Form and function: structural analysis in evolutionary morphology

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Abstract.—A theoretical approach to the analysis of historical factors (Raup 1972) in evolutionary morphology is presented which addresses transformational hypotheses about structural systems. This (structural) approach to testing historical hypotheses about phylogenetic constraints on form and function and structural and functional versatility involves (1) the reconstruction of nested sets of structural features in monophyletic taxa, (2) the use of general or emergent organizational properties of structural and functional systems (as opposed to uniquely derived morphological features), and (3) the comparative examination of the consequences for structural and functional diversity of these general features in related monophyletic taxa.

Three examples of emergent organizational properties are considered: structural complexity, repetition of parts, and the decoupling of primitively constrained systems. Two classes of hypotheses about the evolution of design are proposed. Transformational hypotheses concern historical pathways of change in form as a consequence of general organizational features which are primitive for a lineage. Relational hypotheses involve correlations between structure-function networks primitive for a clade and morphological diversity both between and within terminal taxa. To the extent that transformational and relational hypotheses about form are corroborated, they provide evidence of underlying regularity in the transformation of organic design that may be a consequence of the hierarchical organization of structural and functional patterns in organisms.

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Introduction

The diversity of structure exhibited by life on earth is a recurrent theme in natural history, and it is the task of the morphologist to analyze and order this diversity. Darwin (1859, p. 434) considered morphology to be the "very soul" of natural history and cited the elucidation of "unity of type" as the foremost contribution of morphologists to the study of life: "What can be more curious than that the hand of a man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the wing of the bat, should all be constructed on the same pattern and should include the same bones, in the same relative positions?" Indeed, the theme of unity of plan among organisms was perhaps the cardinal principle of eighteenth and nineteenth century anatomy and received its most complete expression in the work of Cuvier, Geoffroy, and Owen.

The concept of unity of type, and its phylogenetic implication, falls under what has been called the "historical factor" in morphologic analysis (Raup 1972). The constructional approach to morphology (Seilacher 1970, 1979; Thomas 1979) has served to define the three main factors which must be understood in an attempt to explain form: fabricational, functional, and historical. Of these, only the first two have received much attention (see Gans 1960, 1974; Hickman 1980; Seilacher 1973; Rudwick 1964, 1968). Historical factors are usually analyzed only in a very general way. Accretionary growth may appear to constrain the range of possible molluscan forms (McGhee 1980; Raup 1966, 1972) but how can such a hypothesis be tested? The increasing emphasis on the themes of limits to morphologic change, historical constraints, and ontogenetic constraints on possible structural patterns (e.g., Alberch 1980; Fisher 1981; Gans 1966, 1969; Gould 1980a,b; Gould and Lewontin 1979; Raup 1972; Riedl 1978; Thomas 1976) has not focused on an important question: how can hypotheses of constraint (or

the converse, versatility) be tested in evolutionary morphology?

In this paper I present one approach to testing hypotheses of structural and functional constraint and versatility. Four elements are basic to this analysis: (1) the recognition that hypotheses of morphological constraint and versatility are *historical* hypotheses and must be approached within a historical framework, (2) the importance of hierarchical organization for understanding patterns of structural and functional change through time, (3) the distinction between intrinsic explanations for form and extrinsic environmental explanations, and (4) the crucial role of corroborated phylogenetic hypotheses in permitting tests of historical hypotheses.

Morphologic Analysis

For the purpose of discussing the historical approach to form and function, I distinguish two classes of analyses about structural systems: *equilibrium* analyses (see Lewontin 1969), and *transformational* analyses. Equilibrium analyses focus on the relationship between the organism and the environment, and may be either (1) an examination of present-day structure environment correlations (e.g., Wiens and Rotenberry 1980) or (2) a consideration of historical patterns of covariation between environment and morphology. Explanations for structural patterns are *extrinsic* in that factors external to the organism (temperature, resource availability, competition) are held to be the primary determinants of structural change. Transformational hypotheses form a class of questions which have not received much attention from morphologists, and they will be the focus of most of this paper. Historical patterns of structural change are analyzed as a consequence of *intrinsic* organizational properties of structural systems (Whyte 1965; see below p. 434). This class of hypotheses is not the same as the "transformational approach" discussed by Eldredge (1979a) which utilizes an extrinsic explanatory framework. (I use the term structural to emphasize (1) the central role of nested sets of structural features (cladograms) in the study of form and function, (2) the intrinsic nature of explanations for historical patterns, and (3) the focus on structural transformation (Piaget 1970).

This is in contrast to extrinsic explanations for structural change which dominate equilibrium analyses.)

Three aspects of equilibrium analysis relate directly to the study of historical hypotheses in morphology: (1) the inference of historical selective forces to explain morphological change, (2) the use of morphological series as a reflection of the actual historical pattern of structural change, and (3) the explanation of adaptive radiations in terms of key innovations.

Elucidating the selective forces that have produced structures is a widely claimed goal of evolutionary morphology (e.g., Bock 1960, 1980; Bowman 1961; Gans 1974; Lombard and Wake 1976, 1977; Simpson 1953; Williams 1966; see Cracraft 1981). Bock (1980) claimed that it is necessary to know the exact selection force because adaptation is judged with respect to the selection force, and "the selection force must be known before a feature can be considered to be an adaptation." He suggested that a detailed knowledge of the environment is necessary to specify the selective forces by which adaptations are judged. Correlations between hypothesized environmental (selective) factors and structural features of the organism can then be examined. Historical hypotheses of relationship (phylogenies) may have important consequences for the analysis of structure-environment correlations as illustrated in Fig. 1 (phylogenetic analysis is discussed in more detail below). Interpretation of the distributional pattern of taxa in the structure-environment space (Fig. 1A) depends critically on the phylogenetic hypothesis. Given hypothesis 1 (Fig. 1B), that taxa E and F are most closely related to each other, their proximity in the structure-environment space may only reflect common ancestry. The structural features shared by these taxa may reflect the environment of the common ancestor of E and F, and not the environments presently inhabited (environment four in Fig. 1A). If hypothesis 2 (Fig. 1B) is the pattern of phylogenetic relationship, then taxa E and F are only distantly related and their proximity in the structure-environment space calls for additional explanation. A phylogenetic hypothesis allows the reconstruction of the historical sequence of structural change through time and thus serves as a null hypothesis from which significant deviations may be
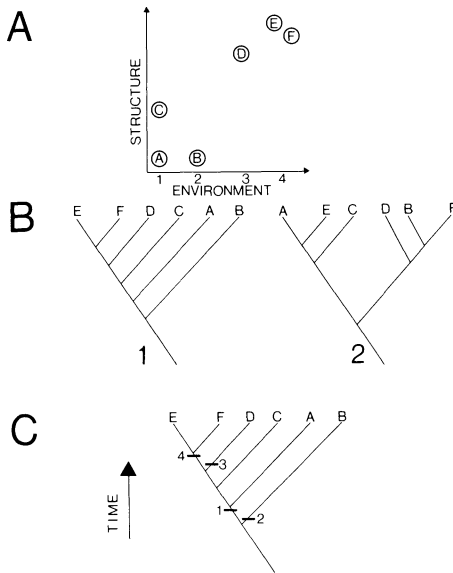
FIGURE 1. A: Bivariate plot of six taxa (A through F) in the structure-environment space. These taxa cluster into four distinct environments. B: two alternative historical hypotheses of relationship for taxa A through F. Interpretation of the clustering of taxa in the structure-environment space depends critically on the historical hypothesis of genealogy. In hypothesis 1 taxa E and F are each other's closest relatives and the commonality of position in (A) may merely reflect the retention of primitive (ancestral) character states, perhaps evolved in a different environment. In hypothesis 2 taxa which are closely related are widely separated in this particular space. C: prediction of the temporal sequence of environmental change if the hypothesis of correlation in (A) and hypothesis 1 in (B) are correct. Given a hypothesized structure-environment correlation and a corroborated hypothesis of relationship, predictions of the historical sequence of change in environments can be made.

detected and indicates the appropriate level of generality at which structure-environment correlations must be explained. That is, both convergent maps in the structure-environment space (e.g., taxa F and E, cladogram 2, Fig. 1) and congruence between ancestral characters and the environment emerge from a consideration of the genealogical sequence of structural change.

A phylogeny may also allow a very general test of the structure-environment correlation by allowing a prediction of the actual temporal sequence of environmental change (Fig. 1C). Congruence of the pattern of historical change in environment with the pattern predicted from phylogeny would corroborate a proposed relationship between form and environment. The

methods that have been used in historical analyses of adaptation appear to be very similar to those used in contemporary equilibrium analyses. Historical patterns of structural change are viewed as explicable on the basis of correlations between structure and environment within the limits imposed by general phylogenetic constraints. Historical equilibrium hypotheses are only testable in so far as environmental changes through time can be precisely determined, a requirement that may be difficult to meet in many paleobiological investigations.

A genealogical hypothesis of relationship has one other important implication for the analysis of form and the inference of historical causes of change in structure. "Morphological series" are often constructed in an attempt to understand the historical process of structural change in a lineage (Bock 1970; Gutmann 1977; Gutmann and Peters 1973; Gutmann et al. 1978; Valentine 1975). Taxa are arranged in a series, usually corresponding to order of appearance in the fossil record or notions about the direction of character transformation (from short teeth to long teeth, for example, or from the simple to the complex) (Fig. 2A). Interpretations of historical selective factors and morphological and functional trends in character complexes are then based on this constructed series.

Bock (1979) discussed the conceptual basis for this type of analysis and an example is provided in his (1970) study of the Hawaiian honeycreepers. Bock's methodology is to formulate a "pseudophylogeny" (Bock 1979, p. 57), interpret the structural changes suggested by the morphological series as adaptive, and then transpose the series into a "phylogenetic" one. The morphological series of honeycreepers (Bock 1970, Figs. 1, 5, 6) which shows relatively minor differences between closely paired taxa, is then taken as evidence that a gradualistic (microevolutionary) process is sufficient to explain the observed morphological differentiation.

The morphological series, however, may bear no relation to the historical sequence of structural change, which can best be approximated by the construction of a phylogeny explicitly based on shared derived features (Fig. 2B; Hennig 1966). The fallacies of the morphological series, then, are (1) the non-historical nature of the constructed sequence which is an artificial se-

FIGURE 2. Diagrams illustrating the difference between two approaches to reconstructing morphological transformations. A: A–F is constructed on phenetic comparisons, stratigraphic sequence, or the assumption that change has proceeded from the simple to the complex. B: genealogy. The cladogram in B illustrates the probable lack of congruence between a morphological series and the historical pattern of change in characters inferred from an hierarchical arrangement of shared derived features. Hypotheses of pattern transformation will differ depending on whether morphological series or a nested set of shared derived features are used as a basis for interpretation. That is, the historical sequence of structural transformation as inferred from a morphological series (A) will differ from the sequence constructed from the cladogram (B) using inferred ancestral character states (from the most parsimonious arrangement of characters 1 to 9) at the branching points. This point is discussed from a slightly different point of view in Vrba (1980, p. 69). Investigations using morphological series as a basis for evolutionary analyses include Bock (1970), Gutmann (1977), Gutmann et al. (1978) and Valentine (1975).

Stanley (1968) attributed the success of infaunal bivalves to a specific morphological feature: "the development of siphons was without question the key feature in the adaptive divergence of infaunal bivalves during the Mesozoic and Cenozoic," and "once siphons appeared . . . it would seem that the radiation was inevitable." This method of explaining the evolutionary success of lineages assumes a close link between the possession of a particular morphological feature and speciation rate, a relationship for which there is little evidence. Cichlid fishes and bivalves are thought to be so speciose because they possess a structural innovation that enables individuals in these lineages to outcompete members of other taxa that lack the morphological innovation. The method by which "key" adaptations are recognized has not been made explicit but two criteria apparently need to be satisfied: the occurrence of a speciose taxon to serve as the basis for analysis, and the presence of a feature shared by most members of the taxon that performs a major function apparently related to the pattern of diversification.

The Structural Analysis of Functional Design

The goals of a historical approach to structural transformation are (1) to generate testable historical hypotheses about the way in which form changes and (2) to discover general regularities in the transformation of organic design. This research program focuses on the limits to change imposed by structural, functional, and epigenetic interactions within the organism and on a search for *generalized historical pathways (tracks) of structural change.* In this respect, a structural approach embodies the concept of a lawlike history in which patterns of change in form follow general pathways as a consequence of structural and functional interactions within organisms (examples are given below; also see the discussion of Svertsov in Adams [1980] for a similar concept in Russian morphology). Historical analysis in morphology becomes the search for general patterns of structural transformation which may apply to a wide variety of organisms. Simpson (1964), Berlin (1979), and Popper (1964) have argued the opposite view: that the search for general historical patterns (laws) is futile because of the uniqueness of historical events.

quence of equilibrium points, and (2) the inference of historical processes from this equilibrium series (selective forces, microevolutionary processes, etc.). Hypotheses regarding historical processes require at the very least a historical data base.

The most common explanation for the adaptive radiation of a clade is that the early members possessed a "key innovation" (Liem 1973) or an evolutionary novelty (Mayr 1960) that gave them a competitive advantage over related individuals (see Stanley 1975; Stanley and Newman 1980; Stebbins 1973, 1974). For example,

Key questions in the search for a nomothetic theory of biological organization are: what are the consequences of certain aspects of design (e.g., metamerism, mechanical complexity) for possible directions of structural change? Does the possession of certain features or complexes of features canalize change in form? And, how do interactions of structural, functional, and epigenetic hierarchies affect potential transformations of design? One consequence of having a theory of structural organization would be the ability to erect null hypotheses of structural change in an analogous fashion to the role of allometry in interpreting changes in size and shape: a standard can be established from which significant deviations in structure can be determined. In a highly constrained system in which the structural elements are tightly coupled by both functional and morphogenetic interactions, certain types of structural modification might be predicted to occur given a certain initial morphology, regardless of the nature of the extrinsic factors. These patterns of change do not require deterministic explanations and are largely due to the network of constraints within the initial system.

This approach complements equilibrium analyses of form by using a different explanatory framework (intrinsic) and by concentrating on a distinct level of morphological novelty. Equilibrium analyses attempt an explanation of specific (unique) features in relation to extrinsic environmental factors whereas a structural approach to the transformation of form and function examines general (emergent) organizational features. Clearly, both approaches are necessary for the full explanation of form, but equilibrium analyses are limited in explanatory power for interpreting historical changes.

At least two assumptions underlie a structuralist view of morphology: first, that organisms possess features that may be ordered into nested sets (a cladogram), and secondly, that this nested pattern is a reflection of a historical process of descent with modification (although no assumption is made about the nature of the process that produced the modification). The unit of structural analysis is the monophyletic group.

Phylogeny.—Fundamental to historical analysis is a genealogical hypothesis which allows nested sets of structural features to be used as a basis for interpretations of change in form. Methods of constructing phylogenies have been described in a number of recent papers, as have the pitfalls of using a non-genealogical basis for historical interpretation (Cracraft 1974; Eldredge 1979b; Eldredge and Cracraft 1980; Farris 1977; Nelson 1972; Patterson 1977; Patterson and Rosen 1977; Schaeffer, Hecht, and Eldredge 1972; Wiley 1976). In general, similarities between taxa are discovered and these similarities are ordered into the most parsimonious nested set. This arrangement may be modified by the addition of ontogenetic information on character generality (Nelson 1978) and by the inclusion of outgroups in the parsimony analysis. Hypotheses of character homology are derived from the cladogram and are considered to be synapomorphies. Convergences are thus recognizable only a posteriori as characters which are not congruent with the preferred hypothesis (Gaffney 1979). It is only by having a corroborated hypothesis of phylogeny that testable generalizations about historical changes of form will emerge.

Hierarchical networks within the organism.— After phylogeny, a second key element for the analysis of historical patterns consists of determining structural, functional, and epigenetic interactions within the organism. There are extensive interactions both developmentally, whereby a change in one feature may influence the size and shape of a large number of adjacent features, and functionally, whereby conflicting demands imposed on a morphological system constrain changes that can occur in any individual element (Dullemeijer 1974; Wimsatt 1974). The view that an organism is composed of an interacting network of constraints (Liem 1980; Pattee 1970; Simon 1962; Weiss 1970; Whyte 1965; Whyte et al. 1969) is of key importance in understanding patterns of structural diversity (or uniformity) in nature. However, the determination of these constraints interacting among elements of the structural and functional network is the most difficult and time-consuming aspect of the analysis of morphological patterns.

The structural network within the organism is defined as the spatial relationships of the distinct anatomical elements and the interconnections between these structural elements. The

functional network is composed of the set of functional demands imposed by structural elements on each other as a consequence of movement or morphogenesis. The interaction of structural and functional networks within the organism produces an observable hierarchy of structure-function relationships (see Bock and von Wahlert 1967; Dullemeijer 1958, 1968). This hierarchy results in constraints and limitations on change which can occur in structural and functional elements (Jacob 1977; Walker 1979). The possible pathways for change in design are thus limited by the nature of interacting constraints within the hierarchy of structure-function relationships. These restraints on possible directions of change appear to arise as a consequence of hierarchical organization (of structure and function) in that the existence of multiple levels and the nature of the connections between levels places limits on change of the entire system (Pattee 1970, 1972; Salthe 1975; Weiss 1971).

Four complementary methods may be used to analyze a network of structural and functional constraints. (1) Comparative morphological and functional analysis reveals the range of variation of the entire structural pattern and of the component parts. The experimental analysis of form (functional morphology) allows the structural and functional networks within the organism to be determined. Functional analysis is crucial to understanding the network of interacting constraints in organisms. (2) Experimental modification of the structural system and a comparison of the modified network with the undisturbed network contributes to understanding the functional interactions between elements in the pattern. (3) A model of the network may be constructed to predict the consequences of altering either supporting or connecting components of the network. Finally (4), ontogenetic analyses may give fundamental insights into developmental connections between elements in the structural pattern (Alberch et al. 1979; Lovtrup 1977). The study of normal development, experimentally induced perturbations, and, especially, naturally occurring deviations (see Zuckerkandl 1976) contributes significantly to the clarification of constraints on form.

These methods allow the construction of a corroborated model of structural and functional interactions within the organism. In order to generate testable historical hypotheses about change in design, the network of structural and functional interactions must be determined for three or more taxa and then examined in a phylogenetic context. Using a phylogeny as a basis, the historical sequence of change in the constraints on the pattern can be determined. This procedure is outlined in Fig. 3. Nested sets of similarities (Fig. 3A) are used to construct a cladogram, and the most parsimonious arrangement of the similarities is used to indicate convergent and homologous features (Fig. 3B: character b). The cladogram indicates the consequences of the inferred pattern of genealogical relationship for structural and functional changes in a clade and allows these structural and functional attributes of the terminal taxa to be examined in a historical context. Ancestral states and the historical sequence of structural or functional transformation can also be reconstructed from the phylogeny.

Using the historical pattern of structural change in a monophyletic lineage as a basis, the consequences of structure—function hierarchies for change in design can be examined. That is, the effect of emergent organizational properties of structural and functional networks (Z in Fig. 3C) on the subsequent history of morphological transformation can be determined. Isolating a particular element, functional relationship, or larger component of the structure-function hierarchy which is inferred to be primitive for a lineage allows the subsequent course of change in form to be used to test hypotheses of constraint, versatility, or canalization. I distinguish between two types of hypotheses. *Transformational hypotheses* (H_T, Fig. 3C) concern the relationship of historical tracks of change in form to primitive elements of the structure-function hierarchy for the lineage. *Relational hypotheses* (H_R, Fig. 3C) involve correlations between aspects of the primitive network (Z in Fig. 3C) and morphological diversity (both within and between terminal taxa). Transformational hypotheses thus concern historical *pathways* of change in design while relational hypotheses concern historical *consequences*. These hypotheses may be tested by repeating the procedure outlined above for another monophyletic lin-
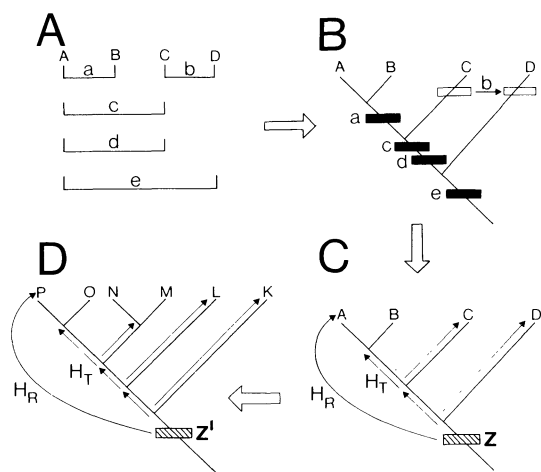
FIGURE 3. Outline of a structural methodology (see page 435) for testing historical hypotheses about the transformation of design. Nested sets of similarities (A) are ordered into the most parsimonious cladogram (B). Incongruent characters (b) are then recognized as convergences while the congruent characters (such as c and d) are recognized as homologies for the taxa they define. The corroborated cladogram is a hypothesis of the phylogenetic relationships (C) of the terminal taxa (A, B, C, and D) and provides a basis for reconstructing the historical sequence of structural transformation in any particular set of characters. Given a corroborated genealogy, the set of structural and/or functional data which were present in ancestral taxa (branching points) are then reconstructed by determining the most parsimonious fit between the attributes of the terminal taxa. This furnishes a very powerful tool for the analysis of form and function, as the *historical track* (pathway) taken by structural and functional networks in organisms is available for testing hypotheses of constraint, canalization, or versatility. Transformational hypotheses (H_T) concern the historical sequence of structural and functional change as a consequence of general (emergent) organizational properties of the structural and functional network within the organism (Z). Three examples are discussed in the text. Relational hypotheses (H_R) involve correlations between primitive emergent features (Z) and structural and functional networks in the terminal taxa A, B, C, and D. Note the importance of having a set of information corroborating the phylogeny which is independent of the structural data being used to formulate and test relational and transformational hypotheses. Maximum parsimony analysis of structural gene nucleotides (Fitch and Margoliash 1967) provides one such independent corroboration. Historical (structural/transformational) hypotheses may be tested by examining the relational and transformational consequences of similar emergent features (Z') in other monophyletic groups (D).

eage (Fig. 3D). It is important to realize that it is the use of emergent, general features of design (Z and Z' in Fig. 3C,D) which allows testing in independent lineages. The study of unique, specific morphological attributes does not permit testing by comparison (see discussion of

"key innovations" below). Similar aspects of the primitive structure-function network should have similar consequences for patterns of morphological diversification in other lineages. Tests of historical hypotheses about form must involve monophyletic lineages, and nested sets of characters that reflect ancestry and descent are fundamental to tests of transformational hypotheses.

The methodology outlined above permits several general questions to be posed for future consideration. Are there, in fact, general historical patterns (tracks) in the change of integrated complexes of features? What happens to structurally adjacent elements when a functional complex is altered? And, can a level of functional integration be defined that correlates with the rigid maintenance of character complex identity despite the alteration of surrounding elements?

I now consider three related generalities which exemplify the type of hypotheses contained in a structural approach to historical biology. Note that these hypotheses involve a historical relationship between emergent structural properties that are primitive for a clade and the subsequent pattern of structural and functional diversification. The analysis is thus purely structural in that morphological patterns within a clade are compared and that it does not involve concepts of taxonomic diversity (cladogenesis) or "adaptive" radiation.

Three hypotheses about structural patterns.— (1) *Decoupling of primitively constrained systems.* Vermeij (1973), Liem (1973, 1980), and Lauder (1982) (also see Strathmann 1975) have correlated diversity in body plan with an increase in the number of mechanical pathways or in the number of parameters controlling form. The concept underlying this generalization is the increased number of possibilities for arranging an increased number of elements. In certain actinopterygian (ray-finned fish) lineages, for example, an increase in the number of kinematic pathways governing movement of the jaws is related to an increase in diversity of jaw structure. Decoupling of primitively coupled biomechanical linkage systems of muscles and bones is correlated with greater diversity of jaw structure and function (see Fig. 4) than occurs in fishes with coupled systems. This sug-

STRUCTURAL NETWORK
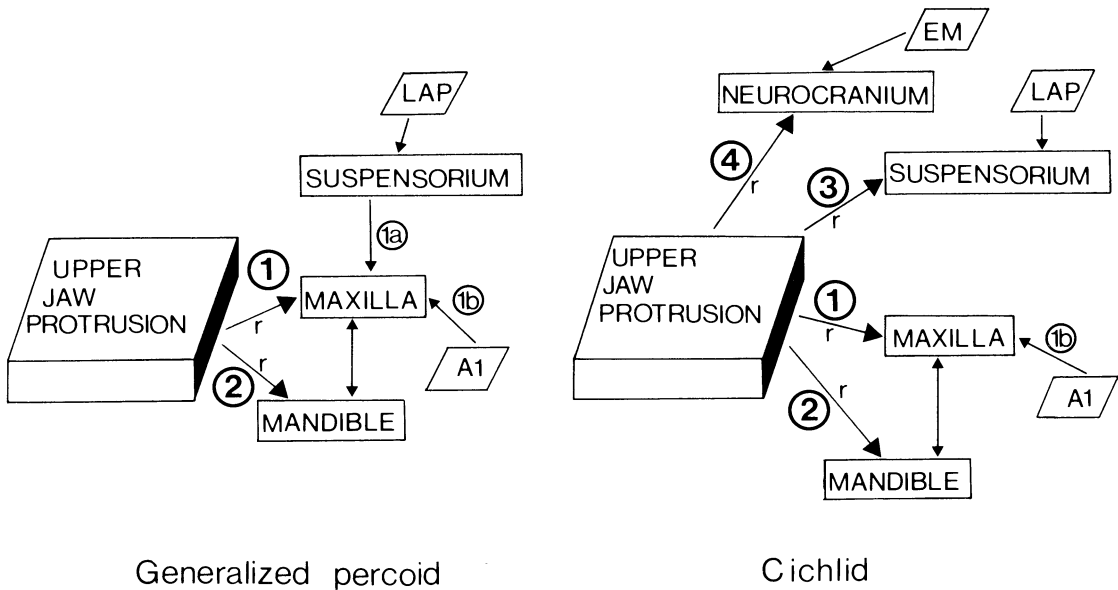

Generalized percoid   Cichlid

FIGURE 4. Comparison between the structural network in the head of a generalized percoid fish and in a cichlid fish to illustrate the concept of biomechanical decoupling and its consequences. In generalized percoids, two biomechanical pathways mediate upper jaw protrusion: mandibular depression and maxillary rotation (pathways 1 and 2). Suspensorial movement influences the upper jaw by an intermediary articulation with the maxilla (pathway 1a). In cichlid fishes (modified from Liem 1980), suspensorial movements can effect upper jaw protrusion independently of maxillary motion and the suspensorium has thus been mechanically *decoupled* from the maxilla (pathway 3). An additional mechanical pathway controlling upper jaw protrusion, neurocranial elevation by the epaxial muscles (EM), is also present (Liem 1980). A consequence of the decoupling of suspensorial movement (elimination of pathway 1a) and the increase in number of kinematic pathways controlling the function of upper jaw protrusion is greatly increased functional versatility and increased diversity of jaw morphology in comparison to generalized percoid lineages. This example illustrates both decoupling of a primitive biomechanical link (pathway 1a), and a proliferation in the number of mechanical pathways controlling a function. Both modifications correlate with an increase in diversity of the structural network. A1: Part A1 of the adductor mandibulae muscle; LAP: levator arcus palatini muscle; r: realization of the function of upper jaw protrusion by the indicated pathway.

gested correlation is a relational hypothesis (H_R, Fig. 3C) between decoupled elements (a general structural property) of the primitive network (Z, Fig. 3C) and morphological diversity in the terminal taxa. In analyzing the consequences of decoupling, taxonomic diversity must be clearly separated from morphological diversity. I make no claim that a release of previously constrained or coupled structural systems results in an increase in speciation rate, and thus higher taxonomic diversity, but I do emphasize the apparent inverse correlation between morphological diversity in a lineage and the number of constraints on the pattern. This hypothesis may be expressed as follows: primitive members of a morphologically diverse monophyletic lineage possess functional, structural, or morphogenetic networks which have a greater number of independent elements as compared to similar networks in closely related but less morphologically diverse monophyletic lineages. This hypothesis says nothing about the temporal sequence of morphological change; it only predicts a correlation between morphological diversity in a structural system and certain general features of the functional, structural, and morphogenetic pattern. This hypothesis may be refuted by demonstrating that two related lineages, preferably sister lineages, have different network constraints but similar patterns of morphological diversity. The hypothesis is not circular because decoupling of elements in the network need not necessarily result in morphological diversity; i.e., it is not true by definition. Tests of

this hypothesis should involve comparisons between monophyletic lineages and will have greater power if the networks of structural and functional interactions are determined for outgroups in order to provide a comparison with the lineages under analysis (Fig. 3).

The converse of the predicted effects of decoupling may be hypothesized to occur for a reduction in the number of independent pathways or elements in the pattern: an increase in the number of constraints (i.e. a decrease in independent structural elements or functional units) is predicted to correlate with reduced morphological diversity within a lineage, and the analysis of repeated independent cases of reductive evolution would provide a further test of the decoupling hypothesis.

(2) *Duplication and repetition of parts*. The consequence of the repetition of similar segments (metamerism) for morphological diversification is perhaps one of the oldest elements of a theory of pattern, having been recognized by Aristotle, Cuvier, Owen, Darwin and many morphologists in this century (Lankester 1904; Goodrich 1913; see articles by Gasc (1979) and Clark (1980) in two recent symposia on segmentation). The principle that a repetition of elements allows independent specialization of some segments while other segments retain the primitive structural and functional associations has recently been generalized to include the important phenomenon of gene duplication in evolution (Markert et al. 1975; MacIntyre 1976; Ohno 1970; Zuckerkandl 1976). Markert et al. (1975) note that duplication provides a path for generating new information from previously existing information, and they and Ohno (1970) have illustrated the importance that duplication of genetic material has had for the evolution of diversity in vertebrate proteins. I suggest that initially (primitively) repetitive systems have played an equally important role in allowing morphological diversification within lineages by enabling new functions to be acquired without disrupting a primitive functional complex. The consequence of repeated elements of form for the subsequent morphological history of a taxon is a key aspect of a theory of structural transformation and needs to be studied in much greater detail with a historical hypothesis as a basis. Both relational and transformational hypotheses may be formulated. Given a duplication in structural elements that is primitive for a monophyletic lineage, the historical sequence of divergence in structure between repeated elements can be followed (a transformational approach). Relational analysis might involve testing the association between the presence of primitively duplicated structures or functions and the pattern of structural or functional diversity in the terminal taxa.

Hypotheses about the consequences of metamerism or repetition of elements may be among the most general to emerge from a structural approach. Arthropods, fishes, plants, genes and even metabolic pathways in bacteria (Lin et al. 1976) provide examples of the consequences of repeated elements for structural and functional diversification. The task ahead is to make precise predictions about the historical tracks and final result of the transformation of redundant structural and functional elements.

(3) *Complexity and its consequences*. A final important aspect of structural transformation, not entirely independent from the previous two topics, is the influence of structural complexity in a lineage on the pattern of diversification. The phenomenon of structural decoupling discussed above may be of greater significance in governing pathways of change in those aspects of organisms which are mechanically complex (fish jaws; arthropod limbs—see Flessa et al. 1975), while the decoupling of elements in the epigenetic hierarchy may be a more common method of increasing versatility and thus morphological diversity in mechanically less complicated aspects of form (mollusc shells; mammal jaws). Complexity may be defined as the number of parameters needed to describe form (see Raup 1966; Schopf et al. 1975; Vermeij 1971; i.e., highly complex morphologies require many descriptors), as the number of independently movable elements, or as the number of links in the structural network (also see Saunders and Ho, 1981; Wicken, 1979). Only a very few investigators have explicitly considered the potential influence of complexity of organization on patterns of morphological change, yet this concept is particularly important for the analysis of structural transformation. One of the most basic aspects of biological organization,

the number of structural elements and the number of connections between the elements, may exert a profound effect on the type and extent of possible changes in design. This influence may extend even to determining which level in the hierarchy of possible processes produces morphological change in a given lineage.

Complexity of organization may also exert an influence on the pathway of structural transformation. Simon (1962) has noted that the level of complexity of organization may be related to the number of stable intermediate states. More complex systems can have more potentially stable intermediate states and thus may have more options for change in design. Less complex systems may have fewer potential pathways and fewer stable states within each track. Thus, variation in complexity of organization and in the hierarchical organization of complex systems may contribute to differences in the way lineages fill up morphological space.

The key innovation reconsidered.—Within the context of historical hypotheses of adaptation, a key morphological novelty or innovation is often causally associated with the adaptive radiation of the group possessing the novelty. These associations are generally untestable because of the unique nature of the morphological features invoked as causally related to clado-genesis (e.g. bivalve siphons, Stanley 1968). If "key innovations" have evolved only once, how can alternative scenarios explaining "adaptive" radiation be tested?

The structural approach to historical patterns outlined above suggests an alternative view of morphological novelties. A key innovation represents, at some level of generality, a shared derived feature for the lineage under consideration. As such, it can be considered as the subject of transformational and relational hypotheses, as outlined in Fig. 3, if it can be incorporated into a general emergent structural framework. This differs from previous discussions of the key innovation (Liem 1973; Mayr 1960) in that the analysis is purely structural and does not involve relating the presence of a specific morphological feature in a clade to an increase in speciation rate (e.g. Stanley 1968). A key innovation, then, is just one component of the structural network that has been traditionally isolated because of a belief that it plays an exceptionally important role in the biology of the lineage. Testable hypotheses of the consequences of possessing a particular structural pattern may be constructed only within a historical hypothesis of relationship (Fig. 3) and only if the "morphological novelty" has general attributes that are present in other unrelated lineages. Unique features with no general properties admit only particularistic explanations that are as untestable as hypotheses of the causal basis of adaptive radiation.

Conclusions

The theory of evolution by natural selection has had a peculiar effect on the science of morphology. In its role as the central organizing principle of research in natural history, particularly in this century, the concept of modification of form by the process of natural selection has greatly stimulated morphological research. After all, so many of the favored topics of evolutionary biology such as tempos of change, macroevolution, and adaptive radiation, depend on a morphological data base. In particular, paleontological data have been perceived as having an especially important role to play in understanding the action of natural selection.

On the other hand, the "Modern Synthesis" has defined the goals of morphological research to be the study of adaptation and the selective forces which produce change. Darwin focused the attention of morphologists on the evolutionary process and in so doing inhibited the study of evolutionary patterns per se, an area in which morphology is most likely to contribute basic concepts and generalizations about the diversity of life on Earth. The relatively rapid change in focus from pattern to process questions at the end of the nineteenth century nipped in the bud a nascent theory of pattern developed mostly by Owen, Cuvier, and Goethe. Many of the major generalizations about patterns of structure in organisms date from the pre-Darwinian morphologists who developed the basis of a theory of pattern without a concept of natural selection or descent with modification. Indeed, the three topics singled out above as the most important generalizations to emerge from the analysis of structural patterns—duplication, decoupling, and complexity—owe their initial formulation to pre-Darwinian morphologists (Bronn 1858;

Gegenbaur 1876; Milne-Edwards 1834, 1851; Coleman 1976).

In this paper I have emphasized the need for an approach to morphological patterns that is mechanism independent. My aim has been to show how historical hypotheses about patterns of form and function can be proposed and tested, and to point out several hypotheses that may have general implications for the transformation of organic design. Nearly all post-Darwinian morphologists have had as their stated goal the elucidation of mechanisms of structural change (see Davis 1958; Coleman 1980), and this mechanistic emphasis is perhaps related both to the rise of causal embryology in the late nineteenth century (His 1888; Roux 1888; see Allen 1975; Coleman 1977; Russell 1916) and to the influence on research methodology of the concept of natural selection as an extrinsic explanation.

The structural approach outlined here is historical in focus and the goal is the analysis of general historical pathways of change (tracks) in form and function which are a consequence of emergent organizational properties. This is in distinction to equilibrium analyses in which the focus is on extrinsic explanations and specific (unique) structural features. Ultimately, transformational and relational hypotheses should provide general insights into the evolution of structural and functional networks in organisms. By combining historical analysis with the study of structural and functional interactions within organisms, morphology as a discipline may contribute major generalizations about the transformation of design and about patterns in the diversity of life.

Acknowledgments

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