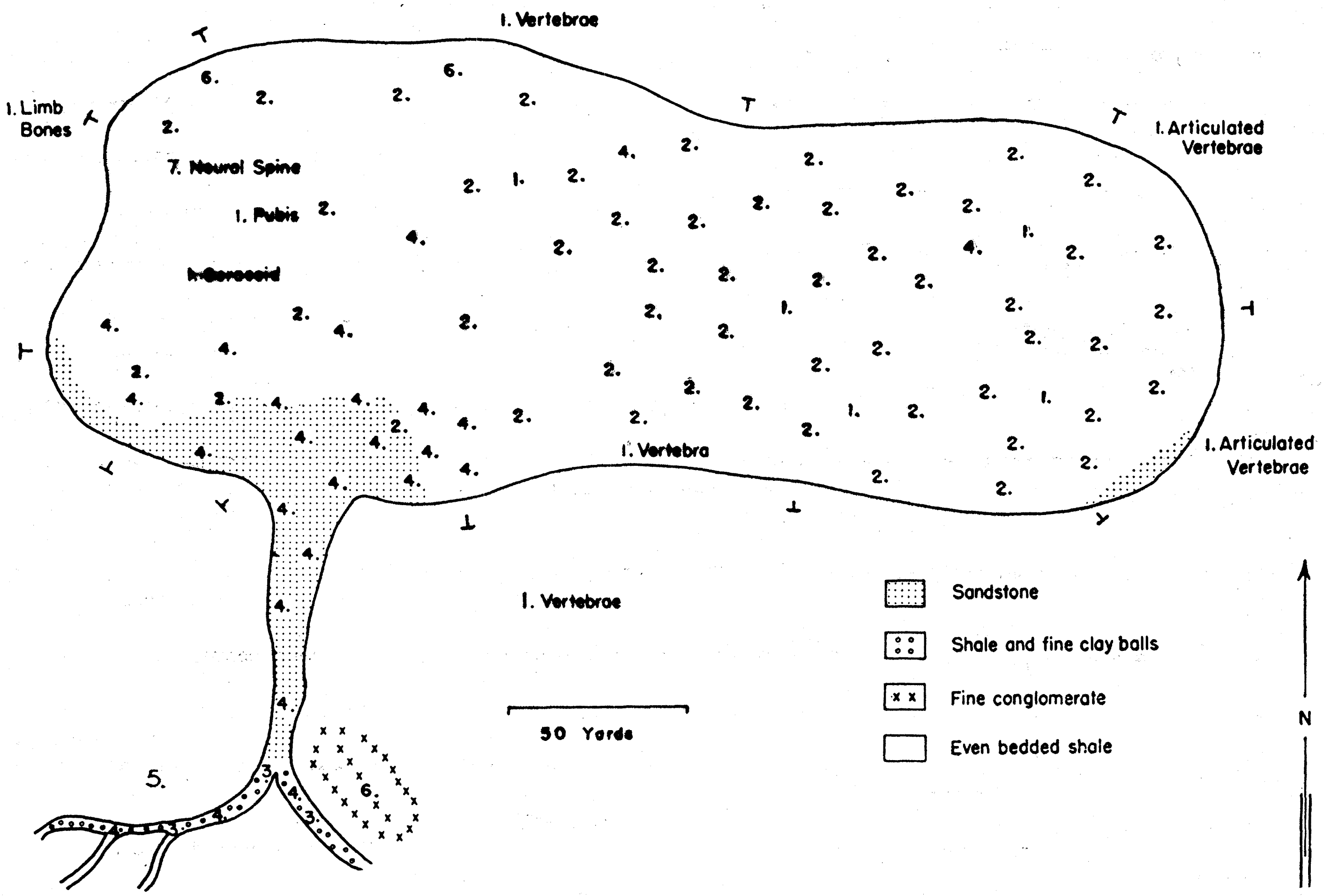

Fig. 5. An example of paleoecological data and interpretation. The map represents a Permian pond, its shore, and a small tributary stream, now represented by sediments, as keyed at lower right. The numbers indicate precise sites of discovery of different kinds of fossil vertebrates. Correlation of kinds of fossils with the ecological situation is evident. [After E. C. Olson]

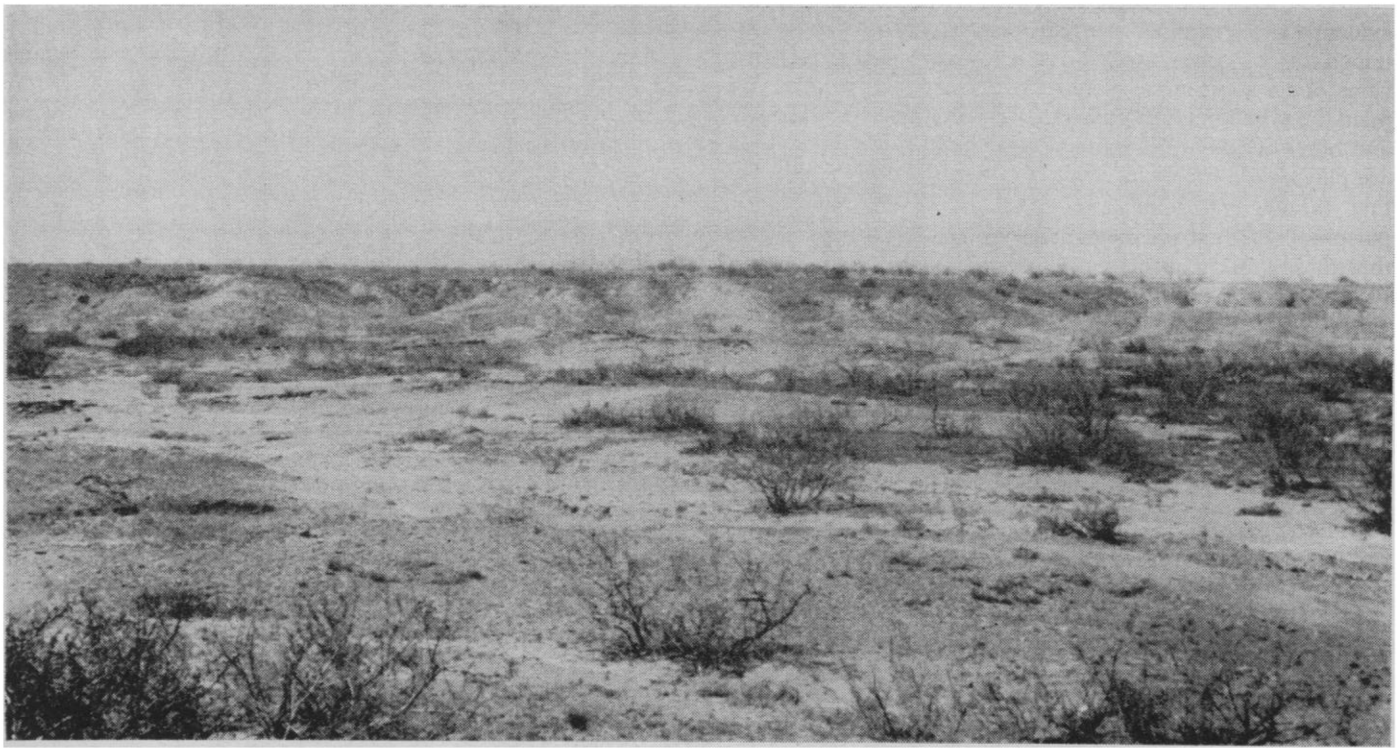

Fig. 6. Sediments of a Permian pond as exposed today in Texas. This is the exposure of the fossil deposit mapped in Fig. 5. [Hitherto unpublished photograph by E. C. Olson, University of Chicago]

law" (*35*), that repeated similar structures in individual organisms tend in the course of evolution to become less numerous and functionally more differentiated (*36*). Both are frequently general tendencies, though there are numerous exceptions.

Such generalizations are still part of the interpretive instrumentation of vertebrate paleontologists, and it is not quite true that they no longer believe in what used to be called "laws of evolution." It is, however, true that this approach has proved rather sterile, has produced no really novel and striking ideas in the last generation or so, and probably deserves its present unpopularity. The whole effort to find laws in this field analogous to the laws of the physical sciences was methodologically mistaken.

Most of the early contributions of vertebrate paleontologists to theories of evolutionary factors and forces (as opposed to the descriptive generalizations that were mistaken for laws) also now seem sterile in retrospect. Cope developed his own form of Neo-Lamarckism, popular for a time but now wholly discredited. Osborn espoused a somewhat nebulous, idiosyncratic, vitalistic-finalistic theory never accepted by any of his colleagues. After making a good start in it, Scott abandoned the whole field of evolutionary theory as futile. Broom called in familiar spirits to explain evolution. Matthew took a somewhat naive form of Neo-Darwinism for granted and did little to test or to advance the theory. In each of these and in many other cases that could be cited, a significant factor is that the vertebrate paleontologists were operating in an almost watertight compartment. They tended to neglect and were sometimes quite ignorant of the progress of theoretical biology in other fields.

The situation now is very different. The main (not the only) body of evolutionary theory today, sometimes called "Neo-Darwinian" but usually and more appropriately "synthetic," arose largely as a synthesis between genetics and systematics, but it immediately expanded to embrace other and eventually all fields of the life sciences. Vertebrate paleontology early began to play a large and in some respects crucial role in that development, a role in which it is not compartmented but is firmly integrated with almost all the branches of biology. (Other paleontologists have of course also contributed importantly, but up to now more has been done by vertebrate paleontologists than by the others, probably because they tend to be more biologically oriented and because for certain groups they have particularly good bodies of pertinent and well-analyzed data.)

In terms of the broadest aspect of its role, paleontology shows what has happened in the course of evolution over large groups of organisms and through long periods of time. In other words, paleontology specifies what really has to be explained by any explanatory theory of evolution. Put in its weakest and most negative form, the conclusion now most generally supported is that there is nothing in the fossil record that cannot conceivably be explained by the synthetic theory, or at least by an expanded and probably somewhat modified form of the theory. A note of caution and even in some respects of opposition has been sounded by some students, notably by Olson among vertebrate paleontologists (*37*). In broadest essence, the criticisms point out that other explanations are *possible* and that the synthetic theory has not clearly explained *everything*—propositions that must certainly be granted by all reasonable students of the subject. The position of those of us who do open-mindedly support the synthetic theory is simply that no other explanations yet advanced seem to us nearly as probable, and that so far no phenomenon clearly established as real is plainly inexplicable under the synthetic theory or definitely contradicts it.

Within the general field of synthetic theory, paleontology provides concrete evidence and examples that can be obtained in no other way, covering periods of time not observable by experimentation or by neosystematics. Olson and other critics are certainly right and are playing a useful part in pointing out that *all* the phenomena revealed by paleontology do have to be explained, that these could conceivably controvert parts, at least, of the synthetic theory (although they have not done so), and that they must inevitably both expand and modify evolutionary theory.

One basic aspect of these problems is the firmer integration of paleontological and neontological studies and improvement of genetical interpretation of the fossil record. That involves especially studies of variation and heredity of characters that can be observed in fossils and for which control studies can be made on recent animals. Along with an increasing number of other students, Bader has recently devoted attention to this subject (*38*). Work on morphological integration and structural correlation, previously mentioned, is also pertinent here. In a related field, Kurtén has been able to measure the intensity of mortality selection in some fossil populations and has found, as have a number of neontologists in parallel studies, that the intensity of natural selection on apparently trivial characters may be amazingly great (*39*).

More peculiarly paleontological is the study of long-term and, as it turns out, usually changing trends in evolution. The literature of that subject is already very extensive and hardly needs exemplification, but fully adequate review and synthesis are still lacking (*33*). A major necessity here is to establish unequivocally that an assembled morphological sequence does truly follow a temporal evolutionary sequence. Former belief in orthogenesis was largely bolstered by ignoring data on time sequence, and the same criticism may justly be leveled at some current work by vertebrate paleontologists of the "pure" morphological school.

The study of evolutionary rates is another complex subject that, in the nature of things, is almost entirely in the province of paleontology. Bader and Kurtén are among those who have made important recent contributions to the subject, in works already cited (*38*, *39*). Still more recently, Kurtén has devised an ingenious half-life method of making quantitative estimates of average rates in whole faunas—a method particularly well adapted to the kind of data now actually available (*40*). With some other problems of rates, such as that of rate distributions within large taxa, a start has been made (*33*) (see Fig. 7), but recent progress has been disappointing because immediately usable data are inadequate, even though such data could be obtained and appropriate methods for analyzing them have already been devised. In all studies of evolutionary rates the greatest present impediment is the inaccuracy of estimates of absolute dates and lapses in time in years. Radioactivity dating is the best method available, but reliable long-half-life dates (for example, from uranium-lead) are still too few and too poorly tied in with fossil faunas, and reliable short-half-life dates (for example, from carbon-14) do not cover enough time. Some recent work, particularly with potassium-argon, does hold out hope for eventual solution of this problem (*41*).

A still more complex whole field of primarily paleontological evolutionary

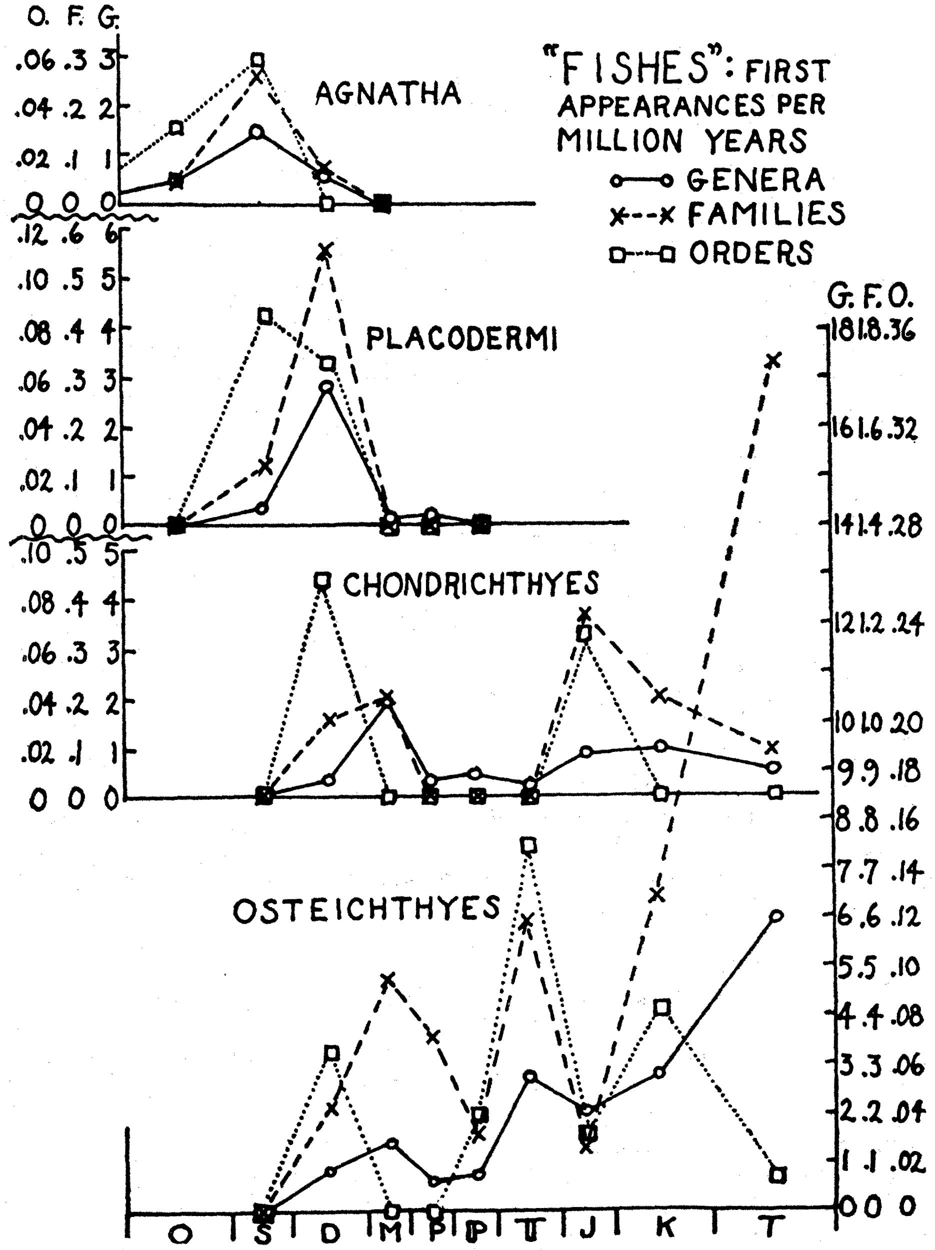

Fig. 7. An aspect of changing rates of evolution in the four classes of primarily aquatic vertebrates (fishes, in a broad sense). The scale along the abscissa, indicating approximate relative durations of geological periods from Ordovician (left) to Tertiary (right), is the same for all four classes. The numbers of known first appearances of orders (*O*), families (*F*), and genera (*G*) are scaled separately for each class on the ordinates. Besides variations in rates of appearances of new groups, successive "explosive" episodes are evident, as well as a tendency for later groups to replace earlier groups.

problems concerns numerous intricately interrelated subjects: the rise of higher taxa and the evolutionary nature of higher categories; their duality of diversification and divergence; the occurrence of "explosive" episodes of diversification; the prevalence of parallel evolution throughout many high taxa and problems of polyphyly arising therefrom; patterns of early radiation in such groups as fishes, therapsids, and rodents. It is perhaps in this general field that vertebrate paleontology faces its most important problems of evolutionary theory and is making (or is capable of making) its greatest contributions to that subject. Even to exemplify these problems adequately and to cite the most important recent work on them would require another article longer than this one. Among other essential problems that can be barely mentioned here is that of extinction, about which a great deal has been written but very little can be said to be firmly known.

Philosophy

The history of life and the processes of its evolution have a crucial bearing on philosophy—on our understanding of ourselves and of the universe in which we live. This is a subject that greatly transcends vertebrate paleontology, but here, too, vertebrate paleontology has or should have an essential role. Its area of main concern is a part of the history of life, and the most pertinent part, since it includes the ancestry of man from jawless fish onward. Vertebrate paleontology also participates with other life sciences, in the elucidation of the processes by which we and the whole world of life evolved.

Among the great philosophical problems on which evolution and, therefore, also vertebrate paleontology bear are those of order in the universe, of utility or teleology, of progress, and of purpose or finality (*33, 42*). Decision on any of those problems must depend largely on what one considers to be the principal directive forces of evolution—whether natural selection (largely a resultant of interaction between organisms and environments), primary action of the environment itself, purely internal forces (especially gross mutations, irrespective of the environment), or metaphysical, nonmaterial, or divine impulses and finalities. One can hardly speak in an absolute sense of proving or disproving any of those views on evidence from vertebrate paleontology, but such evidence certainly bears on which views should be considered more and which less probable.

These questions are always approached on the basis of a priori postulates, seldom frankly stated, often nonscientific and sometimes even antiscientific. In the Soviet Union, purely political postulates forced support of Michurinism, a form of Neo-Lamarckism, even though most Russian biologists knew all the time that accumulated evidence has made that theory extremely improbable. Orthodox Christian, and particularly Roman Catholic, postulates are often, but not necessarily, construed as demanding vitalistic and finalistic control of evolution. Other views inevitably have their overt and covert postulates as well. The important thing is that those postulates should at least be consistent with and appropriate to the scientific approach—otherwise the contribution of vertebrate paleontology or any other life science to philosophy is negatived or stultified from the start. Unfortunately the postulates are not scientific in the most conspicuous recent contribution of a vertebrate paleontologist to this field: the mystical works of the late Teilhard de Chardin, a Jesuit priest, who departed from purely metaphysical postulates and rejected scientific evidence opposed to them (*43*). A few vertebrate paleontologists have spoken for more strictly scientific postulation and inference, but most of them are publicly silent on philosophical questions and probably try to ignore them even in private. They may thereby be losing, by default, the opportunity to explore the most profound problems and values of their subject.

References and Notes

1. Although the number of vertebrate paleontologists in North America is still small, there has been a considerable percentage increase in recent years, and the number continues to rise slowly. In contrast, Lehman estimated in 1957 that the number of vertebrate paleontologists in Europe was then about the same as in 1900. Strictly speaking, there has never been a professional vertebrate paleontologist in Australia, and there is only a handful each in Asia, Africa, and South America.
2. Selection of topics and point of view are necessarily personal, but within the limited scope of this account I have tried to include the interests of others. I have done this largely on the broad basis of years of conversations, correspondence, and exchange of publications. In addition, I have sought explicit advice, in preparing this article, from a small sample of vertebrate paleontologists of varying interests and approaches, including some I might otherwise have missed. Among those who responded to that appeal are R. S. Bader, J. R. Beerbower, B. Kurtén, J. P. Lehman, M. C. McKenna, E. C. Olson, B. Patterson, A. S. Romer, D. E. Savage, B. Schaeffer, J. A. Shotwell, E. Simons, R. A. Stirton, and L. Van Valen. It has not been possible to include all their suggestions, and they are not responsible for the necessary omissions.
3. For a strong but reasonable appeal for emphasis on the morphological approach, see J. P. Lehman, *Bull. muséum natl. d'hist. nat.* (Paris) **29**, 363 (1957).
4. See J. P. Lehman, *L'Évolution des vertébrés inférieurs* (Dunod, Paris, 1959); E. Jarvik, *Théories de l'évolution des vertébrés reconsidérées à la lumière des récentes découvertes sur les vertébrés inférieurs* (Masson, Paris, 1960).
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7. Among many others, see A. S. Brink, *Palaeontol. Africa* **4**, 77 (1957); A. W. Crompton, *Proc. Zool. Soc. London* **130**, 183 (1958); E. C. Olson, *Evolution* **13**, 344 (1959); D. M. S. Watson and A. S. Romer, *Bull. Museum Comp. Zool.* **114**, 37 (1956). Much still unpublished work in this field was reported at Oxford in 1960.
8. Proceedings of the Brussels symposium, which reviewed most of the recent work on the subject, will be published. See also B. Patterson, *Fieldiana. Geol.* **13**, 1 (1956).
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12. On this and other topics discussed in this section, see G. G. Simpson, *Principles of Animal Taxonomy* (Columbia Univ. Press, New York, 1961); on the statistical principles involved, see G. G. Simpson, A. Roe, R. C. Lewontin, *Quantitative Zoölogy* (Harcourt, Brace, New York, 1960).
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14. J. A. Shotwell, *Ecology* **39**, 271 (1958).
15. R. W. Wilson, *Univ. Kansas Publs., Paleontol. Contrib., Vertebrata* (1960).
16. For different viewpoints on the problem for Mammalia, see L. Van Valen, *Evolution* **13**, 304 (1960); C. A. Reed, *ibid.* **13**, 314 (1960); G. G. Simpson, *ibid.* **13**, 389 (1960).
17. Among numerous current workers on this subject are P. M. Butler, S. B. McDowell, Jr., M. C. McKenna, and B. Patterson. The most crucial work is not yet published.
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19. J. H. Quinn, *Univ. Texas Publ. No. 5516* (1955). As a matter of principle Quinn used taxonomic methods unacceptable to many of his colleagues, and his conclusions have not been widely adopted, but they certainly indicate that the classic phylogeny of the Equidae must be changed in many details. M. F. Skinner is currently working intensively on this subject.
20. G. Haas, *Am. Museum Novitates, No. 1729* (1955). Further examples of still broader and in part new approaches to functional analysis of fossil (and recent) skeletons are provided by R. J. G. Savage, *Proc. Zool. Soc. London* **129**, 151 (1957); J. M. Smith and R. J. G. Savage, *School Sci. Rev.* **40**, 289 (1959).
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33. On this section in general, see G. G. Simpson, *Major Features of Evolution* (Columbia

Univ. Press, New York, 1953); G. G. Simpson, in *Evolution after Darwin*, S. Tax, Ed. (Univ. of Chicago Press, Chicago, 1960), vol. 1, p. 117.

34. Although not a paleontologist, Rensch has become the authority on "Cope's law"; see B. Rensch, *Evolution above the Species Level* (Columbia Univ. Press, New York, 1960).
35. The eponyms of all these "laws" are inappropriate; other workers had expressed them in one form or another before they were advanced by Dollo, Cope, or Williston.
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37. E. C. Olson, in *Evolution after Darwin*, S. Tax, Ed. (Univ. of Chicago Press, Chicago, 1960), vol. 1, p. 523.
38. R. S. Bader, *Evolution* **9**, 119 (1955); ———, *Quart. J. Florida Acad. Sci.* **19**, 14 (1956); ——— and J. S. Hall, *Evolution* **14**, 8 (1960).
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41. D. E. Savage, G. H. Curtis, J. F. Evernden, *Bull. Geol. Soc. Am.* **71**, 1966 (1960) [abstract; full text in press (New York Academy of Sciences)].
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Sounds Emitted by the Bottlenose Dolphin

The audible emissions of captive dolphins under water or in air are remarkably complex and varied.

John C. Lilly and Alice M. Miller

Some of the sonic (audible to human beings) emissions of the bottlenose dolphin of the east coast of the United States (*Tursiops truncatus* Montagu) have been described (*1*). One of the classes of emissions (the clicks) has been studied situationally in the limited context of their use in echo-location (*2–4*). Some of the supersonic components of these clicks have been measured (*2, 3*). In this article we present evidence that the dolphin's audible sonic emissions can be divided into at least three classes: (i) sine-wave type whistles; (ii) slow trains of clicks (buzzings); and (iii) a class of complex waves emitted in bursts (quacks, squawks, blats). It can be shown that these classes of sounds are emitted under different environmental conditions and states of need. It is shown that each animal probably has at least two sound-producing mechanisms available for simultaneous use. The dolphin's now well-known use of click trains (creaking, and so on) as "sonar" is not under discussion here and has been eliminated as far as possible in the experiments (*5*).

The methods of investigation were briefly as follows: A captive animal was restrained and confined in water 10 to 15 inches deep, in a space 15 inches wide and 7.5 feet long, with polyurethane foam 1 inch thick along one side of the water box to attenuate echoes somewhat. (The same animal was also observed and the emissions were checked under conditions in which the dolphin could swim more freely.) A hydrophone, with preamplifier (*6*), was placed beside the animal's beak (rostrum). The animal could not move its head more than 6 inches (one wavelength at 10 kilocycles per second in sea water) from its mean position relative to the hydrophone and walls. The output of the hydrophone was amplified and recorded on a magnetic tape recorder at 60 inches per second (*6*). The pass band of this configuration is determined by the hydrophone (upper limit, about 33 kcy/sec) and a high-pass filter (1 kcy/sec). For analytical purposes, the tape recording was played back (slowed down 8 to 16 times), analyzed electrically, and recorded with an ink writer or a mirror galvanometer oscillograph, or both (*6*).

The sounds recorded were those emitted (i) spontaneously in solitude, or (ii) on hearing sounds of another animal nearby in a similar water box, or (iii) in response to maneuvers on the part of the observer. Most of the findings reported here are based on observations of four animals studied intensively (every day for 3 to 6 months) and of ten others observed for periods of from 24 hours to 6 days.

In solitude an animal emits whistles and clicks and, very rarely, quacks or blats. In response to, and in exchange with, another dolphin at a distance, an animal emits whistles and trains of clicks (at a relatively slow repetition rate) and occasional quacks. In violent play, courtship, and intercourse, in close quarters, each may emit all three classes of sounds, with fairly frequent squawks, quacks, and blats.

The sounds that an observer can elicit from a restrained dolphin can be of any of the three classes, depending on the tactics of the observer. As described previously (*1–4*), placing a fish or any object in the box sets off trains of clicks of a particular kind (creakings). A loud whistle by the observer elicits whistles. Bodily manipulations (gentle to painful) can elicit whistles or quacks or blats. In the presence of an observer an animal can and does shift from emitting sounds under water to emitting sounds in the air, by raising its blowhole out of the water. The whistles in the air are faint and occur at the blowhole slit; they are accompanied by small bubbles, which are lacking in most underwater emissions. To make loud clicks, blats, squawks, and quacks (and other air-borne sounds not here described), the animal opens its blowhole and releases the internally produced sounds into the air.

Simultaneous Clicks and Whistles

Here we present analyses of only the underwater sounds and the underwater sonic components of the air-borne sounds. Figure 1 is a graphic amplitude record (*6*) of simultaneous underwater emission of a slow train of clicks and a whistle. The clicks occurred at a rate

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