The Use of Functional and Adaptive Criteria in Phylogenetic Systematics

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SYNOPSIS. The controversy over whether functional data can contribute to phylogenetic inference has grown in recent years. Steps can be taken toward its resolution if the relevance of functional data is judged for each component of phylogenetic analysis. These components are (1) recognizing of basic taxa (species or superspecific taxa), (2) formulating hypotheses of homology followed by character analysis, (3) evaluating character phylogenies, (4) formulating phylogenetic hypotheses, and (5) evaluating alternative phylogenetic hypotheses. It can be shown that functional data do not play a necessary or unique role in any of these components of phylogenetic analysis. Arguments to the contrary have failed to provide a rigorous, repeatable method to incorporate functional data; proponents of a functional approach to phylogenetic reconstruction rely too often on subjective, authoritarian argumentation.

Students of functional evolutionary morphology frequently have failed to understand the kinds of information necessary to study or apply the causal process of adaptation via natural selection. This information, required by the very nature of the theory itself, includes knowing the pattern of heredity of the phenotypic characters being studied, relating intrapopulational phenotypic variability to variation in fitness, and knowing a sufficient amount about population structure to specify the components of natural selection. Studies within functional evolutionary morphology are not designed to satisfy these requirements. Functional evolutionary morphology uses the concepts of adaptation and natural selection axiomatically, and thus such studies contribute nothing to our understanding of the evolutionary process because hypotheses about that process are not being evaluated. This also suggests that, if functional evolutionary morphology wishes to engage in analyses of the evolutionary dynamics of the phenotype, a reorientation of its research strategy and goals will be necessary.

INTRODUCTION

Since the times of Linnaeus and de Candolle in botany and Cuvier in zoology, systematists have pondered the relevance of functional data for the recognition of natural groups. Cuvier held that "Comparative anatomy is therefore the division of the natural sciences which tends to generalize, to erect the theory of organization" (Coleman, 1964, pp. 62-63). His four embranchements—vertebrates, molluscs, articulates, and radiates—were founded on what he termed "important characters," and although he placed countenance on the constancy of characters within and between groups, he clearly envisioned functional criteria as the prime reservoir of methods from which these "important characters" were to be recognized. According to Coleman (1964, pp. 80-81), Cuvier's misgivings about the empirically determined use of constant characters, as advocated by the botanist Antoine L. de Jussieu, were reinforced by his belief that the functional approach was to be preferred for philosophical reasons: Plants are immobile, animals are active, and thus the study of animals demands a functional attitude.

Cuvier's functional approach appears to have had little lasting influence on the practice of systematics: The recognition of groups has generally been based on the correlated occurrences of characters. To be sure, almost every systematist, before and after Darwin, has perceived that sometimes similarities in structure can result from similarities in function and consequently that those groups possessing these structures do not constitute a natural group. Perhaps the best example is eyes in arthropods and eyes in vertebrates. But it is not the functional data themselves which

have allowed systematists to solve this problem; rather, it is the observation that these two types of eyes are correlated with two completely different sets of similarities defining two groups, and not one characterized by eyes.

In recent years a belief in the applicability of a functional approach to the questions of systematics has undergone a minor renaissance. Some advocates of this approach have claimed that knowledge of the functional and adaptive nature of morphology is an absolute prerequisite—the *sine qua non*—for systematic practice (see examples below). It is my interpretation that the results of 200 years of systematic research are sufficient to falsify this claim. It does not follow, of course, that functional data can play no important role in systematic biology. I would make one observation, however: It is my perception that this role, to whatever degree it exists, has neither been clearly defined nor justified, nor has a precise systematic methodology based on functional data been articulated. It is the purpose of this paper, therefore, to examine the basis of my perception and to evaluate the relevance of functional data within systematic biology.

I wish to approach the subject by characterizing the goals of systematics within the context of two sets of hypotheses: first, those about the *pattern* of the history of life, and second, those about the *processes* that might be proposed to explain the genesis of the pattern. The pattern aspect of systematics pertains to deciphering phylogeny, that is, the recognition of natural groups. The causal process producing the pattern is of course evolution, but there may be alternative hypotheses about the nature of that process. I will not be concerned here with evaluating these alternatives *per se*, but it is not possible to ignore problems of process analysis when considering the importance of functional data in systematic practice, for the very reason that advocates of their use rely heavily on arguments about process, specifically about adaptation and natural selection. In doing so, I believe, many workers have confounded process analysis with pattern recognition. Hence, one of my purposes is to attempt to unravel the confusions inherent in their argumentation. The focus of the problem seems to be the use of functional data in the analysis of adaptation and its implications for the efficacy of natural selection as a causal mechanism of that adaptation. Knowledge about adaptation, it is claimed by some, is a necessity before phylogenetic relationships can be inferred. But this logically leads to a still more fundamental question, one that cannot be ignored here: what is the relevance of functional data to the analysis of the process of adaptation? Thus, the problem being raised is whether functional biologists have adopted lines of investigation and reasoning that can truly elucidate the evolutionary process. The solution to this problem has obvious, far-reaching implications for the research program of the newly created field of "functional evolutionary morphology," as it is called by its practitioners.

This critique of current work obviously does not apply to the entire field of functional morphology. Most functional morphologists are not engaged in systematic studies, but rather are concerned with how structures work (function). Furthermore, most functional morphologists do not undertake primary investigations of the evolutionary process. But as the citations below will show, many workers use particular viewpoints of process in an explanatory context which tacitly assumes that the data collected actually bear on the issue of process when, in fact, they do not.

**Some Definitions**

Before beginning it is necessary to explain how certain terms will be used. What, exactly, are functional data? No precise meaning seems possible or universally acceptable. Bock and von Wahlert (1965), for example, run counter to tradition and define function in terms of the physical and chemical properties arising from the form of a structure. Traditional biology has viewed the function of a structure in terms of its action or use by the organism (Bock and von Wahlert would call this the biological role; see also Bock, 1977a). Tra-
tion thus implies that for a structure its function is its purpose, what it is designed to do.

While I have no major disagreements with the terminology of Bock and von Wahlert, I am inclined to follow tradition only because fewer misunderstandings may arise. In any case, I do not perceive serious conceptual or methodological problems which may result from following tradition. But there is one aspect of function that does appear relevant to systematic practice, namely the distinction between function and behavior. The relevance relates to the problem of defining what is meant by a systematic character. Functions of structures generally have not been thought of as characters, whereas ritualized behavior patterns have been utilized as characters for many years. For example, an avian bill may have a particular shape and may function (be used) to obtain food, to obtain mates and maintain pair bonds (by bill clapping, for instance), to build a nest, or for defense. For each of these functions there may be a stereotyped behavior pattern that is species-specific or shared with other species. That there may be one or more functions for a structure does not imply an associated stereotypic behavior pattern for each function; it is the behavior pattern, then, and not the function, which constitutes a systematic character. I believe this distinction is within systematic tradition, and I will follow it here.

An additional term in need of discussion is adaptation. Once again I follow the tradition of Darwinism and refer to a morphological adaptation as a structure, its functions and biological roles, which have evolved under the influence of natural selection because they confer some advantage to the organism possessing them. Recently, some authors (e.g., Gould, 1978, p. 532; Clutton-Brock and Harvey, 1979, p. 548; Gould and Lewontin, 1979, pp. 592–598) have used adaptation more broadly, even referring to phenotypic characteristics which lack a genetic basis or which have not evolved via natural selection as adaptations. I wish, however, to make the distinction between perceived design and the question of whether that design is an adaptation in the traditional Darwinian sense. To be sure the workers just cited are also aware of this distinction, but in my opinion it is imperative, both for semantic and scientific reasons, not to refer to perceived design as an adaptation. Within contemporary biology design is essentially defined as an adaptation, but it is conceivably that design has frequently evolved by non-Darwinian processes, as the above workers so cogently argue.

The Recognition of Natural Groups: Functional Data and Phylogenetic Inference

Within systematics the concept of pattern has had a fairly unambiguous meaning: It is the representation of genealogical relationships and the distribution, with respect to those relationships, of the similarities and differences among the included taxa. Some biologists also would want to add to this concept of pattern information about adaptation, temporal environmental characteristics, or even natural selection. However, these are all aspects of process analysis, and to maintain clarity as to just what it is we think we can do with functional data, it is best to reinforce the separation between hypotheses about pattern and those about process.

Space does not permit an extended discussion of the methodology used to reconstruct pattern, that is, to formulate hypotheses of phylogenetic relationships (the reader is referred to Hennig, 1966; Wiley, 1975, 1981; Eldredge, 1979; Gaffney, 1979; Eldredge and Cracraft, 1980; Nelson and Platnick, 1981). Rather, I want to list the procedures that are considered most important by the majority of workers who have studied the problem and then examine the applicability of functional data to each procedural step. The process of erecting phylogenetic hypotheses includes:

(1) the preliminary acceptance of hypotheses about the taxonomic limits of the included taxa,

(2) the recognition of similarities among
these taxa, that is, formulation of provisional hypotheses about homology,
(3) the use of one or more methods to postulate the hierarchical level at which
homologues are primitive and at which they are derived,
(4) the creation of hypotheses about nested sets of taxa, which are defined in
terms of shared derived similarities, and
(5) the comparison and evaluation of alternative phylogenetic hypotheses.

These five steps result in hypotheses about phylogenetic pattern. All five steps
are independent of various hypotheses of process which might be postulated; the
only assumptions are that evolution has taken place and that changes in intrinsic
characters (morphology, physiology, behavior) have occurred during the course
of evolution (i.e., there has been descent with modification). Many workers have
argued the necessity of functional data for one or more of these methodological steps
of pattern analysis; let us now evaluate these claims.

The recognition of basic taxa

All studies designed to reconstruct the phylogenetic relationships of a group of
organisms generally assume the individuality of certain basic taxonomic units and
from this starting point discuss their interrelationships. By individuality is meant
that (a) the basic taxa are assumed to be "real" in a monophyletic sense, and (b) in
the study in question, the basic taxa are not to be decomposed further into subtaxa. It
is now generally accepted that species-taxa are the lowest, basic taxonomic unit, and
it is further recognized that the acceptance of basic taxa—whether of species or supraspecific rank—constitutes a hypothesis and as such is subject to critical evaluation.

Because this entire discussion is directed toward the characterization of a methodology designed to formulate and test phylogenetic hypotheses among species and
groups of species, my present remarks will be concerned with the use of functional data to delimit species.

A species can be viewed as a diagnosable cluster of individual organisms within
which there is a parental pattern of ancestry and descent, beyond which there is not,
and which exhibits a pattern of phylogenetic ancestry and descent among units of
like kind (Eldredge and Cracraft, 1980). The recognition of species has two components, one involving reproductive continuity and the other phenotypic distinctness. Obviously, a species might be defined by the possession of some unique, derived character; if it is, then that species cannot, without admitting character reversal, be considered ancestral to any other species. Unlike supraspecific taxa, species do not
have to be defined by synapomorphies but may be characterized by shared primitive
characters (sympleiomorphies). This is merely a reflection of the evolutionary process: If we are to accept an ancestral-descendant hypothesis, an ancestral species must share one or more synapomorphies with its descendants but also must be pleiomorphic relative to them in all other phenotypic characters; in this case the pleiomorphic ancestral species, of necessity, will be defined by postulated reproductive continuity and not synapomorphies (Eldredge and Cracraft, 1980).

What, then, can be said about the role of functional data in defining species limits? I will defer discussion about the use of functional data in recognizing synapomorphic characters and will ask here whether such data have a role in identifying the presence or absence of reproductive continuity. A question about reproductive continuity—that is, about conspecificity—might arise under three conditions: (1) when there are two identifiable, sympatric phenotypes which are sufficiently similar to cause the systematist to suspect they might only be morphs of the same species, (2) when there is some suspicion that what was first perceived to be a single species population occurring sympatrically is in
fact two or more reproductively isolated units, and (3) when there are allopatric populations, incapable of interbreeding, and the systematist wishes to make a decision about their specific status. In the first case, the systematist has already made some judgment regarding a similarity in phenotype ("they are different, but perhaps not that much"), and the critical question is whether there is evidence of interbreeding. In the second case the systematist
apparently has some evidence that there is a difference and more than one morph is indicated; thus, evidence of interbreeding is again important. Finally, in the third case, the systematist is asking whether the allopatric populations, based on their phenotype, can be judged capable of interbreeding if they were sympatric. Functional data would seem to play no necessary or unique role in determining the capacity to interbreed. The primary observation in the case of sympatry is whether the morphs do or do not interbreed. To be sure, the function of a stereotyped display behavior may be to attract conspecific mates but conspecificity is demonstrated, not by attraction, but by de facto interbreeding. The function of one behavior, or the functions of several behaviors, in themselves do not constitute the data used by systematists to infer specific status.

In the case of allopatric populations it is conceivable that functional data might play a role in deciding specific status. If, for example, two isolated populations exhibited identical stereotyped displays, but these displays were used for different purposes in the two populations, a systematist might take this as indicating specific distinctness, especially if it were known that this behavior is involved with species recognition. While it might be that behavior changes first by modification of the functions of the display, I know of no examples in which such functional differences have been used to decide the specific status of isolated populations. It is a difference in behavior, not its function, that typically characterizes species.

I have focused this discussion on behavioral characteristics because they are most directly concerned with isolating mechanisms of phenotypically similar species. I am unaware of any example in which the functional parameters of a morphological character, rather than the attributes of the character itself, have been used by a systematist to define species.

Hypotheses of homology and character analysis

Perhaps no concept within systematic biology has been so misunderstood and misused as has been that of homology. The problem, it would seem, is not with differences in definition—most would agree that, in principle, homology refers to characters inherited from a common ancestor—but with the practical application of the homology concept to systematic problems. I would like to suggest that the solution to the problem is deceptively simple: A statement about homology is basically a statement about similarity, more specifically about the hierarchical level at which that similarity, postulated to be a synapomorphy, defines a set of taxa. Any interpretation of the evolutionary history of the similarity is dependent upon the particular phylogenetic hypothesis one is willing to accept. Thus, it is illogical to claim that one can apply the evolutionary component of the conventional definition of homology—inheritance from a common ancestor—prior to the formulation and evaluation of alternative phylogenetic hypotheses. In terms of phylogenetic methodology a hypothesis of homology is simply a perception of similarity and the working assumption that the similarity will define a set of taxa and thereby facilitate further comparison. A classic example is the hypothesis that the three ear ossicles of mammals are homologous with a series of bones in the jaws of other gnathostomes. Why do we entertain such a hypothesis of homology? Their adult structural differences are irrelevant as are their differences in function. It is their similarities in development that have led biologists to invoke homology.

It might be supposed that morphological and/or functional differences observed for two structural characters can be used to infer nonhomology. Indeed, statements to this effect abound in the systematic literature. I suggest, however, that these statements entail a basic misunderstanding of the homology concept, which is that homology is based on similarity not difference. Homology does not imply identity, only similarity, thus homologues will be different. Likewise, the concept of nonhomology itself implies similarity, otherwise why were the structures compared in the first place? A hypothesis of nonhomologous similarity is neither inferred from nor supported by differences—this would entail a logical contradiction. Then what
From the standpoint of the above remarks and arguments, how are we to evaluate the claims of some biologists that functional data are required or are an important adjunct in recognizing homologous versus nonhomologous characters? Zusi (1971, p. 81), for example, states that "features evolving in parallel may be recognized by the close similarity in function and biological role of most or all features of a functional complex . . . convergence can be recognized by differences in superficially similar functional complexes serving similar biological roles." As "parallel" characters are taken by virtually all biologists to be nonhomologues in the strict sense (it is assumed the ancestor did not possess the character of the descendants), we may ask how a systematist is to use similarity to recognize "parallel" characters on the one hand as compared to true homologies on the other; logically, one cannot have it both ways. Likewise, as pointed out above, homologies can be different and thus the use of differences to infer convergence is also logically suspect.

Bock (1977b, pp. 889−890) has expressed opinions similar to Zusi in his explication of a method purported to distinguish between homologues and convergences (nonhomologues). To him homologous attributes will be those that serve (p. 890) "in a wide range of biological roles rather than having a single biological role because the probability of a feature serving a wide range of roles evolving independently two or more times is less than one that has only a single biological role and tight correlation with a single or narrowly delimited environmental factor." Furthermore, Bock claims, homologues will be features "whose evolution depended upon the interworkings of a complex pattern of structural and functional relationships rather than a feature with few such structural interrelationships for the same reasons."

Along with Zusi and Bock other authors have stated their belief that functional criteria are useful in discerning homology from convergence (e.g., Mayr, 1974, pp. 118−118; Hecht, 1976; Hecht and Edwards, 1976, 1977; Van Valen, 1978), and all seem concerned with establishing the

constitutes evidence that two characters are nonhomologous similarities? Simply that both similarities are interpreted to be derived but within the context of a given phylogenetic hypothesis these similarities define different sets of taxa, that is, they are convergent similarities. This implies, of course, that the judgment of nonhomology is based on the acceptance of a phylogenetic hypothesis constructed in terms of other characters. But it is also clear that a judgment of homology is also based upon the compatibility of the two characters with the nested taxa of a phylogenetic hypothesis: One of the homologues (the primitive one) defines a set of taxa which includes a subset defined by the other homologue (the derived one).

Bock (1977b, p. 882) has recently written that "shared similarity is the only valid empirical test of homology" (italics his), but it should be obvious from my discussion that similarity is not a test of homology. Rather, similarity is the factor which compels us to postulate homology; the test of homology is related to the compatibility of characters and their characteristic of defining sets of taxa such that the postulated synapomorphies are not interpretable as convergences.

Given this background on the homology concept, what role can be envisioned for functional data? Obviously, that role must be restricted to recognizing similarity (i.e., postulating homology), for the evaluation of homology is strictly a matter of the logic of phylogenetic analysis. But, upon reflection, it is apparent that functional data cannot be applied in any logical manner to the recognition of similarity. To be sure, similarities in function sometimes parallel similarities in structure, but it is the similarity in structure that is the primary empirical basis for a hypothesis of homology. Moreover, any systematist or morphologist can list numerous structural similarities, highly corroborated as homologies, which have very disparate functions. And there is no reason to believe that a similarity in function necessitates a similarity in structure, and certainly not a homologous similarity. So I conclude that functional data play no relevant role in either postulating homology or in its evaluation.
The probability level of some shared similarity being homologous. None of these workers do more than claim the efficacy of functional criteria, and they provide us with no concrete methodology. The issue seems to be a misunderstanding about the concepts of homology and convergence. They believe—and state explicitly—that there ought to be methods to identify homologies prior to comparative procedures of phylogenetic inference. What their functional criteria are really saying is that structurally complex characters are less likely to evolve independently than less complex characters (and in reality, functional data play a minimal role in establishing the degree of complexity of form). But how can one assess that probability level other than by an appeal to authority? In the final analysis, proponents of this functional method ask us to suspend critical judgment and accept that their experience in investigating the functional properties of systematic characters can establish probability levels of similarities being homologous. By focusing on probability statements these workers, consciously or not, adopt a philosophical worldview such that their methodology is designed to establish the truth of their scientific statements. I would submit that phylogenetic analysis has nothing to do with calculating the truth value of statements about homology or of phylogenetic relationships.

It is often said that knowledge of function or of “functional integration” is important in defining the limits of taxonomic characters (see for example, Gruen, 1970, p. 97). The implication is that functional data point to correlations among structures and that whereas a conventional systematist might see a number of characters, a functionally-oriented systematist will recognize only a single “integrated” character. Although this argument may sound intuitively reasonable, functional biologists supporting it are faced with a number of serious problems. Surely one must ask what is meant by “functionally integrated” and how does one objectively define the structural limits of this integration? Functional integration would have to be defined independent of correlated change in order to avoid circularity. A further problem is that one can always make up a story, if one tries hard enough, to “explain” why structural change in two features might be correlated functionally. Take, for example, the often cited case of change in dentition and foot structure in Cenozoic horses. In some lineages, it appears both change more or less at the same time, and functional stories (“adaptation to grasslands,” etc.) have been invented to explain this correlated change. Are there one or two systematic characters? And can we push the example to the extreme and include correlated changes in muscle structure, postcranial and cranial bone shape, gastrointestinal changes, and so on (provided they could be documented), as a single character? The point is, if we believe that organisms are integrated functionally in the totality of their structure, then it becomes impossible to define the limits of this integration objectively except at the level of the whole organism; and, to perceive all change as one character is a reductio ad absurdum. Systematic analysis would become impossible.

In summary, advocates of a functional approach to character analysis have not yet provided a methodology whereby discrete characters can be recognized in an objective manner. In fact, the problem seems intractable using functional criteria, because any such solution would appear to rely solely upon the subjective opinions of the individual researcher. The problem may not be as serious as some functional biologists would have us believe, for within the present literature on phylogenetic analysis, decisions about numbers of characters would seem not to have influenced the results of systematic studies to any significant degree.

The evaluation of character phylogeny

Most systematists now agree that monophyletic groups can be defined only by the possession of shared derived characters, consequently there is little or no debate over the need to erect corroborated hypotheses about character phylogeny. As is well known, however, there is no unanimity of opinion regarding the methods of constructing the hypotheses.

The concept of a character transforma-
tion is simple: it means that at some time during the phylogenetic process of branching and divergence a character, \( A \), becomes modified (call it now character \( B \)). Characters \( A \) and \( B \) are homologues, and \( A \) is primitive relative to \( B \). The most important aspect of character \( A \) is that it defines a set of taxa which includes as a subset those taxa defined by \( B \). Of course, character \( A \) itself is a modification (a derived condition) of some other character which defines a still larger set of taxa. The problem of discerning character transformations is merely one of deciphering the hierarchical level at which postulated homologues characterize a set of taxa. I do not wish to discuss here the literature on character transformation. I will note, however, that two criteria in particular—outgroup comparison and ontogenetic character analysis—are now generally recognized by systematists as being the most reliable for investigating character transformations. My goal at this point is to evaluate the claims of some biologists that functional data may be useful in interpreting primitive-derived character sequences.

Two functional biologists in particular have argued forcefully that such data are critically important. Let us examine their position. Bock (1977b, pp. 886–887), for example, recognizes only two criteria for determining polarity, one associated with functional-adaptive information and the other with stratigraphic distribution. He does not mention outgroup comparison and ontogenetic data, the two criteria accepted by virtually all systematists, cladists and non-cladists alike. If we are to determine polarity sequences, Bock (p. 887) claims, we must know “as much about the function, adaptive significance and other aspects of the biology of the feature as possible.” Why do we need such information? Because, then we will have “a comprehension of the probability of evolutionary change in one direction as opposed to the probability of change in the reverse direction.” His example is instructive as to his method and its application: “evolution from an akinetic vertebrate skull to a kinetic skull is so highly improbable that it would invalidate any morpholine expressing this direction of change.”

W. F. Gutmann (1977) is even more resolute in his insistence of the primacy of functional data. His method of phylogenetic analysis centers around the reconstruction of the adaptive history of lineages. Thus (p. 646), “only those features and characters whose functions are known and for which the value of the adaptational changes can be assessed, can be utilized in phylogenetic reconstruction.” His use of polarity sequences is not directed so much toward the identification of shared derived characters as to point the way toward what is perceived by him as an adaptive story of whole organism transformation. Nevertheless, he is concerned with character transformation (p. 649):

One can start with morphoclines which might be representative of stages in a phylogenetic lineage. The polarity of morphoclines can then only be decided on the basis of adaptational interpretations. These have to be reconstructed on the basis of insight into the working of the structural components. Those transformations that increase efficiency may be assessed as advantageous. A decision on the direction of the adaptational process is reached only in this way.

A conviction that functional criteria are important in recognizing character transformation is not restricted to evolutionary systematists. For example, the phylogenetic systematist Crowson (1970, p. 91) notes, without further elaboration, that:

From the point of view of the phylogenetic systematist, information about behavior may be even more important, in that it can help us to an understanding of the functional significance of structural and physiological characters, which in turn may lead to a sounder estimate of the likelihood of various postulated evolutionary sequences.

The arguments of Bock, Gutmann, Crowson, and others with similar views are unconvincing, and rely primarily on sub-
jectivism and authoritarianism. Their criteria and methods—little more than statements of belief—consist of a request for us to accept their judgments about character transformation, but we are not provided with a specific, logical basis on which to evaluate these judgments. Consider their statements. For Bock, functional data allow us to comprehend "probability levels" that evolution proceeds in one direction as opposed to another. What are the premises underlying this argument? What does he mean by "probability"? How do we go from functional data to probability levels? My interpretation is that the statement "the probability that evolution went from A to B is X" is totally untestable; in cases such as this, there is no way to evaluate the probability of a character transformation using functional data. Evidence for this evaluation is also to be found in his own example: to Bock the transformation from an akiton to a kinetic is "highly improbable" and this probability level "invalidates" this transformation for use as systematic data. This conclusion is astounding, for our present knowledge of vertebrate phylogeny assuredly indicates that a kinetic skull is a derived condition in numerous groups. Does Bock mean to imply that the vertebrate skull is primitive-ly kinetic? Or that only the akitin skull is derived within the vertebrates? Also, we are never told which functional data facilitated the determination of this "probability level," or how he used those data in the determination. In other words, no method is described or applied.

Gutmann's statements about character transformation are open to the same criticisms, but they are subject to additional problems because they are tied so closely to his conceptions of adaptation and its analysis. Gutmann's view of evolution is that it relentlessly improves structure and function through time (Gutmann, 1977, is replete with examples). His method of character transformation is to study this improvement by proposing to measure the increase or decrease in efficiency. Further comments about Gutmann's method of adaptational analysis will be given below. In short, his approach cannot produce rigorous, testable statements about character transformation. Furthermore, as I will argue shortly, it is doubtful whether we can obtain the necessary data to permit meaningful interpretations about the adaptive nature of morphological features. If so, Gutmann's method of character analysis cannot be used.

Formulating phylogenetic hypotheses; evaluating alternative phylogenetic hypotheses

Very few functional biologists claim that functional data _per se_ can be used directly to construct or evaluate phylogenetic hypotheses. This is understandable because comparative biologists realize that similarity is used to form groups within groups; to most functional biologists, functional data are employed to weigh the importance of observed similarities.

Gutmann (1977) is one of the few functional biologists who believes functional-adaptive criteria play a direct, and essential, role in formulating phylogenetic hypotheses. His concept of phylogenetic relationships is not strictly that of hypothesizing groups within groups but of reconstructing the gradual functional-adaptive transitions between different bauplan. In one sense, then, he is not formulating and evaluating phylogenetic hypotheses; he is constructing stories of what might have happened. His general philosophical approach to phylogenetic analysis is revealed in Gutmann (1977):

Phylogenetic theories can only be formulated by reconstructing sequences of adaptational changes and tracing the diverging lines leading to existing organisms and their characters . . . . Phylogenetic theory is never contained in a dendrogram but only in the phylogenetic model based on a reconstruction of the adaptational process . . . . A dendrogram remains an empty scheme if the phylogenetic theory on which it is based is not clearly outlined . . . . So both aspects of selection and adaptation, the environmental and the functional relations within the organism, have to be inherent in the phylogenetic reconstruction . . . (p. 646).
Neither comparison alone nor character analyses can by themselves disclose phylogenetic relationships. Only the reconstruction of the process of phylogeny as a series of adaptational transformations of the organism in the course of time can solve phylogenetic problems. The task of the phylogeneticist is not to erect systematic entities or to design dendrograms but to reconstruct the continuous process explaining it in adaptational terms and thereby basing the decisive arguments on requirements of the evolutionary theory (p. 664).

I will show in the next section of this paper that functional biologists do not study adaptation within a historical context except in a trivial sense; that argument itself will constitute a severe criticism of Gutmann’s phylogenetic method. At another, fundamental level I believe Gutmann has misunderstood what it is that systematics has sought to do for over 200 years, namely, to reconstruct the pattern of the history of life, to attempt the delineation of natural groups. Thus, systematics is not primarily concerned with imagining intermediate stages among all the fossil and extant taxa—although this idea has its origins with pre-Darwinian nominalists and with Darwin himself (Cracraft, 1979)—but with using similarity relationships to reconstruct nature’s hierarchy. Gutmann operates at what Eldredge (1979) has called the scenario level of evolutionary analysis. Eldredge has cogently pointed out that one cannot operate effectively at the scenario level without, first, considering hypotheses at the cladogram level, and second, without then evaluating hypotheses at the level of evolutionary trees. Gutmann begins at the level furthest removed from an empirical database, creates a series of functional reconstructions of hypothetical intermediate organisms, superimposes a mélange of speculation about natural selection, adaptation, and the environment, and then concludes that the adaptational pathways which have been described are the only way that evolution could have proceeded (see Gutmann, 1977, pp. 657–662, for repeated assertions that the chordate body plan could only have evolved the way he has reconstructed it). If this were the case, then further consideration of the problem would be superfluous.

In summary, I have tried to argue that functional biologists have not made a strong case for the need for functional data in phylogenetic analysis. It may be that functional data are important, but this has not yet been demonstrated effectively. When one dissects the arguments of functional biologists, one discovers the absence of a rigorous, repeatable method; instead one is presented with a belief system relying primarily on an appeal to authority. In this critique I have raised a number of specific questions that should be addressed by those functional biologists who continue to claim the importance of functional data in systematics.

**Functional Evolutionary Morphology and the Analysis of Adaptation**

One of the avowed goals of functional evolutionary morphology is to interpret the phylogenetic history of organisms in terms of change in function and adaptive modification. Certainly this goal can be traced back as far as Darwin, and he proposed his theory to explain two phenomena: the origin of taxonomic diversity and the origin and maintenance of phenotypic design. His answer to the latter problem was adaptation by natural selection.

I wish to propose two lines of argumentation regarding current approaches to adaptational analysis within functional evolutionary morphology: First, that functional evolutionary morphology does not study adaptation in a strict sense because it cannot. I will support this thesis by considering the kinds of knowledge which are minimally necessary to justify hypotheses about adaptive change. The argument will be that functional evolutionary morphology cannot obtain this knowledge about the past, and the extent to which such knowledge is lacking creates severe constraints on the scientific usefulness of many contemporary approaches to historical evolutionary analysis.

Second, that many, if not most, discus-
sions about the evolutionary history of form and function within the context of adaptational analysis convey little or no knowledge either about the nature of adaptation or about the evolutionary process. I will support this thesis by examining the logical structure of some of the best functional morphological studies which attempt to interpret their findings in terms of adaptation and the evolutionary process. If weaknesses are found in the reasoning of the best studies, then we are justified in concluding that my argument applies to the field of functional evolutionary morphology as a whole.

The use of the term adaptation antedates nineteenth century evolutionary biology by more than 200 yr. It has always implied a fit of one thing to another: something is designed for a purpose. The nearly universal usage of adaptation in modern biology considers this design to be the result of Darwinian natural selection. Hence, it is easy to find statements within functional evolutionary morphology to the effect that “structure X is an adaptation for purpose Y and the evolution of this adaptation was caused by natural selection.” A critical component of such statements is that they are historical in nature: reference is to historical events, not ongoing processes. Are we justified in referring to this design as an adaptation in the Darwinian sense and thus projecting a specific causal mechanism into the past? One approach to answering this question is to consider the kind of knowledge which is required by the theory of natural selection itself in order to analyze the ongoing evolutionary dynamics of a phenotypic characteristic. The following list, although certainly not exhaustive, summarizes some of this knowledge.

1. Knowledge about heritability. Does the phenotypic characteristic we are studying have a genetic basis? To what extent is the phenotype controlled by nongenetic factors?

2. Knowledge about genetic variance and its relationship to intrapopulational phenotypic variability. Given that a phenotypic characteristic has some genetic basis and is thus heritable, we want to know, first, how much genetic variance is present, and second, how this manifests itself in intrapopulational phenotypic variability. Does the observed phenotypic variance have an underlying genetic basis?

3. Knowledge of the relationship between intrapopulational phenotypic variation and variation in fitness. An argument that a phenotypic characteristic evolved by natural selection and is therefore an adaptation implies that phenotypic variability is directly related to variance in fitness. If variance in a phenotypic characteristic cannot be related to differences in fitness, then it cannot be claimed that the characteristic is an adaptation whose evolution was mediated by natural selection.

4. Knowledge about the nature of natural selection. Most functional evolutionary morphology has a very simplistic view of natural selection. Because of the parochial interests of investigators, adaptive stories are usually restricted to “my favorite part of the phenotype.” But what is the unit of selection? As Lewontin (1979) has questioned, can a whole organism be decomposed into separate phenotypic units and to what extent is it valid to examine the evolution of each unit from the standpoint of natural selection?

One implication of these adaptive stories is that survival, reproduction, and/or fecundity are nonrandom with respect to the variance of the phenotypic characteristic being studied. What is the evidence, derived from information about the population structure of the species, that these components of fitness are not simply random with respect to the pattern of phenotypic variation being studied? And if the correlation between phenotypic variation and fitness is nonrandom, what is the evidence that differences in fitness are a direct result of that particular phenotypic variation?

If the above kinds of knowledge are required to study the process of adaptation, it should be fairly obvious that functional evolutionary morphology—as well as most other areas of evolutionary biology—is not engaged in the study of adaptation. There can be no question that functional evolutionary morphology is concerned with discovering why organisms seem designed
the way they are, but there is no compelling reason why these findings must be tied to a specific theory of causal process. The causal process is outside the realm of analysis for those investigating historically-based events. The critical factor in the scientific study of any phenomenon is that explanatory hypotheses should be susceptible to criticism, that explanations should be evaluated by empirical tests of some sort. As far as I can see, statements of the type that "phenotype x is an adaptation, evolved via the agency of natural selection" are thoroughly untestable. The necessary data needed to refute such an assertion cannot be gathered, and we are more or less forced to accept it as an article of faith rather than as a scientific statement.

The current problems of adaptational analysis seen within functional evolutionary morphology can be illuminated more fully when some of the best studies are examined as to their logical structure. I suggest that the following general scheme of argumentation is adopted wholly or in part by most of these studies:

1. PREMISES
   1. Observations:
      a. Species 1 possesses phenotypic characteristics $P_{1,1}$, $P_{1,2}$, ..., $P_{1,N}$.
      b. Species 2 possesses phenotypic characteristics $P_{2,1}$, $P_{2,2}$, ..., $P_{2,N}$.
      c. In species 1 the phenotypic characteristics have functions $F_{1,1}$, $F_{1,2}$, ..., $F_{1,N}$.
      d. In species 2 the phenotypic characteristics have functions $F_{2,1}$, $F_{2,2}$, ..., $F_{2,N}$.
   2. Inferences:
      a. Based on methods of phylogenetic reasoning, species 1 is hypothesized to be relatively primitive and species 2 relatively derived.
      b. Because of $F_{1,1}$, $F_{1,2}$, ..., $F_{1,N}$ and $F_{2,1}$, $F_{2,2}$, ..., $F_{2,N}$ and because of environmental constraints $E_1$, $E_2$, ..., $E_N$, phenotypic characteristics $P_{1,1}$, $P_{1,2}$, ..., $P_{1,N}$ and $P_{2,1}$, $P_{2,2}$, ..., $P_{2,N}$ serve the following biological roles, $R_{1,1}$, $R_{1,2}$, ..., $R_{1,N}$ and $R_{2,1}$, $R_{2,2}$, ..., $R_{2,N}$.

II. AXIOMS
   A1. Natural selection is the causal agency of evolutionary change in form, function, and biological role.
   A2. Any biological role (a form-function-environment interaction), if it has been evolved by the process of natural selection, can be termed an adaptation.

III. CONCLUSIONS
   C1. There has been change through time in the homologous structures $P_1$, $P_2$, ..., $P_N$ (from IIA, IIB, I2A).
   C2. There has been change through time in the functions of homologous structures (from IIC, IID, I2A).
   C3. There has been change through time in the biological roles of homologous structures (from I2A, I2B).
   C4. The form, functions, and biological roles of species 2 evolved from conditions similar to those of species 1 because of the agency of natural selection (from C1, C2, C3, IIA1).
   C5. Biological roles $R_{2,1}$, $R_{2,2}$, ..., $R_{2,N}$ in species 2 are adaptations (from C4 and IIA2).

I recognize this scheme is simplistic in some respects. For example, the determination of phenotype or function may be highly inferential, particularly with fossil organisms. However, the scheme depicts a hierarchy of reasoning. Statements about phenotype and function are closest to the "data base," the organisms themselves. Statements about change (conclusions C1, C2, C3), without specifying process, are more remote from the data base in that they rely upon some method of comparative analysis and phylogenetic reasoning. Still further removed from the data base are statements about process (conclusions C4 and C5). In fact, within functional evolutionary morphology—and evolutionary
biology as a whole—conclusions C4 and C5 are dependent upon acceptance of certain axioms, propositions adopted as being true in order to achieve a causal "explanation." As such, conclusions C4 and C5 are explanations only in an axiomatic sense: Much of the content of C4 and C5 is already embedded in the premises and axioms. This method of reasoning is not objectionable per se as long as the axioms or general laws are themselves highly corroborated hypotheses. My perception of the present state of evolutionary biology is that natural selection cannot be claimed to be a universal causal mechanism for the origin and maintenance of phenotypic diversity and design. This is not to say, of course, that natural selection is not operating or that it is unimportant in evolution, only that it cannot be applied as a general law in evolutionary explanations. The point worth stressing in the present context is that studies within functional evolutionary morphology are permeated with axiomatic reasoning and that this does not increase their explanatory context. Some examples will illustrate this.

Among the best comparative functional work in recent years has been that of Liem on cichlid fishes (Liem, 1973, 1978; Liem and Osse, 1975). Using detailed description and modern experimental techniques, he is producing an important body of knowledge about the form and function of the musculoskeletal system within the vertebrates. In several of his papers, he has also sought to provide an evolutionary perspective on his results, and I wish to focus my discussion on this aspect. In particular, we can examine his 1973 study in which he attempted to depict the evolution of the cichlid feeding mechanism from the more primitive percoid type.

Liem first characterizes the generalized percoid pharyngeal jaw apparatus by describing the morphology and a series of elaborate and excellent functional experiments. He then does the same for a generalized cichlid jaw mechanism (Haplochromis burtoni). This part of his study would conform to 11a–d of my scheme discussed above. Next he makes an inference about the direction of evolution (12a): based on outgroup comparison he reasons that the percoid condition is primitive, the cichlid condition derived.

It is at this point that he endeavors to provide evolutionary interpretations, some of which follow:

1. The cichlid jaw apparatus "represents a major adaptive complex" (p. 432).
2. "The entire conversion has been accomplished by a modification of pre-existing structural elements, which, when functionally integrated, give rise to a new and vastly improved character complex of high selective value" (p. 435).
3. "Natural selection has produced all possible types" (p. 437).
4. The cichlids, because of their new feeding mechanism, possessed "a distinct selective advantage" (p. 438).
5. "During adaptation, under control of the selection forces for food preparation and manipulation, the new adaptive complex is perfected" (p. 439).

Finally, he proposes a general hypothesis: that the seemingly gradual emergence of the cichlid adaptive complex . . . took place by rapid salutary steps under influence of strong selection pressure acting not on a single gene but on the minor reconstruction of the genotype which is involved in the necessary evolutionary changes of the controlling ontogenetic mechanisms" (p. 439).

I suggest the lines of reasoning in his analysis of cichlids are fairly typical of those within functional evolutionary morphology. Whereas his conclusions about change in form, function, and biological role are well supported and have a close tie to the original data, those about adaptation and causal mechanism are entirely axiomatic.

Liem's work is the subject of my criticism only because his functional morphological analyses are so distinguished and because he is providing a solid foundation for considerations of evolutionary change in form and function. But I seriously question the significance of his statements about process; my interpretation is that studies like his do not increase our knowledge or un-
understanding of the mechanism of evolution, they do not answer the evolutionary why and how of phenotypic design.

Liem, of course, is not alone. Many other excellent studies are conceptualized in the same terms. Bramble (1978, p. 272), for instance, in his important contribution on mammalian feeding biomechanics, identifies a number of key issues, one of which is "What was the relative importance of selection for improved hearing ability, versus that for feeding competency, in shaping the course of mandibular evolution in mammal-like reptiles?" How could this question possibly be answered?


One study within functional evolutionary morphology purporting to investigate natural selection directly is the analysis of Webster and Webster (1971) on Kangaroo Rat (Dipodomys) predator avoidance (in their later study on heteromyids, 1975, process is viewed axiomatically). They experimentally reduced the middle ear volume of Kangaroo Rats and found significant loss in recapture rates, thus suggesting the action of rattlesnakes, but only during the dark phase of the moon. If light is available, Kangaroo Rats apparently avoid predation even when ear volume is reduced. They conclude (p. 321) that "two sensory mechanisms [i.e., eyes and ears] to detect predators, which can be used either together or separately, provide this animal with a distinct adaptive mechanism for survival..."

The study of the Websters can serve as the epitome of the functional evolutionary morphologist's dilemma: What questions are we trying to answer? Are we concerned primarily with description of form and function? Are we attempting to identify the biological roles of morphological features? Or are we asking questions about process, about the evolutionary dynamics of the phenotype? The Websters have focused at the level of form, function, and biological role, but the design of their study cannot answer questions about process. For example, one obvious question is the extent of intrapopulational variability in the form and function of the middle ear and its relationship to fitness. Even a definitive answer to this question still leaves open the problem of identifying other aspects of the phenotype and their contribution to fitness. Perhaps the problem is ultimately intractable.

The obvious rebuttal to the above remarks will be to ask what all the fuss is about. Am I not being impossibly restrictive with my requirements for studying process? My response is that, yes, perhaps I am restrictive, but the restrictions are set by the theory of natural selection, not me. I only urge functional evolutionary morphology to undertake realistic studies of process. There are other reasons for adopting my viewpoint. First, axiomatic reasoning, as it is employed by functional evolutionary morphology, simply does not increase our knowledge about process. It seduces investigators (particularly students) into thinking they are working on questions of general importance when they are not. Second, this form of axiomatic reasoning leads to an abundance of untestable statements in the literature. And, if scientific statements are not open to rational criticism, how can progress be made? Third, axiomatic acceptance of the causal process of natural selection diverts attention away from the truly important question of determining the components of evolutionary dynamics of the phenotype. Natural selection as a causal mechanism is widely accepted within evolutionary biology more for heuristic, common-sense reasons than for any real understanding of its action in natural populations. Moreover, it is clear that statements about natural selection should be restricted to the intrapopulational level of analysis; extending natural selection to specific and supraspecific levels, as do
nearly all of the above cited studies, further confuses the issue of process analysis (Eldredge and Cracraft, 1980).

CONCLUSIONS

Two major arguments have been proposed in this paper. First, a convincing case has not been presented that functional data are a necessary component of phylogenetic analysis. Moreover, the history of systematics demonstrates conclusively the ability of workers to produce corroborated hypotheses of relationships in the absence of functional data. Any malaise which exists in the consciousness of systematists regarding our inability to reconstruct the history of life can be traced, in my opinion, to an unfamiliarity with the fundamentals of comparative phylogenetic reasoning. Patterson (1977) has provided detailed documentation of this in the history of teleostean phylogeny and systematics, and I believe this observation is applicable to systematics in general. Certainly there is nothing in the writings of those advocating a functional approach to systematics to make us believe they have a cure for this malaise.

Second, functional evolutionary morphology employs axiomatic reasoning in its treatment of causal process, primarily in statements about natural selection and adaptation. Because of the kinds of data needed to relate intrapopulation phenotypic variability to variation in fitness, as required by the theory of natural selection, our ability to apply process explanations to studies which are historical in context is severely limited. This does not mean, of course, that we cannot study evolutionary change in form, function, and, to a lesser extent, biological role. That functional evolutionary morphology is limited in its ability to study process phenomena suggests that more discussion about its research strategy and goals would be highly desirable.

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