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GEOLOGY

AUG 13 1964









# FIELDIANA

## Geology

Published by Field Museum of Natural History

Volume 33, No. 19

June 29, 1976

This volume is dedicated to Dr. Rainer Zangerl

### Functional Morphological Models: Evolutionary and Nonevolutionary

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#### INTRODUCTION

The widespread use of formal models for gathering data and reasoning about fossils has sharply altered the direction of much paleontological research. The nature of models is complicated, and models are viewed philosophically in various ways by different investigators (Schopf, 1972, p. 12; Kitts, 1974) and in different disciplines. Models used in paleontology have been drawn from such diverse subfields as ecology, biogeography, genetics, morphology, and biochemistry. This paper especially considers functional morphological evolutionary models.

Here the many philosophical ramifications of models will be avoided. Instead, the operational aspects of models are stressed. Thus, models are assumed to be hypotheses, which predict the data to be gathered. Of course, ultimately, a model is modified, accepted, or rejected as a result of data gathering. Formal models are relatively new to paleontological research, and therefore many paleontologists are a bit awkward with them, and may not have pondered the implications of their use. Some paleontologists have viewed models as goals to be attained only after we gather enough unbiased data. In fact, all paleontologists—like all scientists—use models in data gathering, although they may not be formally devised, and the investigator may even deny that any model is being used (Eldredge and Gould, 1972, p. 86). Data unbiased by a model do not exist.

Vertebrate paleontologists have always used formal models in morphological studies, because they used the methods of compara-

*Library of Congress Catalog Card Number: 76-8310*

tive anatomy, which enabled them to point out many important comparisons in widely different groups (e.g., birds *vs.* reptiles). Thus, evolutionarily continuous structures in divergent groups were found with very different shapes and functions. Such interesting comparisons are less possible among invertebrate fossil groups, and this has greatly reduced the use of formal comparative anatomy models in their study. In fact, because of the complicated homologies of vertebrate paleontology, a vast literature has accumulated on the formal methods of comparative anatomy (e.g., Zangerl, 1948). However, except in some limited instances (see below), the use of formal models in vertebrate paleontology has not been extended to function.

This paper reclassifies functional morphological models into two differing styles: (1) static or nonevolutionary models, and (2) evolutionary models. Evolutionary models are restricted to those that use differentials, where the mathematics is directly related to function, and therefore some of the variables used are moment arms, force vectors, position vectors, etc. It is hoped that such a restriction and reclassification will encourage us to develop the kinds of models most likely to give us insight into the evolution of function (see Gould, 1970; Schopf, 1972, for different classifications). Differentials have been very little used, so far, but I believe them to have enormous potential in the study of the evolution of morphology because they enable us to study optimal change. This is important because evolution presumably refers to optimal change in function in addition to optimum function at any one moment.

### UNIFORMITARIAN MODELS

The traditional formal model of paleontology has been based on the phrase, "the present is the key to the past." Early in the history of paleontology, this strategy led to useful and interesting conclusions in that it forced comparisons of the strange objects contained in solid rocks to now-living taxa. Once it was established that fossils were the remains of once-living organisms, observations based on such simple comparisons became less interesting, leading only to the identification of structures in fossils. For example, the comparison of the adductor musculature of living articulate brachiopods with that of fossil taxa does not exemplify the most exciting aspects of scientific research because they are the same. The reason that the conclusions drawn from such comparisons are drab is that such an

application of uniformitarianism is to a nonevolutionary situation. The most interesting cases of the application of uniformitarian models have evolutionary ramifications. The brief discussion of two recent studies will explain some of what I mean (Barghusen, 1968, 1973; Stanley, 1968).

Stanley (1968) showed that the Mesozoic radiation of infaunal pelecypods was the result of mantle fusion. This depended on being able to show which fossil species had fused mantles, and, particularly, to demonstrate that fused mantles did not occur in Paleozoic forms. Thus, the comparison of modern with ancient pelecypods required that it be recognized that siphons in living pelecypods functioned in different ways. In effect, it had to be shown that pelecypods with fused mantles should not be used to reconstruct the form and function of Paleozoic pelecypods. The evolutionary lineages of pelecypods are not so well known as some vertebrate lineages (because of the greater discontinuity in the fossil record of pelecypods). Thus, the errors of comparison faced by Barghusen (see below), of comparing the primitive form in its lineage with the advanced form—rather than with other primitive forms—was less likely. The Mesozoic evolutionary radiation had to be isolated in order to make proper comparisons of living with Paleozoic taxa.

Barghusen was faced with a more complex situation in his study of the evolution of the adductor jaw musculature of synapsid reptiles. Vertebrates have more morphological features than pelecypods. This, and the more complete fossil record led to many attempts to construct phylogenies. In fact, Barghusen had a well-established, generally accepted rival model with which to contend. Briefly, Barghusen (1968, 1973) was confronted with the decision of whether primitive mammal-like reptiles should be compared with mammals or reptiles for the purpose of reconstructing their jaw musculature. The rival model constructed by earlier workers (e.g., Parrington, 1955; Crompton, 1963) tended to emphasize the mammal-like nature of the jaw musculature of reptiles. Thus, they opted for mammal comparisons, concluding that the Sphenacodontia had adductor jaw musculature similar to that of mammals. Barghusen, in a series of comparisons, showed the details of the origin and evolution of much of the jaw musculature of mammals to be in the cynodonts. He further determined that primitive mammal-like reptiles—at least with regard to jaw musculature—must be compared with reptiles and not mammals (see Barghusen, 1968). This finally resulted in cynodonts being recognized as the only reasonable candidates

for the ancestors of mammals (Hopson and Crompton, 1969; Olson, 1971).

In these examples of uniformitarian reconstruction (see van Bergeijk, 1966; Hopson, 1966; Thomson, 1966, for other interesting examples), the *evolution* of the structure being reconstructed is eliminated as "noise" from the comparisons, otherwise the strategy cannot be carried out. Thus, although one may learn much about evolution from such models, they are not directly and efficiently evolutionary, and do not predict evolutionary events in a functional framework. They are logical devices for evading the troubles caused by evolution.

### THE PARADIGM APPROACH

Although invertebrate fossils have fewer morphological features and less complicated morphological evolution, it is interesting to note that the first new morphological functional models were suggested by invertebrate paleontologists. Rudwick (1961) pointed out that we can describe the ideal form of a structure if we know its function. This led to the development of the *paradigm* approach, which has been used with some success in a number of groups (Gould, 1970).

Rudwick formalized the method to include some operational rules: (1) given a set of suggested hypotheses to explain the function of some structure that (2) the structure would most resemble the paradigm of the functional hypothesis most likely to be the correct explanation. The best-documented example of the use of this method is Rudwick's (1964a) suggestion that the zig-zag commissure of many brachiopods was useful in preventing the entry of particles above a certain size. The paradigm for this function enabled him to predict more of the structures of brachiopods than could the paradigm for any other function (see Carter, 1968, for *Arctostrea*, and Westermann, 1964). Thus Rudwick's idea is the one most accepted (see Gould, 1970).

But, although the paradigm approach can help us choose a function for a given structure, it gives us no rules with which to begin our study. How is the paradigm constructed? How do we decide what the possible functions were? In the end, we are left with original thoughts, but no operational definitions to help us solve further problems.

Moreover, the paradigm is not placed in an evolutionary context. Thus, in the example given above, the paradigm works well for ex-

plaining the fully developed zig-zag commissure, but is useless for explaining its origin, since the earlier forms of the structure were probably not effective for the stated function, and probably involved some additional function. Perhaps the structural idea of Westermann (1964) should be expanded using the more formal models based on statics and dynamics suggested below. In any case, the paradigm approach works only in instances where evolution of a structure from one function to another does not occur or can be eliminated. In effect, evolution interferes with the application of the paradigm approach.

### DESCRIPTIVE MATHEMATICAL MORPHOLOGICAL MODELS

Raup (1966) described a more specific strategy for deciphering the function of past morphology (see also Raup and Michelson, 1965). He described the morphology of coiled shells with only four parameters, using equations to describe three of these—distance from the coiling axis, expansion rate, and translation rate. Using a fixed shape of generating curve, a computer was programmed to simulate many different coiled shells—some of which have evolved, some of which have not. Then, the limited possible range of all the forms that evolved was examined in order to determine the reasons for the limits of coexisting variability of the various parameters described by the equations. Thus, Raup was able to distinguish reasonable limits for univalve and bivalve regions, and to show that some interesting questions could be asked about the restrictions of some coiled shells (e.g., brachiopods and pelecypods) to certain narrow regions. In a later study, Raup (1967) showed, in addition, that many of the detailed restrictions of ammonoids were rational. Presumably, this sort of detailed study could be extended to other animals with coiled shells in addition to ammonoids.

Without question, the Raup technique has the power to help us discover the function of the shapes of fossils; it has been used for studying the organization of dentitions (DeMar, 1972, 1973), the paths of burrowing tracks of infaunal sediment feeders (Raup and Seilacher, 1969), echinoderms (Raup, 1968), and in some other situations. However, there are two significant weaknesses in the system: (1) the equations used are individual for each study attempted, and (2) the equations used do not directly connect function and morphology. Thus, only vague rules of operation can be discerned by learning about prior work of this kind. Each worker oper-

ates almost in isolation; his work has only limited significance to others contemplating similar problems. What is more, as will be further discussed below, it is only vaguely stated how we must discuss function.

D'Arcy Thompson's (1942) transformation grids greatly resemble the Raup system for describing morphology in that the manipulation of a very few variables leads from one morphology to another (Gould, 1970). He believed that the simple manipulation of a rectangular grid would simulate and serve to describe and explain the evolution of morphology. But, because there was no set of equations that could be used for deriving one morphology from another, Thompson's original methods did not measure up to their promise.<sup>1</sup> This difficulty has been partly circumvented by Sneath (1967); however, his set of equations have no set of restrictions based on the reality of animal shapes, in sharp contrast to the equations of Raup (1966) for coiled shells and DeMar (1972, 1973) for dentitions.

Neither those techniques resembling Raup's methods, nor those resembling Thompson's use equations that directly relate function and morphology. The Sneath method (see also Oxnard, 1973, for comparable, if not similar, methods)—unlike Raup's method—has the advantage of enabling one to transform any morphology to any other morphology with a similar set of equations. However, Raup's method—in those studies where equations have been developed—is generally more useful in discussing function because the investigator usually has some notion, however vague, of what the function of the morphology is. Thus, the limitations imposed by the equations crystallize intuitive thoughts. For example, it was already known that bivalves had to open their shells, but it was desirable that the shells should not be easily forced open; and that univalve shells served for protection, but it was not desirable to waste shell-making material, long before Raup (1966) related these issues to mathematical statements about coiled shells. Similarly, the function of dentitions (see Edmund, 1960; Romer, 1961) was known before DeMar (1972, 1973) related gaps in the tooth rows to specific arrangements of teeth.

<sup>1</sup>It is interesting to note that Thompson (1942, p. 1,096) viewed *On Growth and Form* as an introduction to the naturalist of "a few mathematical concepts and dynamic principles," but as an introduction to the mathematician of "a field for his labour—a field which few have entered and no man has explored." It seems obvious that he believed the solutions of morphological problems would come from mathematicians, not from naturalists.

In all of these techniques, evolution is simulated by changing the variables in equations so that one shape is gradually transformed into another. A gradual transition may be made from any one morphology to another by changing a variable only slightly, and a very large number of the possible shapes can be examined by utilizing a computer program. In mathematics, this strategy is sometimes called "brute force." It means, approximately, that the solution to the problem is not elegant—that is, if one has not developed a precise set of reasoned equations and limits for examining a given phenomena, an approximate solution can be achieved in a more cumbersome, time-consuming way. The point is that the revelation of critical evolutionary events by the techniques described above takes place only after a multitude of the possible combinations are portrayed and examined. Not only is function not specifically included in the original mathematical statements, but there is no use of differentials described below. Therefore, change (which is what evolution concerns) and function can only be considered by examining and comparing many static morphologies in the hope that the fundamental features of evolutionary change will be revealed. Thus, none of the above models are truly evolutionary models without the relatively inefficient use of "brute force."

### EVOLUTIONARY MODELS

Thus far, the only model combining function and morphology with equations containing differentials is one describing jaw mechanics in synapsid reptiles (DeMar and Barghusen, 1972). In part of this model, the height of the coronoid process, the position of the jaw articulation, the line of muscle action, and the length of the force moment arm are related by using the Pythagorean theorem. These variables are, in part, directly related to function (e.g., force moment arm) and are the kind of variables that would be used in a static (nonevolutionary) functional model (Maynard Smith and Savage, 1959; Ostrom, 1964).

What makes it an evolutionary model as defined here is that the Pythagorean equation, and others from related trigonometric functions are differentiated so that the ratios of the differentials (e.g., the change in the length of the moment arm compared with the change in the height of the coronoid process) may be compared, given different values of the original (undifferentiated) variables. This allows the function of *change* (which is evolution) to be directly

examined (e.g., see DeMar and Barghusen, 1972, fig. 4). In addition, it allows the optimal manner of making a change to be considered.

The weaknesses of this model will be considered below, but first I want to consider several recent models that give hints that other truly evolutionary models are emerging. These include an explanation of "Cope's Rule" (Stanley, 1973), a measure of the rate of evolution (Lerman, 1965), and a mechanical rationale for the position of certain skull sutures in labyrinthodonts (Bolt, 1974).

Stanley (1973) has shown, in a complex discussion of optimal size, why it is reasonable that animals of optimal body size are more likely to make major adaptive breakthroughs because they have not taken on the special structures required by large (or small) size. In effect, optimal size is related to greater evolutionary flexibility. Thus, allometry—in this instance—enables one to predict statistically the kind of animal most likely to evolve, but does not specify the possible direction of evolution, or which particular species will evolve. In addition, there are no specific functional statements or limitations included in Stanley's discussion of Cope's Rule, and therefore it does not predict anything specific about the evolution of function. Of course, allometry has been used in many situations besides Cope's Rule (Gould, 1966, 1969, 1974). In cases where the number of variables considered is low enough, allometry can be used for specific predictions (unlike the vague statements of Cope's Rule).

Lerman (1965) measured the statistical "distance" in units of standard deviation between the means of characters of populations of pelecypods, equids, ammonoids, and oreodonts. He then obtained a differential equation relating this to distance in each case, thus getting a measure of the rate of evolution of these organisms. Unfortunately, this measure of evolutionary rate was not connected with function; this leaves one asking what was happening during a rate of evolution.

Bolt (1974) constructed a complex model to explain why the skull sutures in the Dissorophoidea (temnospondylous labyrinthodont amphibians) had certain special features. This model contains forces, moment arms, and fulcra so that function and morphology are related. The variables are not drawn together into equations so that the full relationships may not be simultaneously studied, and, of course, no differentials may be obtained. However, since I believe the variables chosen to be reasonable, it seems to me that this scheme lacks only formal mathematical and mechanical analysis to become an evolutionary model.

## DISCUSSION

What operational rules can we develop so that we can construct evolutionary models? As mentioned above, the methods used by Rudwick (1961, 1964a, b), Raup (1966, 1967), DeMar (1972, 1973, 1974), and many others are often clever solutions of problems. However, except for vague statements about searching for the optimal morphology for a particular function, we are given no operational rules for further investigations. It is especially important to emphasize that none of the equations published are useful beyond their limited morphological or taxonomic areas.

Our aim should be to make models that (1) use common equations—that is, ones which are applicable to many functional situations in many taxonomic groups—where (2) these equations have variables that relate function and morphology, and (3) these equations should be differentiated so that *change* in function and morphology can be compared. I believe that the way to achieve such models is to perceive morphological structures as the result of a tendency for selection to make them perform optimally according to one or more physical laws. The most useful set of laws is, I believe, that related to statics and dynamics. In this set of laws, models could be formed in the realm of forces, strength of materials, and work. These variables may generally be put into equations, provided that we can reasonably simplify the situation being examined<sup>1</sup> (DeMar and Barghusen, 1972) into moment arms, force vectors, and fulcra.

I further consider prior models (notably DeMar and Barghusen, 1972) to be very naive, in that they are not put into the form a free-body and inertia vector diagrams (a convenient means of accounting for all forces acting on a particle) during all times of stress (Hibbeler, 1974). Future models should attempt to use the standard models of statics and dynamics. Some interesting nonevolutionary studies using such models have been done (e.g., Frazzetta, 1962; Alexander, 1968; Bock, 1968; Oxnard, 1973). These and other comparable studies contain interesting information, but they cannot be put readily into a general form. Usually, they are attempts to study only one species of animal, and in some cases the simplifying assumptions should be re-examined.

<sup>1</sup>The far-sighted Thompson (1942, p. 1032) pointed out that “we must learn from the mathematician to eliminate and to discard; to keep the type in mind and leave the single case, with all its accidents, alone; and to find in the sacrifice of what matters little and conservation of what matters much one of the peculiar excellences of the method of mathematics.”

The tetrapod skull can serve as a model to discuss some of the difficulties involved in using the strategy of static and dynamic models. The skull typically contains 40 or 50 separate bony elements. This number is very stable, in a general way. Thus we can be very sure that there are feedbacks that maintain constancy in the number of bones. Moreover, we can be very sure that part of the explanation for the number of bones and the positions of the sutures (and the implied feedbacks) is to maintain some kineticism with enough strength to maintain the integrity of the skull against various stresses. The physical stresses involved can be put into the form of free-body diagrams and equations can be written that will compare various optimum arrangements of bones under various stresses with the *actual* arrangements. Unfortunately, the skull is exceedingly complicated, so that many simplifying statements must be made (see Thomson and Bossy, 1970; Bolt, 1974). However, there is a further large complication; the position and nature of the sutures and relative sizes and shapes of the bones of the skull have many other functions in addition to kineticism and strength. Some of these are (1) to allow growth, (2) to transmit sound, (3) to channel fluids, (4) to allow feeding, and (5) to enhance display behavior. It will be difficult to separate the effects on the morphology of the skull of these different functions in constructing a mathematical mechanical model of the skull. This difficulty should not overwhelm us. Bolt (1974) was partially successful, although his approach was a rather primitive form of an engineering model. The use of more powerful analytical tools should be more successful.

All the *evolutionary* functional morphological models discussed here depend on the idea that some combination of mass, strength, velocity, force, and acceleration is involved in the morphology of many organic hard parts. Other morphological models have been constructed based on other physical parameters. Thus, we have nonevolutionary optimality models of vision in trilobites based on optical theories (Clarkson, 1966a, b; Clarkson and Levi-Setti, 1975), models of swimming in pecten (Stanley, 1970, p. 41) and cephalopods (Kummel and Lloyd, 1955) based on hydrodynamic laws, and a model of flying in pterodactyls (Bramwell and Whitfield, 1974) based on aerodynamic laws. Although none of these fits my description of an evolutionary model, some are very elegant and are based on physical principles. As a result, eventually we should be able to write sets of equations which will lead to evolutionary models which can be applied to those taxa whose morphology has resulted from conformance to comparable physical laws.

The enlightened use of physical laws will lead us to new insights into evolutionary processes. Just as trilobites were able to avoid spherical aberration by shaping their lenses like those described by Huygens and Des Cartes (Clarkson and Levi-Setti, 1975), so other animals shape their bones, shells, etc., according to mechanical principles. Of course, we should never belittle the problems involved in constructing such models. Earlier models (evolutionary and non-evolutionary) have been aimed at analyzing the simplest morphological features: coiled shells, tooth replacement organization (see Edmund, 1960, for descriptions of the ordered relationship), and jaw mechanics are—at least as a first approximation—much simpler than most other morphological features of animals. Nonetheless, I believe the techniques of statics and dynamics to be sufficiently powerful that much more complicated situations can be handled.<sup>1</sup>

At this stage in the history of paleontology, the ways of examining data have changed sharply (Gould, 1970; Raup and Stanley, 1971; Schopf, 1972); those who look at data in new ways are generally optimistic, in that they are often willing to make simplifying assumptions that they cannot fully justify because they believe new insights will develop from the new relationships that are perceived.

This new optimism has an interesting historical perspective, in that many paleontologists were temporarily in despair when early hopeful attempts to increase the objectivity of information gathered from the fossil record (Boucot, 1953; Johnson, 1957; Olson, 1957; Boucot et al., 1958) seemed to show that biases in the fossil record were so pernicious that little could be learned about growth, coexisting species, or relative abundances of individuals. Fortunately, Johnson (1960, 1972), Valentine (1961), Warne (1969), and others eventually developed a defensible position that much useful information was still available in fossil deposits and that we can make conclusions on rational bases about the biological interactions of past organisms.<sup>2</sup>

<sup>1</sup>As Rudwick (1964b, p. 33) has remarked, "The range of our functional inferences about fossils is limited not by the range of adaptations . . . possessed by [living] organisms . . . , but by the range of our understanding of . . . engineering."

<sup>2</sup>One of the early truly optimistic studies was that of Zangerl and Richardson (1963) who described "bitten off tail fins," "gastric residue spatter," "gastric residue pellets," and "chewed remains," etc. Such phenomena might have been dismissed as being the result of diagenesis by earlier investigators, and, as a result, no interpretation would have been attempted.

Nonetheless, naive hope is not enough; models must be tested objectively. In this paper, I have suggested reclassification of models as evolutionary and nonevolutionary, and specific recognition of the need to make function and *change* in function directly related to mathematical models of morphology because I believe this will generate operational strategies for making new models. This will lead to new insights. But we must develop tests of our models; I believe the tests will come from the use of the paradigm approach of Rudwick. Its weakness is in generating ideas about function, but once these ideas are generated, it should serve very well as a test of the quality of the idea.

### ACKNOWLEDGMENTS

I have gradually come to a dim understanding of models in paleontology by interaction with a great many people. Sometimes this interaction has been mainly by reading their papers. Some of the most important people have been Herbert Barghusen, Werner Baur, John Bolt, Dennis Bramble, Robert Bryant, Stephen Gould, James Hopson, Everett Olson, Jeffrey Osborn, Charles Oxnard, David Raup, and Rainer Zangerl.

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