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Historical Biology and the Problem of Design

GEORGE V. LAUDER

Department of Anatomy, The University of Chicago, 1025 *E.* 57*th Street, Chicago, Illinois* 60637, *U.S.A.*

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Organisms are historical entities in that their past history plays an important role in shaping the properties they exhibit today. While this fact is widely acknowledged, little attempt has been made to develop a testable approach to the analysis of the historical factor in evolutionary morphology. The analysis of extrinsic environmental factors may reveal the limits imposed by the environment on biological design, but the intrinsic phylogenetic component of design may severely constrain the directions of structural modification that can occur. The importance of history can be assessed with (1) a phylogenetic hypothesis of genealogical relationship, (2) the use of emergent structural or functional attributes with general properties, and (3) the testing of historical hypotheses by the comparison of general properties between monophyletic lineages. The synthesis of a structural/phylogenetic approach to historical morphology with the analysis of extrinsic limits to form may provide the level of resolution needed to generate testable mechanistic hypotheses regarding the distribution of extant organismal forms in the hyperspace of possible morphologies.

1. Introduction

The problem of biological design is one of the oldest topics in biology. It has been clear, at least from the time of Aristotle, that organisms possess a "unity of plan" or underlying commonality of structure, and that the function of biological features bears some relationship to their form. E. S. Russell in his classic book (1916) has interpreted the history of morphology as an attempt to understand the relationship between form and function.

The concepts of commonality of structure and functional design play prominent roles in modern evolutionary morphology. Yet we seem to have made little progress toward a synthetic approach to biological structure, or towards a "science of form" (Gould, 1971). In this paper I will recast the dichotomy between form and function into a somewhat different framework, that of historical vs. equilibrium analysis, suggest how a synthesis might be achieved (and why it is necessary), and outline a set of

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outstanding problems that must be examined if a general theory about the transformation of biological design is to be developed. Two related general questions can be considered to underly this discussion. (1) Why does the range of extant phenotypes, when mapped onto a theoretical "morphospace," fill so little of it (Raup, 1966; McGhee, 1980)? (2) Is it possible to produce testable explanations for why certain morphologies (such as vertebrates with wheeled appendages) have not evolved?

To approach these questions, two classes of morphological analysis may be distinguished: equilibrium and historical. Equilibrium analysis (Lewontin, 1969; Lauder, 1981) is by far the dominant approach to the analysis of biological design in the fields of functional morphology, ecology, and population genetics. Organisms are considered to be in equilibrium with the environment and present-day environmental correlates of structure are sought in an attempt to explain morphology (e.g. Wiens & Rotenberry, 1980). An equilibrium approach may also have a time axis in that changes in the environment through time are related to the morphology of those organisms inhabiting the environments, and structural change is described as an adaptive modification to changing external conditions (e.g. Valentine, 1973, 1975).

Historical analysis is concerned with the evolutionary transformation of intrinsic organizational features (Lauder, 1981) and not with the relationship between form and the (extrinsic) environment. A crucial element in analyzing structural transformation is the phylogenetic reconstruction of nested sets of homologies which indicate the historical sequence in which new morphological features were acquired in a lineage (Eldredge & Cracraft, 1980). A phylogenetic approach to the analysis of design reveals the historical pattern by which any particular combination of structural features was constructed. (In this paper I define *design* as the organization of biological structure in relation to an hypothesized function. *Adaptation* (following Lewontin, 1978; Cracraft, 1981) is restricted to features that have arisen by means of natural selection.)

If an understanding is ever to be achieved of the pathways by which form has diversified to fill the occupied phenotype space, or of the mechanics underlying these evolutionary patterns, then a synthesis of both extrinsic environmental limits to form and intrinsic structural and functional properties must be achieved within a phylogenetic (historical) framework.

2. Extrinsic Determinants of Design

There is little doubt that the environment poses at least general constraints on the design of organisms (Lewontin, 1978) and the fields of

biomechanics and functional morphology have been largely devoted to analyzing the relationship between biological structure and environmental forces experienced by organisms (e.g. Gans, 1974; Wainwright, 1980). For the most part, this work falls under the equilibrium method defined above. Two main contributions have emerged from this approach: (1) a reasonably precise characterization of the structural principles and systems necessary to meet particular functional situations, and (2) the delimitation of boundary conditions to biological design. As an example of a structural property found widely in biological systems, consider helically-wound collagen fibers. In many organisms in which resistance by the skin or body surface to radial expansion is necessary, while retaining body flexibility and/or the ability to elongate, helically-wound fibers occur in the body surface (Wainwright *et al.*, 1975). A crossed helix is formed with fibers at a helical angle of from 30° to 70°. This arrangement permits lateral bending and elongation but resists radial expansion and buckling due to internal pressure changes. The diversity of organisms in which this system has been found (sharks, teleost fishes, squid, earthworms, nematodes, plants) attests to its generality as a constructional principle, and Wainwright *et al.* (1975) propose this concept as one of their six design principles for biological systems. As a second example, Webb (1978) has examined the functional tradeoffs between rapid accelerations and steady swimming in teleost fishes. The theoretical optima for each locomotor mode is definable by a mechanical analysis. Rapid accelerations are best achieved (in part) by increasing depth along a flexible body, while steady swimming efficiency increases with body stiffness, caudal fin aspect ratio, and reduced total caudal fin area. Webb (1978) was able to demonstrate experimentally that fishes of different body shape have very similar fast acceleration performances due to the tradeoffs in different species between lateral body profile and the mass of body musculature. This type of analysis is of interest because of the relatively well-defined mechanical theory underlying the interpretation of design, and the consequent utility of these analyses in making precise comparative predictions about the relative performance of unstudied species.

Boundary conditions on the range of possible morphologies may also be revealed by a biomechanical analysis. McGhee (1980) has shown that much of the "morphospace" available to brachiopods is unfilled because of geometrical constraints on shell growth. McGhee defined the theoretical morphospace available to brachiopod shells by elaborating a geometrical model of shell growth and ascribed the limited distribution of actual shapes within the theoretical space to two factors: the fact that the two valves of brachiopods must articulate and thus cannot overlap, and small size imposed by the ratio between surface area and internal volume.

While these examples illustrate the utility of an extrinsic explanatory framework for understanding the relationship between structure and function and limits to design, there are important restrictions on the explanatory power of this approach. What of the unoccupied phenotype space that is not prohibited by mechanical factors? How do we explain the absence of certain morphologies when there appears to be no mechanical, functional, or structural reason why such an organism might not have existed? Finally, how is an observed lack of correlation between the structures possessed by organisms and environmental factors to be interpreted? If an organism predicted on the basis of a mechanical argument to have a helically-wound fiber system does not, how can this discrepancy be explained? The traditional escape is to interpret the absence of predicted features, the lack of a predicted structure–environment correlation, or an unfilled portion of the morphospace in terms of the original equilibrium premise. An additional unanalyzed component of the system has prevented the close concordance of structure and environment; or in the case of the morphospace, the requisite historical pattern of environmental change has not been present to generate the selective forces necessary to produce the new morphologies (Raup & Stanley, 1971). But these explanations beg the historical question: might there not be intrinsic, phylogenetic constraints on form that canalize or facilitate certain evolutionary transformations? In order to evaluate this possibility, we need a testable program for historical research.

3. Historical Morphology: Intrinsic Determinants of Design

The study of evolutionary morphology has been dominated by the search for explanations of unique structural or functional aspects of design. The difficulty with this approach is that while a reasonable hypothesis may be formulated for why any particular unique structural feature has evolved, it is difficult if not impossible to test the hypothesis. The foundation of a scientific approach to historical events lies in testing by comparison. Hypotheses of structure–function relationship in any group of organisms can be tested by finding similar structures in another group that has acquired them independently, and determining if the predicted functional correlate is present. If not, then the hypothesis is refuted. But this procedure is impossible if the structures or functions selected for analysis are unique.

The most clear-cut cases in evolutionary biology of attempts to explain unique features involve discussions of the causal basis for the origin and "adaptive" radiation of major lineages. The usual procedure is to identify some morphological or physiological feature that seems to play an important role in the biology of a group, and then to maintain that this feature is

causally related to both the morphological change and subsequent speciation pattern of the taxon. One example is the analysis of the adaptive radiation of multicellular organisms provided by Stebbins (1973). Stebbins identified the "most significant determining characteristics" of adaptive radiation such as a rigid cell wall and the presence of cellular polarization. These structural properties are then invoked as being causally related to the adaptive radiation of multicellular organisms. A similar approach to other taxa may be found in Liem (1973), Stanley (1968), and Lewis (1972). The difficulty with these discussions is the untestable nature of the premise: that a particular structural feature can be identified as having caused adaptive radiation. How would one choose between two different structural attributes of a taxon, each cited by different authorities as being *the* feature that caused adaptive radiation?

An alternative approach to the historical analysis of design is possible, however, and I suggest three principles for a scientific (testable) approach to the evolutionary transformation of structure. (1) Explanation must be for general properties of a structure or functional complex, and not for unique features. (2) A phylogenetic hypothesis of relationship that depicts the nested hierarchy of structural features in the historical sequence they were acquired (a cladogram) is fundamental to the analysis of historical patterns. (3) Historical hypotheses are tested by the examination of related monophyletic lineages. Hypotheses about classes of evolutionary events thus are tested by repeated attempts at refutation via the phylogenetic history of individual lineages.

As an example of how these concepts might be applied, consider the interesting hypothesis of Vermeij (1973*a*) that

> "*the potential versatility of a given taxon or body plan is determined by the number and range of independent parameters controlling form.*"

This hypothesis has stimulated considerable interest and yet has not been explicitly tested, although Vermeij (1973*b*) has listed several cases which seem to support it. In order to test Vermeij's explanation for morphological diversity, it is necessary to realize that the hypothesis is fundamentally historical in nature. That is, a specific evolutionary pattern (an increase in structural versatility) is predicted to occur as a consequence of a change in structural organization. This is exactly the general type of hypothesis that can be tested with respect to nested sets of structural features in a class of monophyletic clades. As increasingly restricted sets of taxa (cladistically more derived forms) are considered, an increase in structural diversity should occur for those clades which primitively possess an increased number

of parameters controlling form. To state Vermeij's hypothesis explicitly: primitive members of morphologically diverse monophyletic lineages possess an increased number of independent parameters controlling form compared to closely related (sister) lineages whose primitive members lack the increased parameters. The hypothesis is refuted if these related lineages show similar patterns of structural diversification to the taxa with a primitively greater number of morphogenetic pathways. When stated in this way, it is clear that a test of this hypothesis is possible by the repeated examination of sister lineages (lineages more closely related to each other than to any other lineage) which differ in the number of parameters controlling form. If the initial relationship is corroborated, then there should be a positive correlation between the number of controlling parameters and the degree of body-plan versatility as expressed in morphological diversity. Ideally, such tests should span a wide range of diverse taxa differing in general bauplan to determine the generality of the phenomenon.

The basic theme underlying this approach to historical morphology is that general aspects of structural organization such as the number of functional linkage systems, the number of epigenetic pathways controlling form, or complexity of organization, canalize historical change in morphology and restrict (or, possibly, increase) the potential structural and functional diversity of descendent taxa. Thus, when a potential morphospace is found to be partially unoccupied, the explanation may not lie with a lack of appropriate selection pressures or with mechanical reasons for why morphologies in the unoccupied area would not work, but rather in the phylogenetic constraints on possibilities for morphological change. This possibility is usually acknowledged (e.g. Rensch, 1959; Riedl, 1978; Seilacher, 1973), but a testable research program in historical morphology has not yet been applied to the distribution of structure in the theoretical phenotype space.

An interesting consequence of a phylogenetic/historical approach to biological design is the possibility of elucidating general laws of structural change in organisms. To the extent that a repeated examination of the historical consequences of intrinsic organizational properties of organisms in many monophyletic lineages reveals substantial regularity, then a law-like deterministic view of structural evolution is corroborated. This result would be particularly important in the light of recent stochastic simulations of morphological evolution (Raup & Gould, 1974; Raup, 1977; Gould *et al.*, 1977; see Schopf, 1979). These investigations have shown that simple stochastic models of morphological evolution in randomly generated clades produces patterns of clade organization, extinction, and morphology that are extremely similar to those observed in biological systems. The con-

sequence of these results for deterministic explanations of morphological evolution is severe: if observed patterns in nature cannot be convincingly distinguished from stochastically generated ones, then the dominant explanatory framework in evolutionary biology today would appear to have limited utility. Despite this challenge, there does not appear to have been a convincing reply. Evolutionary morphologists have continued to explain structural patterns within a deterministic framework.

But congruent patterns of structural transformation in unrelated monophyletic lineages provide the possibility of testing the importance of stochastic vs. deterministic factors. The repeated similarity of evolutionary structural modification in unrelated groups corroborates intrinsic phylogenetic constraints as important determinants of biological design as it refutes both stochastic and environmental (extrinsic) deterministic explanations.

The analogy between this approach to historical patterns of form and the emerging science of historical biogeography is very close. Historical biogeography (Nelson, 1969; Nelson & Platnick, 1981) is concerned with the distribution of organisms in space as related to both historical events of earth geography and the phylogenetic (genealogical) relationships of the earth's biota. Congruence between the pattern of environmental fragmentation in space and time (vicariance) with the pattern of genealogical branching (Rosen, 1978) supports a causal connection between genealogical diversification and environmental change. Thus, to the extent that genealogical splitting is congruent with patterns of environmental fragmentation, then unique dispersalist scenarios for how each lineage came to occupy its present range are rendered unparsimonious. A stochastic explanation of biotic distribution is also rejected with increasing confidence with higher congruence between geology and the phylogenetic histories of unrelated lineages. Invoking dispersal to explain the distribution of each species while failing to see if a general pattern that is congruent with geological and environmental history is present, is comparable to adducing unique selection pressures and historical sequences of environmental change to explain the forms of each evolutionary lineage. Such interpretations are rendered unparsimonious if general historical patterns common to taxa with widely differing bauplans are found.

4. Conclusions and Prospectus

The problem of biological design is fundamentally a historical one. Without an understanding of the past history of organisms, there is little hope of effectively analyzing the relationship between form and function

and the interaction between organisms and the environment. The past constrains and determines future directions of structural change and organisms carry with them, through the retention of primitive characters, a record of their past history.

Yet it is precisely the historical element that has been missing from explanations for biological design. To be sure, the existence of historical constraints is widely mentioned, but there have been few attempts to directly grapple with the testing of historical hypotheses, or the influence of intrinsic factors on the design of biological systems. (Nowhere is the lack of a historical framework more evident than in D'Arcy Thompson's, 1942, *On Growth and Form*, and the widespread influence of his approach to design is evidence of the minor role historical factors have played in the explication of organic form.) The failure to consider adequately this class of explanations is particularly apparent in two areas of research: (1) optimal modelling of structure, ecology, or behavior, and (2) the "deductive" approach to morphology (Dullemeijer, 1974; Gutmann, Vogel & Zorn, 1978).

Optimal models explicitly neglect the historical component of biological systems and treat the organism–environment relationship as though the system were in equilibrium, evidenced most clearly by the widespread use of the *ceteris paribus* assumption (Lewontin, 1978). The "constraints" inherent in optimal models reflect the initial assumptions about the equilibrium situation, and not historical factors or intrinsic phylogenetic limits to optimality. In so doing, these models reveal little about the potential transformation of design, and the conclusions tend to be a reflection of the initial factors selected for analysis (Lewontin, 1978).

"Deductive" models for the evolution of design (e.g. Gutmann, 1977; Gutmann *et al.*, 1978) utilize an *a priori* functional model or mechanical analysis to predict a morphological transition between different structural types. The method of this approach (see Gutmann, 1977) is to (1) hypothesize selective factors that have governed morphological change, (2) propose a gradual series of "adaptive" structural and functional modifications that will transform one bauplan into another (annelid into brachiopod, for example), and (3) claim that this morphological series of "adaptive" changes reflects the actual process by which evolutionary transformation took place. The basis of this approach is the assumption that selective forces can be identified in the historical record and that an alternative model, equally consistent with simple structural and mechanical principles, will not provide as convincing a demonstration of structural transformation. Without a phylogenetic hypothesis independent of the hypothesized transformation series of designs, the model cannot be tested. Thus, this approach is circular

because the test of the proposed biomechanical model requires the very phylogeny the model was used to construct.

With this background of what I perceive to be several of the methodological problems and logical difficulties with some current approaches to the analysis of biological design, three inter-related issues may be defined that may provide a focus for future research.

(1) Are there historical laws of morphologic change? To the extent that clades of differing bauplan exhibit historical congruence in basic pathways of structural and functional transformation attributable to a common general organizational property (such as complexity), then stochastic or individual selectionist explanations become of less generality. Simpson (1964, p. 128) maintained that

> "*the search for historical laws is . . . mistaken in principle, . . . historical events are unique, usually to a high degree, and hence cannot embody laws defined as recurrent repeatable relationships.*"

This characterization of history is a recipe for the continued search for individual explanations and untestable historical scenarios as have characterized biogeography for much of this century. Historical events are not unique, organisms exhibit a commonality of structure as a result of conservative epigenetic pathways (Alberch, 1980), and thus general properties of biological design are available for analyzing the occurrence of repeated transformations of structure and function.

(2) What is the null hypothesis for extrinsic explanations of design? One of the values of stochastic modelling of morphological change (Raup, 1977) is that a null hypothesis is provided from which deviations in structure can be determined. In a similar fashion, general patterns of structural transformation in lineages that are shown to be the consequence of intrinsic organizational properties, become the null hypothesis for extrinsic environmental explanations for structure. These explanations must be assessed against the "expected" properties of design that result from intrinsic phylogenetic determinants of form. The demonstration that intrinsic properties have played an important role in governing the transformation of design does not rule out the possibility that selection and changing extrinsic conditions ultimately drive change. However, the historical record provides only limited access to extrinsic data, while it does provide the opportunity of examining intrinsic factors.

Finally, (3) is it possible to test explanations for why certain designs have *not* evolved? To some extent, yes. Overlapping valves in brachiopods appear to be a prohibited morphology for simple mechanical reasons.

Similarly, coiled cephalopods do not look like submarines (despite the close similarity in functional requirements) because of constraints associated with accretionary growth of shells (Raup, 1972). On the other hand, a large portion of the unoccupied morphospace is not prohibited by mechanical restraints, and I can conceive of only three possible explanations for this: chance, environmental determinism, or intrinsic constraints. Intrinsic explanations may reveal that canalization of the direction of morphological change in evolution is severe and that chance plays a relatively limited role. Invoking the lack of proper selection pressures and environmental change to produce morphologies in the unoccupied morphospace produces an untestable explanation, as our ability to analyze these factors even in present-day environments is very restricted.

If intrinsic constraints are revealed to be very course and only to provide broad limits to the potential pathways of structural change, then chance factors may have played an important role in generating the range of extant phenotypes.

The key to discovering the limits to deterministic explanation in the historical record will be the extent to which general historical pathways in the transformation of biological design are revealed by a phylogenetic analysis of structural and functional patterns.

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