FUNCTIONAL MORPHOLOGY AND SYSTEMATICS: Studying Functional Patterns in an Historical Context

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INTRODUCTION

The study of function is a neglected area of systematic and historical biology. Over the last 20 years, systematic biology has expanded to include in its purview the study of many different kinds of patterns, and structural features of all kinds have been the subject of phylogenetic analyses. In addition to macroscopic structural features that have been the traditional source of characters reflecting patterns of ancestry and descent, systematists have increasingly relied on DNA base and amino acid sequences, electrophoretic banding patterns, and ontogenetic sequences of character transformation to sort out genealogical patterns (e.g. 21, 51, 63, 72, 111). Morphological features of organisms have been used by systematists as the basis for biogeographic (120, 157, 158), morphometric (17, 134), ontogenetic (1, 54, 55, 72), and quantitative genetic analyses (130) as well as for studying speciation patterns, and ecological and coevolutionary interactions (18–20, 27, 104). But data on organismal function have been both the least used and the least understood class of information about organisms in systematic biology.

There are three main reasons why the form-function relationship, long a central dichotomy in biology (124), has been so heavily weighted toward the

study of form in systematic and evolutionary biology. First, comparative phylogenetic analysis arose historically from a morphological tradition in the nineteenth century, while functional analysis became part of the research tradition in physiology. Since the divergence of the morphological and physiological research programs near the turn of the century (5, 6, 25), little interaction has occurred between them, and functional analysis has played a relatively small role in phylogenetic research. Second, functional analysis is often extremely time consuming, and obtaining even limited functional data for many species within a clade may take years. Thus, only rarely are functional data available for broad comparative investigations. Thirdly, the inference of function from morphology and the heuristic use of functional concepts have often been substituted for the direct experimental measurement of functional attributes in living organisms. While many general discussions have recognized the importance of data on organismal function (13–15, 41, 43–45, 62, 74, 83, 97, 137, 149, 151), a large number of papers have presented "functional analyses" based primarily on the study of structure (e.g. 11, 12, 33, 34, 59, 98, 99, 129, 136, 137). Relatively few papers have actually quantified function in living animals *and* provided direct examples in which measured functional attributes of organisms are useful for understanding problems in historical biology. Thus, despite many statements in the literature supporting the importance of functional analysis, only a small number of papers use *both* experimentally determined function and phylogenetic analysis. Many discussions of the utility of functional analysis present purely morphological data and then infer rather than measure function.

The central theme of this article is that the direct experimental measurement of organismal function in living animals provides insights, not obtainable by other means, into *(a)* the uses of structural characters, *(b)* how and why characters are distributed the way they are on a cladogram, *(c)* interactions and correlations among characters, *(d)* the nature of organismal diversity, and *(e)* historical patterns to organismal design.

WHAT ARE FUNCTIONAL DATA?

The study of function is the study of how structures are used, and functional data are those in which the use of structural features has been directly measured. Functions are the actions of phenotypic components (34, 47, 48, 83, 84). For example, the sequence of amino acids in an enzyme constitutes structural (morphological) data on that enzyme. The maximum rate of catalysis (V_{max}) or the affinity of an enzyme for its substrate (K_m) constitutes functional data on the enzyme. Similarly, structural data on a muscle might include the morphology of the sarcoplasmic reticulum, the amino acid sequence of the myosin molecules, changes in the electrophoretic banding

pattern of muscle myosins during ontogeny, the amount of pinnation in the muscle fibers, the cross-sectional area of the muscle, and the length of the muscle. Functional (or physiological) data on muscle might include the time to peak tension, maximum tetanic tension, myosin ATPase reaction rates, work done or oxygen consumption in a single contraction, patterns of electrical activity during animal movement, or how any muscular rate process changes with temperature (Q_{10}). I do not include measurements of muscles such as lever arms or other morphometric features as functional data, even though such information may be interpreted in a functional context and may be useful in inferring functional characteristics.

Functional characteristics may also be measured at the whole animal level. As measurements are made that integrate increasing numbers of lower level functions, functional data become difficult to distinguish from behavioral data. Examples of functional attributes at the whole organism level include resting metabolic rate, maximal running speed, footfall patterns, and preferred body temperature. Functional data may overlap measures of animal performance. Performance measures the ability of an animal to execute a behavior or the effectiveness of an animal at accomplishing a particular task (7, 39, 83, 141). Typical performance measures include maximal swimming speed, the percent of successful feeding strikes, maximal jumping distance, or the largest size of prey that can be crushed. In addition, functional data may form part of a behavioral analysis. For example, behavioral analyses of frog or bird vocalizations often include the study of specific functional attributes of the call or song.

Use of the term "function" is subject to two confusions in the literature. First, ethologists commonly use the term function as a synonym of "selective value" (10, 23, 80). As discussed elsewhere (80) the use of "function" in this way is associated with many difficulties, not the least of which is the necessity of accurately understanding selective forces on a structure before one can speak of its function.

Second, function is often confused with the role that a structure plays during the life history of an organism. Bock & von Wahlert (16) emphasized a useful distinction between the terms "function" and "biological role." *Functions* are the uses of structures, while the *biological role* of a structure reflects the task of a structure during a behavior such as mating or escape from predation. The idea of a biological role is in many ways similar to the use of the term function by ethologists.

FUNCTION AND HISTORICAL BIOLOGY

There are five key areas in which the interplay between functional and historical analysis is likely to be particularly fruitful. These are treated seriatim below, to focus attention on the possible mutual influences of

functional and historical analysis. Mayr (105, 106) has emphasized the distinction between *functional biology,* concerned primarily with understanding how organisms work and proximate causation, and *evolutionary biology,* committed particularly to studying historical pathways and ultimate causation. A major theme to emerge from a consideration of five areas of interplay discussed below is that clear areas of overlap exist between these two approaches that may provide new insights into organismal diversity and the mechanisms that have produced it. Research into the evolution of function increasingly exemplifies aspects of both "types" of biology.

The Evolution of Function

Functional attributes are an important class of organismal characters. How are structures used by organisms, and how has the use of structures changed in evolution? These questions may be addressed by an analysis of both form and function in an historical context. Analysis of structural features alone will provide an incomplete picture of the nature of organismal design. Our understanding of the evolution of gastrointestinal hormones in vertebrates (140), for example, is greatly enhanced if we can, in addition to describing phylogenetic patterns to amino acid sequences, describe how changes in the structure of the active site affect function and reaction rates in each clade. Are certain changes in amino acid sequence uncorrelated with changes in function? Are particular functions retained as primitive characters despite changes in structure? Do certain structural changes at the active site permit new functions while retaining the primitive function?

Figure 1 illustrates a simple hypothetical example of a functional analysis conducted on seven species (A to G) in conjunction with a phylogenetic analysis. The branching pattern of the cladogram (Figure 1B) has been determined from a previous analysis, and structural features of a biomechanical system of muscles and bones are diagrammed in Figure 1A. Each species is studied to determine both the topology of the muscles and bones and the associated electrical activity patterns (motor patterns) of the muscles. The procedure of mapping both structural and functional attributes of the terminal species onto a cladogram allows one to make several observations about the evolution of muscle function. First, the control of bone *d* (Figure 1) evolved by a two-stage process: first ligament 6 arose, followed by ligament 7. Pathway *i* arose first, and species in clades A to E have the capability of moving bone *d* by pathway *i*. Subsequently, pathway *ii* arose by the addition of ligament 7: only clade A possesses pathway *ii*. Note that the activity patterns of muscle 5 have diverged in two clades (D - E; A - B) while clade C retains the primitive functional pattern for muscle 5. The origin of muscle 4 is congruent with its functional pattern (muscle activity pattern D), while activity patterns associated with muscle 3 show convergent evolution between

clade A and clade G - F. Muscle 3 thus exhibits an incongruence between the evolution of structural and functional characteristics.

Three main benefits are to be gained from such an analysis. First, it enables one to define precisely the historical sequence of both structural and functional change that permits an understanding of how a particular biomechanical system was constructed. In any attempt to understand a mechanical system and the causal factors involved in its construction, it is useful to know the order in which a system was assembled, to help determine the interrelationships among the parts (45). In machines constructed by humans, the order of assembly may often be reasonably inferred by the way in which the parts fit together. But for biological systems the interrelationship among structural components alone rarely provides this information. Second, historical analysis of function provides the basis for an analysis of coevolutionary
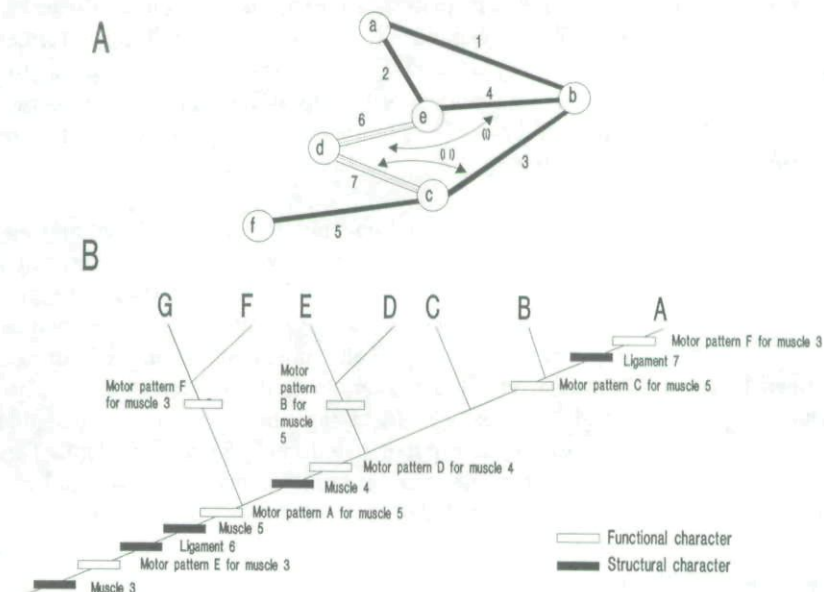

Figure 1 Schematic diagram of a complex biomechanical system (A) and the historical sequence in which it was constructed (B). Circles indicate bones, labelled with lower-case letters, while ligaments are indicated by dashed lines and muscles by black lines. There are two mechanical pathways for moving bone d: i and ii. Pathway i involves muscle 4 and ligament 6. Pathway ii involves muscle 3 and ligament 7. Note that based on the phylogenetic analysis of (B) in which the characteristics of species A to G are mapped onto a cladogram derived from other characters, the muscle activity pattern (motor pattern) for muscle 3 is convergent between clade A and clade G. Note also that functional characters (open bars) and structural characters (solid bars) may exhibit incongruent distributions: e.g., muscle 5 arises with one motor pattern (A) and only the motor pattern is transformed (into motor pattern B and C) during subsequent cladogenesis.

patterns between structural and functional data sets: do historical changes tend to occur congruently in muscle morphology and function, for example? Third, this type of analysis allows an assessment of the conservatism (or lack thereof) in functional data as compared to structural information, and a test of the oft-stated conclusion that functional data tend to be evolutionarily plastic. These last two points are considered in more detail below in sections 2 and 4.

While considerable progress has been made in attempting analyses such as those presented in Figure 1 (22, 46, 67, 74, 80, 81, 92, 94–96, 107, 126, 148, 150), complete data sets of both structural and functional characters are not yet available for many groups (84). In part, this is due to the considerable difficulty in obtaining functional data from a variety of species. Determining mechanical properties of tissues, muscle activity patterns, rates of oxygen consumption, bone movements or deformations, or fluid pressures from three to five individuals in each of a dozen or so species is a formidable task. Many species important in phylogenetic analysis are either rare or found in inaccessible habitats, or they do not respond well to laboratory conditions, further complicating the gathering of functional data. Despite such difficulties, the development of complete case studies of structural and functional evolution would be a significant step forward in attempts to understand the evolution of organismal design.

One additional area where functional and phylogenetic analyses may interact in studies of the evolution of function lies in the framing of specific functional hypotheses. Phylogenetic analyses of morphology may suggest specific functional questions (81, 94, 96, 98, 99, 126) which may then be explored. One example was provided by an analysis of locomotion in ray-finned fishes (81). An analysis on a cladogram of the sequence of character change of muscles and bones in the tail of ray-finned fishes indicated that certain muscles arose prior to the origin of an externally symmetrical tail. This suggested that the action of these muscles might influence the way the tail was used and in fact might be able to change the function of the tail between two alternative states. A functional analysis (measuring bone strain and muscle electrical activity) confirmed this prediction and indicated that previous views on the evolution of the tail in ray-finned fishes may be in need of revision.

Function and Homology

In addition to mapping functional and structural characters onto a phylogeny to conduct an historical analysis of a biomechanical system, functional characters may be used as elements of a phylogenetic analysis and may contribute to the total evidence (71) available for phylogenetic reconstruction. As such, functional characters are not different from any other attribute that might contribute to our understanding of genealogy: functions as well as

structures may be synapomorphies. For example, two species of sunfishes (*Lepomis gibbosus,* the pumpkinseed, and *Lepomis microlophus,* the redear) share a synapomorphic pattern of muscle activity (76, 78) not found primitively in the sunfish clade. Although it has previously been suggested that functional characters are not suitable for systematic analysis (26, 137), recent work has shown that functional characters (such as bone movements or muscle electrical activity patterns) may be used as characters (77, 80, 128, 144) to successfully delineate monophyletic clades.

If a particular functional character (such as: "double burst pattern of electrical activity in the rectus cervicis muscle") is treated like any other character, then clearly functional characters may be homologous or convergent (just like morphological features) and may show complex patterns of phylogenetic distribution independent of their underlying structural basis. An example of muscle activity patterns treated like characters is provided by the sunfishes (Centrarchidae) discussed by Lauder (80). A further implication of treating functional characters just like structural features is that determining the homology or convergence of functional attributes is accomplished by using the same procedures applied to structural characters. Both convergent functions and structures are recognized by their incongruent distribution on a cladogram (42, 80, 109, 110), and the status of particular characters (whether functional or structural) as homologous or convergent is dependent on the topology of the cladogram. Character status may change as the cladogram changes. Figure 2 illustrates this point. In Figure 2A structure 1 and function 1 are homologous and are synapomorphies for clade A - B, based on the topology of the cladogram given. If, however, a subsequent phylogenetic analysis shows that the cladogram topology of Figure 2B is much better supported by available data (so that now clades A and B are unrelated to each other), then both structure one and function one must be interpreted as convergent between these two clades.

When functional attributes are treated like structural features, function is not useful as an a priori guide for determining homology of structures: Function does not take primacy in homology decisions. However, a number of authors have argued that functional analysis does provide an a priori guide to determining the homology of associated structural features (8, 13, 59, 60, 65, 132, 137). Under such a view, it is "impossible for nonhomologous structures to have homologous functions" (8: p. 60), and "Functions . . . should not be spoken of as homologous" (60: p. 323). Tyler (137: pp. 334, 344) has argued that "A complete determination of the probability of homology, however, is not possible on morphological grounds alone; we need a functional analysis to gauge the probability of convergence," and that "Homology applies most appropriately to the structural features, not their functions." In this view the role of functional analysis is primary, and,
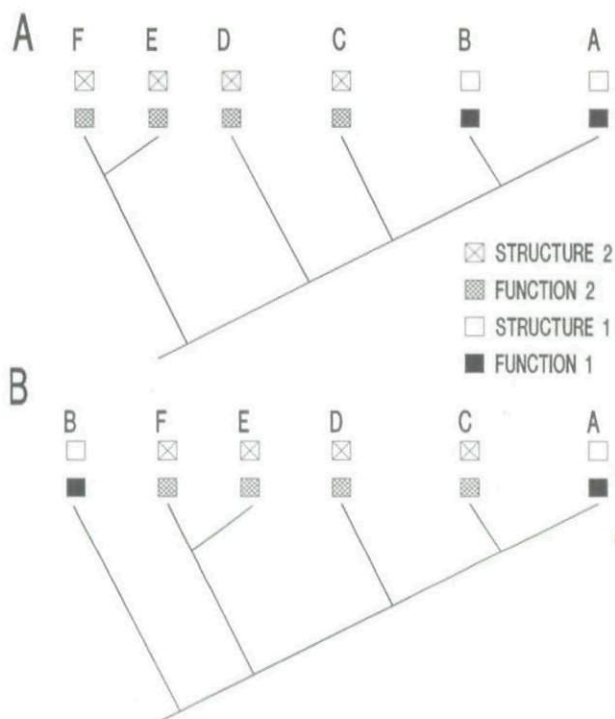
Figure 2 Interpretation of the homology of both structures and functions depends on the topology of the cladogram of the species studied. Panel A: Both structure 1 and function 1 are homologous in clades A and B. Panel B: Given an new cladogram topology with the same pattern of character distribution, function 1 and structure 1 are considered to be convergent between clade A and clade B.

independent of the distribution of characters in other taxa, functional analysis is able to assess homology or convergence of an individual character.

The idea of a priori functional analysis as a guide to homology in systematics suffers from two primary difficulties. First, the "functional" analyses conducted to determine structural homology usually only involve morphological studies. Thus, Tyler's (137) method of "functional hierarchies" involves the heuristic use of functional ideas and hypothesized functions but not the direct measurement of function or the experimental manipulation of structures. Similarly, the methods of Bock (13, 14), Gutmann (59), and Dullemeijer (e.g., 34: p. 227) are based almost entirely on a morphological analysis. Secondly, structural characters determined in some way to be homologous by a functional analysis are not subject to refutation by the discovery of another better-corroborated cladogram. For example, if detailed a priori functional

analysis is applied to two structural characters following the procedures of Tyler (137), Gutmann (59), or Dullemeijer (34), and these two structures are determined to be homologous (e.g. structure one in Figure 2A), what would be concluded if an analysis of DNA base sequences showed that cladogram B (Figure 2B) were in fact correct with a high degree of statistical probability? Would these authors conclude that structure one in clades A and B (Figure 2B) is still homologous?

The Analysis of Correlated Characters

Functional analyses help to address the question of how and why characters are correlated with one another in phylogeny. Patterns of character distribution on cladograms have been the subject of increasing analysis in recent years (e.g. 31, 66, 117, 131, 150), and interest in explaining distributions of characters and determining the significance of correlated character distributions has increased also (18, 20, 24, 37, 38, 58, 66, 67, 130, 157).

One role that functional or biomechanical analysis may play in the analysis of correlated characters is to place boundary conditions on hypotheses of form-function-performance relationships (82). For example, a common goal of comparative functional analyses is to analyze morphology and function as well as the performance of the organism at particular behavioral tasks (7, 39, 101, 141). For example, the jumping performance (ability) of species in a clade of lizards, as measured by maximal jump distance, may be studied by analyzing the structure of the limb bones and muscles in an attempt to explain the evolution of interspecific differences in locomotor ability. One might hypothesize that a particular morphology (such as a long femur) or function (such as coactivation of the rectus femoris and gastrocnemius muscles) in a group of species is causally related to increased jumping performance. In Figure 3A, the clade of species A-B-C is characterized by both a long femur and increased jumping performance (solid circle and square). There is a congruent (correlated) historical origin of these characters on the cladogram. If, after an analysis of femur length and jumping distance for species A to F an incongruent origin was found (Figure 3B) such that the origin of increased bone length precedes the origin of increased jumping ability, then clearly a causal hypothesis of relationship among the two characters is not supported. Greene (58) discusses this pattern of character distribution and notes as a minimal requirement that features thought to be adaptations should have a historical origin concordant with the proposed behavioral advantage.

However, the criterion of historical concordance is not sufficient to establish a causal link between a particular morphological or functional attribute and increased performance. Typically, many derived features will characterize a clade. If, as in Figure 3C, several derived morphological attributes characterize the clade A-B-C, then how are we to choose which
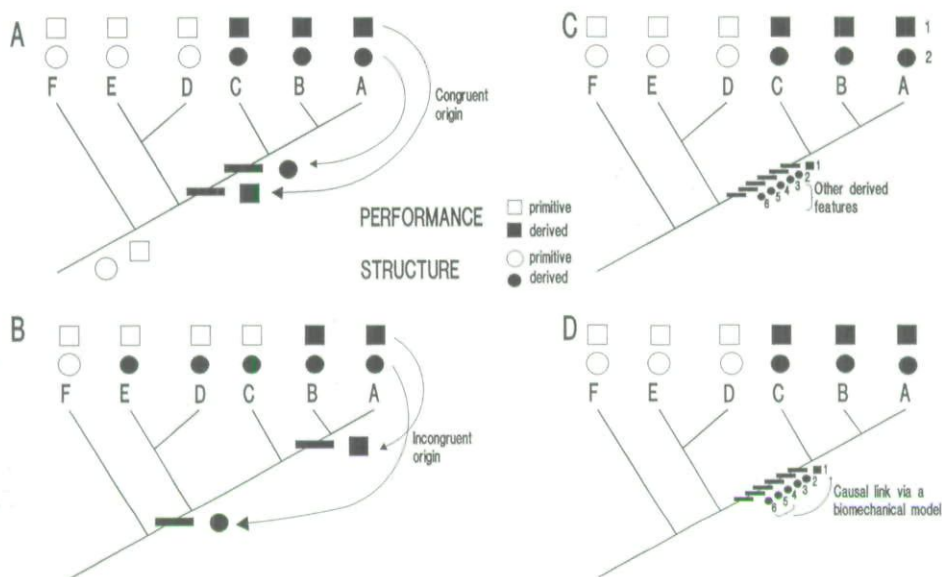
Figure 3 Diagram to indicate how functional analysis may play a role in analyzing the pattern of characters on a cladogram. Although congruent historical origins of performance, functional, or structural characters may *suggest* a causal hypothesis of relationship, a biomechanical or functional analysis can assist in testing a causal hypothesis. Clades will often be characterized by many novelties at each level (panel C) but how are we to distinguish historically correlated characters from those sharing a causal relationship? A biomechanical or functional analysis (panel D) may assist by providing a causal model.

changes in body or limb proportions or which structural characters (features 2-6, solid circles) are *causally* related to the observed changes in performance (feature 1, solid square). Perhaps novelty 3 in Figure 3C is the morphological character "increased lever arm of the biceps muscle." Without some external model or criterion to rely on, there is no way to determine which of the five structural characters sharing a congruent (correlated) historical origin is causally related to the performance change (Figure 3C). The fact that changes in the biceps muscle are not expected to affect jumping ability in any way is only predictable from a causal biomechanical model (37, 82, 160).

A critical role of functional morphology in historical analyses of form and function is to provide an experimental, theoretical, and mechanistic basis for choosing which of several correlated characters are in fact causally related to historical changes in function or performance (Figure 3D). Functional analysis contributes to understanding at a mechanistic, proximate level why characters are historically correlated with one another (37, 82). Thus, only characters 5 and 6 (Figure 3D) might be biomechanically related to increased

jumping performance. Characters 2, 3, and 4 may have nothing to do with performance character 1. As analyses of large data sets in systematics become more common, as patterns of character evolution are increasingly examined using computer programs such as MacClade and PAUP (31, 135), and as interest rises in explaining why characters have the distributions they do, it becomes increasingly important to be able to separate characters that have congruent (correlated) distribution patterns by chance from those that are causally related.

Three main types of functional analysis might be done to assist in the analysis of patterns of character distribution such as those shown in Figure 3C. First, descriptive functional studies such as quantifying patterns of movement, muscle activity, or pressure change in living animals (3, 4, 29, 30, 49, 52, 61, 68, 70, 81, 93, 114, 121, 122, 147, 159) provide a baseline of functional data that may provide a test of proposed causal links among characters. For example, if two muscles attaching to bone A had a congruent historical origin with that bone (as in characters 2, 3, and 4 in Figure 3C), measurement of muscle activity might show that only muscle 1 is electrically active during the stance phase of locomotion. An hypothesis that the correlated historical origin of muscle 2 and bone A is related to acceleration ability in species A, B, and C (Figure 3C) would be refuted as the muscle is not active during the appropriate phase of the locomotor cycle. Thus, even primarily descriptive functional analyses have the ability to provide a decisive test of historical explanations for character distribution.

A second type of functional analysis involves direct experimental modification of structures in animals to test proposed form—function—behavior relationships (e.g. 50, 69, 79, 86, 91; also see Eaton & DiDomenico—36, for a theoretical discussion of manipulation experiments). By cutting a ligament connecting two bones, for example, and monitoring behavioral or kinematic patterns before and after surgery, proposed functional hypotheses may be tested directly. If a novel muscle and increased jumping performance show a correlated historical origin in a clade (Figure 3C), then functional experiments involving cutting of the muscle tendon and the assessment of jumping performance before and after surgery provide a direct test of the causal link between the presence of the muscle and jumping ability.

A third method of assessing the significance of correlated characters is that of modelling (28, 113, 155, 160). By constructing theoretical models of morphology and using such models to generate a range of possible outputs, given known morphological inputs, understanding is gained of the significance of morphological variation in a particular mechanical system. Such models may involve mathematical descriptions of shape or direct measurements of lever arms, muscle masses, and lines of muscle action to estimate the effect of changing one anatomical link in a complex linkage system. Me-

chanical models of the feeding system in mammals (28, 57, 155), for example, have allowed understanding of the functional relationships among the bones and muscles and of the significance of changes in the jaw articulation at the base of the mammalian clade.

In summary, one major role of functional analysis in systematic biology is to contribute to our understanding of how characters interact within the organism. How do we *explain* patterns of character distribution? Why is it that on a particular cladogram two characters appear to have evolved together? Functional morphology by no means provides all the answers to this question as other explanations (not mutually exclusive) also exist: correlated characters may occur because of genetic linkages (40, 127, 130). But functional analysis is able to provide experimental tests, at the phenotypic level, of hypothesized functional dependencies among characters.

Congruence Among Classes of Characters

Functional analyses are important for examining the extent of congruence in change among characters at different levels of biological organization. To some extent, the analysis of congruence among classes of characters is a special case of the analysis of correlated characters considered above. However, the question of the extent of congruence among different types of characters (e.g. behavioral, morphological, ecological) is an issue that is receiving increasing attention from comparative biologists (20, 24, 58, 66, 82, 101). Since the study of function provides the hierarchical link between morphological characters and performance, behavioral, and ecological characters, functional characters form an important class of information about organisms that merits detailed investigation. Table 1 summarizes one possible hierarchy of levels of design. This hierarchy illustrates seven classes of characters that could be investigated if one wanted to obtain an understanding of organismal design from the level of the nervous system to ecological interactions. A critical point is that functional information provides a link between levels 7 and 5 and between levels 5 and 3. An understanding of the morphology alone (levels 7 and 5) is not sufficient to understand the interactions among the levels of organismal design.

With a hierarchy of levels such as that depicted in Table 1 as a starting point, one can address questions about phylogenetic changes at these different levels, the extent of congruent change among levels, and questions of conservatism at any individual level. For example, within a clade are certain levels of design more evolutionarily conservative than others? Do changes in characters at two adjacent levels tend to occur in concert while characters from disparate levels show more divergent specializations? Does any one level exhibit a greater degree of homoplasy than other levels?

Most authors have viewed functional and physiological data as extremely

Table 1 Levels of analysis that might be studied in attempts to analyze historical patterns to character transformation.

Level of analysis	Example of patterns that might be studied
1. Ecological	Intraspecific and interspecific resource use
2. Behavioral	Sequence of behaviors used during mating
3. Performance/effectiveness	Distance moved per unit time; number of prey captured per unit time
4. Functional/physiological: at the level of peripheral tissues	Physiological properties of muscles and the timing of activation; kinematics of movement; enzyme kinetics; biomechanical properties of tissues
5. Structural: at the level of peripheral tissues	Topology of the musculoskeletal system; tissue histology
6. Functional/physiological: at the level of the nervous system	Neuronal spiking patterns; neurotransmitter modulation
7. Structural: at the level of the nervous system	Neuronal morphology; patterns of neuronal circuitry

plastic and subject to considerable homoplasy when comparisons are made across taxa. Level 4 in Table 1, function and physiology at the organismal level, is the class of characters that has been considered the most labile in evolution. Tyler (137: p. 344) asserts that functions vary extensively across clades and that therefore "functions do not constitute reliable systematic characters in their own right." Other authors (9, 64, 152) have advocated the view that physiological data are plastic and exhibit little phylogenetic coherence.

While there is no doubt that certain functional characters may vary considerably across taxa, there are no quantitative data indicating that function is any more or less variable than structural characters on average. When individual functions (such as metabolic pathways) are compared across a wide range of taxa and found to vary considerably, the fact is often ignored that many structural features of these same taxa are also extremely variable. No statement about the historical lability of function has yet been based on a phylogenetic analysis of both structural and functional data.

In fact, growing evidence exists to support the opposite view, that functional characters may often be extremely conservative: Functions may be plesiomorphic characters within a clade that are retained while associated structural features undergo considerable specialization (53, 76, 77, 80, 83, 90, 115, 125, 128, 131, 140, 144). Also, when changes do occur in functional characters, the clades diagnosed by the individual functional character states often corroborate the monophyly of clades diagnosed by structural features.

For example, Mommsen & Walsh (107) show that urea synthesis in

vertebrates has a coherent phylogenetic pattern in which changes in urea synthetic pathways corroborate phylogenetic groupings based on structural features. Goslow et al (53) note that the locomotor system of vertebrates may have retained several basic functional patterns despite substantial changes in the peripheral morphology of the limbs across vertebrates. Dumont & Robertson (35) have argued that many features of neuronal circuit function are highly conserved in evolution despite significant morphological changes in peripheral structures.

Over the last ten years, research on the evolution of function in the feeding and respiratory systems of ray-finned fishes and salamanders has also shown that functional patterns may be conservative (73, 76, 77, 80, 94, 95, 100, 123, 125, 142–145, 156). Figure 4 is a schematic summary of some of the findings from this research which has focused on the evolution of muscle and bone structure and function as a case study in the evolution of levels 2, 3, 4, and 5 in Table 1. Figure 4 illustrates the fact that functional attributes, when treated phylogenetically, may be more conservative than morphological features. For example, sunfishes (Centrarchidae) differ considerably in morphology of the feeding system and are ecologically disparate in the food resources utilized (144). However, as shown in Figure 4A, the muscle activity pattern (or motor pattern) used by the jaw muscles is similar for all species that have been studied. Similarly, the pattern of muscle activity in the pharyngeal jaw muscles is conserved across sunfishes except in two species that share a derived motor pattern (Figure 4B; 76, 78). Many kinematic features associated with prey capture in ray finned fishes have been found to be conserved across phylogeny, as have basic patterns of pharyngeal jaw muscle activity (Figure 4C; 73, 90). Finally, Reilly & Lauder (115) have found that many features of the kinematics of prey transport in vertebrates are conserved across the aquatic-terrestrial transition (Figure 4D): terrestrial tongue-based prey transport uses a kinematic pattern very similar to that used by fishes for hydraulic prey transport.

Functions may also be ontogenetically conservative as shown by an analysis of muscle activity patterns during salamander ontogeny (Figure 5; 88, 89). When tiger salamanders undergo metamorphosis (during which considerable morphological change takes place in the head muscles and bones; 32, 87, 116), the pattern of muscle activity used for feeding in the water remains the same. Thus, the larval motor pattern is retained across metamorphosis, and the terrestrial motor pattern is added onto the previous functional pattern (Figure 5). Weeks & Truman (153, 154) have shown that there is considerable conservatism in the motor patterns used during metamorphosis in the tobacco hornworn *(Manduca):* Even after the prolegs and their muscles are lost at pupation, the motoneurons continue to generate the larval motor pattern.

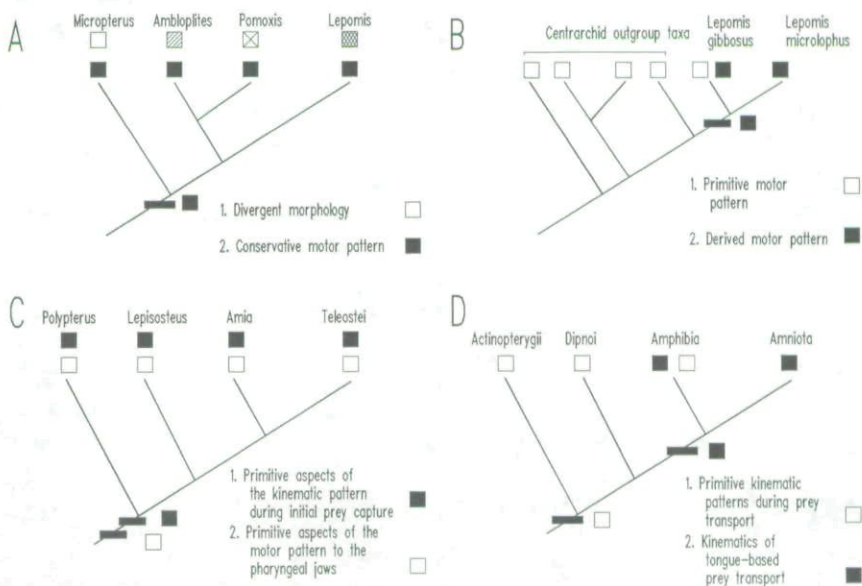Thus, one major conclusion to emerge from research on the ontogeny and

Figure 4   Four examples of studies that provide an historical analysis of both structure and function. Panel A: Results from the research of Wainwright & Lauder (143, 144) showing that within the sunfish family (Centrarchidae) the pattern of muscle activity used during feeding is conserved while the feeding morphology has diverged considerably throughout the clade. Panel B: Results from Lauder (76, 78) showing that two species share a derived motor pattern in the pharyngeal jaw muscles. Panel C: Results from the work of Lauder (73, 77, 79, 90) to show that many functional attributes (of both initial prey capture in fishes, solid squares, and pharyngeal jaw muscle activity patterns, open squares) are conserved throughout the evolution of ray-finned fishes. Panel D: Results from Reilly & Lauder (115) to show that many aspects of the function of the jaws and tongue during prey transport are retained across the aquatic—terrestrial transition in vertebrate evolution (e.g., hyoid retraction occurs during the fast opening phase). Experimental data for amphibians show that they retain many primitive kinematic features and that they possess some derived aspects of prey transport: thus this clade is indicated by both open and filled squares.

phylogeny of muscle and bone function is that functional characters may in fact be more conservative than many structural characteristics. This will not always be the case, but it is certainly incorrect given present data to assert that functional characters are evolutionarily labile.

General Principles of Organismal Design

Functional analyses contribute to defining general patterns and principles in the evolution of design. Central to any attempt to define general principles of organismal design is an understanding of how structural components of the organism are built and function (74, 82, 146). Biomechanical analysis serves
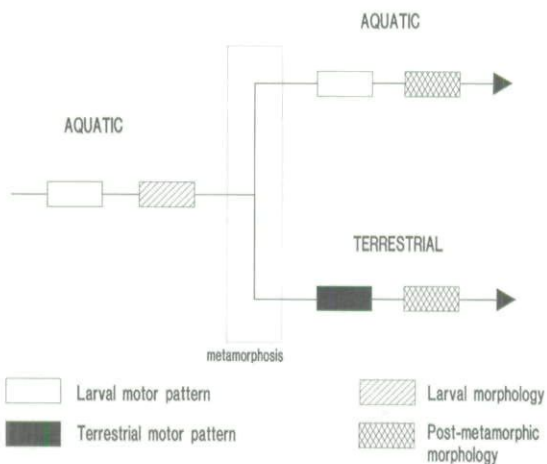
Figure 5 Schematic diagram of ontogeny in metamorphosing tiger salamanders *(Ambystoma tigrinum)* shows that functions may be ontogenetically conserved (88, 89). At metamorphosis a muscle activity pattern used for terrestrial feeding is acquired (black box), but the larval pattern is retained and is used during aquatic feeding (open box). Retention of the larval muscle activity pattern occurs despite the many changes in morphology of the bones and muscles of the head at metamorphosis (hatched boxes).

to define the physical constraints within which organisms must work (56, 75, 147), and a phylogenetic analysis of both form and function allows the historical pathways taken during transformations of organismal design to be followed, and hypotheses about the evolution of design to be tested (74, 75, 97).

Two central contentions of my previous discussions of historical patterns to organismal design (74, 75, 82, 83, 85) are, *(a)* that there are general patterns and regularities to how structure and function change and interact in evolution and that hypotheses about these patterns may be generated and tested, and *(b)* that much of the regularity to historical patterns of form and function stems from intrinsic design features of organisms. Some authors (e.g. 133: p. 128) have argued that historical events are unique and that in the unique history of life there is no place for general patterns or "recurrent repeatable relationships." This view ignores three key facts: *(a)* that many aspects of historical change in organismal design are not unique and do occur over and over again in the history of life (e.g. segmentation of structures, helical fiber organization), *(b)* that organisms exhibit constrained ontogenies that limit the range of possible organismal design solutions to environmental problems (2, 56), and *(c)* that many characters, both structural and functional, are retained throughout speciation events (as plesiomorphies) and thus form part of the historical "burden" (118) of a clade.

One example of a repeatable historical pattern is the repetition of individual structural components of design (other examples are presented in 74, 75, 126, 138, 139). Repetition of structural elements has occurred in many groups of vertebrates, invertebrates, and plants. Vertebrae, limbs, body segments, genes, many aspects of plant structure, as well as numerous other component elements of organisms are all repeated modifications on a common structural theme. Typically, specialization of some of the repeated elements has followed phylogenetically from primitive similarity among the individual components.

What is the significance of repeated design elements for the evolution of form and function? Can we frame testable hypotheses about the evolution of structural diversity? As one example of the historical implications of repeated elements of design, consider the evolution of gene structure and function. If one asks the question: "What is the causal explanation for the diversity of proteins in the family of vertebrate hemoglobins?," it is clear that at least one proximate historical cause is gene duplication early in the evolution of hemoglobin. As has been discussed in detail elsewhere (85, 103, 108, 112, 119), gene duplication is historically permissive in that a primitive gene duplication event allows subsequent specialization of both structure and function in the second gene copy during cladogenesis. While we may have no idea of the ultimate causes of the duplication event itself (or of the selective factors, if any, that lead to gene duplication), without the additional source of structural and functional variability provided by additional copies of functionally important genes, the diversity of functions supported by the multiple variants of hemoglobin proteins would not exist: one copy of a functionally important gene is constrained from change by the critical nature of its product or regulatory function. While gene duplication is not the only mechanism responsible for protein family diversity, it is certainly a critical one for many classes of proteins. Minimally, gene duplication is sufficient for generating protein diversity; it is perhaps also necessary if other genetic mechanisms are not active for any particular family of proteins (108).

Raff et al (112) have discussed another major consequence of protein diversification through gene duplication: the ability to modulate the timing, location, and amount of protein synthesis to a greater extent than when a single-gene copy is present. Gene duplication, then, allows both structural and functional specialization in families of proteins.

Similar patterns of structural duplication are found at the organismal level in many plants and animals, and similar historical consequences may be observed. After the origin of repeated structural elements in a clade, subsequent cladogenesis is typically marked by independent specialization (both structural and functional) of at least some of the repeated elements. The evolution of the feeding system in ray-finned fishes has provided one example in which the evolution of a second biomechanical linkage system in the jaw

has permitted subsequent historical divergence in the morphology and function of the feeding mechanism (73, 74, 85).

It is also possible to define a set of steps by which historical hypotheses about the evolution of morphological and functional diversity may be tested (85). Historical hypotheses are testable by quantitatively comparing ingroup and outgroup taxa with respect to a proposed novelty. As the example of gene duplication illustrates, there are common features to organismal design that appear to have general (and predictable) consequences for subsequent diversification of structure and function.

Emerson (38) has provided the best quantitative test to date of the historical effect of a morphological novelty. Emerson investigated frog pectoral girdles with the aim of assessing the extent of repeatable historical transformation in shape. Specifically, she tested the decoupling hypothesis (74)—that an increase in morphological constraint (and therefore a decrease in morphological diversity) should be associated with a reduction in the number of independent design elements. Eight phylogenetically independent cases of cartilage fusion in the frog pectoral girdle were analyzed. Emerson (38) showed that there were repeated historical changes in shape in each clade following cartilage fusion. These data provide strong support for the idea that historically regular patterns of morphological change do exist.

SUMMARY

Functional data have been both the least used and the least understood class of data in systematics. Compared to the use of morphological features from DNA sequences to gross structural characters, patterns of distribution, and even ecological and behavioral attributes of organisms, functional characters have not been generally thought of as useful for resolving systematic and historical questions.

The current status of functional data in systematics is due to three primary factors, both historical and practical. First, current research in systematics developed primarily out of the nineteenth century morphological tradition while the analysis of organismal function was centered in physiological and experimental embryological research. At the turn of the century these two research traditions, initially complementary, diverged. While several authors have debated the severity of the divergence in research between morphologists (interested in the comparative analysis of *structure,* its development, and phylogeny) and experimental biologists (interested in *function,* physiology, or uses of structures) (5, 6, 102), there is little doubt that these two research areas diverged in the early part of this century and have remained largely separate.

Second, functional data are hard to obtain on a diversity of taxa: Gathering

a range of experimental data on even one small clade is time consuming, and conducting manipulative experiments to understand causal relationships only adds to the difficulty of comparative functional analyses. Third, many so-called "functional" analyses and discussions of the import of function for systematics are in fact purely morphological. The adjective "functional" has acquired a cachet: It sounds quantitative, technical, and sophisticated. As a consequence, it is frequently used by papers in which there is no resemblance of a true functional analysis, where organismal function is directly measured and compared with measured function in other clades. The valid heuristic use of functional ideas should not be a substitute for direct measurement.

A key aim of this paper is to suggest that functional data are in fact critical to understanding five important issues in systematics. Despite difficulties in gathering functional data, the development of even a small number of well-understood case studies would greatly enhance our appreciation of *(a)* historical patterns to functional transformation, *(b)* the use of functional characters to define monophyletic clades, *(c)* the causal basis of character distributions on cladograms, *(d)* the extent to which changes in structural, functional, and behavioral characters are historically congruent, and the extent of evolutionary conservatism at any particular level of organismal design, and *(e)* general patterns and principles in the evolution of form and function.

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