

# 1

## On the inference of function from structure

GEORGE V. LAUDER

### ABSTRACT

Inferring the function of structures in extinct organisms from analyses of morphology has been a goal of many paleontological studies, and several methods have been proposed to guide the inference of function from structure. Success has been greatest where general predictions of organismal behavior or ecology are desired. However, predicting precise aspects of organismal function from morphology depends on the assumption of a close match between structure and function. The central theme of this chapter is that this assumption is unwarranted in many cases. I present three case studies from research on the feeding mechanisms of ray-finned fishes and salamanders that illustrate the difficulties of inferring function from structure. These examples all involve the experimental determination of function in living taxa, and the results in each case may be compared directly to functional predictions based on morphology. The case studies range from broadly comparative phylogenetic analyses in salamanders to intraspecific comparisons of structure and function in sunfishes.

All three case studies illustrate that even when relatively simple predictions are made about function and behavior from morphology, these predictions are often entirely erroneous. Function and structure are often not tightly linked, and we may have been overly optimistic in the past regarding the possibility of inferring function from the morphology of extinct taxa, even where phylogenetically appropriate extant "model taxa" exist. A key reason for the lack of correlation between structure and function in the musculoskeletal system, even in living species, is the lack of information on motor programs in the central nervous system. Identical morphology in two species may be involved in very different functions and behaviors if changes have occurred in the nervous system. Our ability to infer changes in the motor programs of fossil taxa is limited, and for this reason alone we are unlikely to be very successful in making detailed predictions of function and performance from morphological data alone.

### INTRODUCTION

The alliterative appeal of the phrase "form and function" is such that virtually every field has used it to

describe its subject matter. Thus, we may read about architecture in *Form and Function: A Source Book for the History of Architecture and Design 1890-1939* (Benton 1975); about linguistics in the book *Language Development: Form and Function in Emerging Grammar* (Bloom 1970); about literature in *The Phenomenon of the Grottesque in Modern Southern Fiction: Some Aspects of its Form and Function* (Haar 1983), and about digestion in *Guts: The Form and Function of the Digestive System* (Morton 1979).

But the widespread use of the phrase "form and function" has not been accompanied by much understanding of the relationship between form and function. Are form and function inseparably linked? Does form determine function? Does function determine form? This debate has raged for centuries, and is one of the most enduring in biology (Russell 1916). And yet there is little agreement on just what the relationship is between form and function.

The association between form and function is of special importance to paleobiologists and comparative anatomists for whom the primary available data on organisms are structural. If one has access only to structural data, then any attempt to understand how animals work and how they move must involve the inference of function from form. We must then seek methods to infer function from form and a better understanding of how form and function are interrelated.

In much of the literature, form and function are used as closely related concepts that, when considered together, promise to provide a reasonably complete characterization of any heterogeneous system. Many authors believe that these two properties have an intimate relationship and that it is not fruitful to consider form and function as distinct entities (e.g., Arber 1950; Dullemeijer 1974; Thomas 1978).

This view of form and function has a clear implication for the direction of research in functional and evolutionary morphology. If form and function are tied closely together and map onto each other in a relatively simple way, then it should be possible to



make accurate predictions of biological function from a study of form or structure. Similarly, a study of organismal function (or the generation of theoretical models of function) should enable us to predict the design of biological structures associated with those functions. The tightness of the linkage between biological form and function will determine the ease and accuracy with which these types of predictions can be made.

The central theme of this paper is that we have placed unwarranted faith in our understanding of the relationship between form and function, and are thus more confident of our ability to predict function from form than is legitimate, given current data. This is especially true at the organismal level where prediction of organismal function, performance, and behavior from structure is desired. I will argue that biological structures and their associated functions often have a very complex relationship to each other, and, at certain levels of analysis, very little relationship at all. Hence, prediction of one from the other may be extremely difficult. We tend to *assume* that form and function have a mutually predictable relationship even though few specific tests of the fit of structures to *experimentally measured* functions have been conducted. Of particular concern in this chapter are the nature and accuracy of predictions of function from morphology in extinct taxa. In fossil animals the skeletal system makes up the majority of the available preserved material, and thus predictions of function are of necessity derived from skeletal remains. In many cases it is necessary to infer from these skeletal remains the arrangement of muscles and ligaments in order to generate predictions of muscle function, skeletal movement, and thus behavior. The concerns I express here apply equally well to the inference of function from anatomical analyses of the musculoskeletal system in living taxa.

The relationship between form and function in the musculoskeletal system will be the focus of this paper because of the dominant role that bones and muscles play in paleontological and comparative anatomical investigations. First, I will review two general approaches that have been used to study the relationship between form and function (especially in fossil taxa) and I will evaluate the assumptions on which these methods are based. I will also discuss definitions of the terms form and function, as well as the related concepts of performance and behavior. Second, I will briefly present the results of three case studies in different clades to illustrate the difficulties of inferring function from structure even in extant taxa for which structure can be studied comprehensively. These case studies demonstrate the value of experimentally measuring function to test directly predictions from structure. Finally, I will discuss the implications of these conclusions for the

Table 1.1. *Definitions of terms used in Chapter 1*

Term	Definition
Biological role	Role of phenotypic features in a specific environmental or ecological setting (e.g., escape from predators)
Behavior	Actions and/or responses of whole organisms
Performance	A measure of the execution of an ecologically relevant activity (e.g., feeding rate, maximal burst speed)
Function	Use or action of phenotypic features; the mechanical role of phenotypic features
Structure	Topological relationships among phenotypic features; internal organization of phenotypic features

general enterprise of form-function studies, and the extent to which the results from these case studies are likely to be of wide applicability.

## STRUCTURE AND FUNCTION

Before we can evaluate the success with which we might predict function from structure, it is critical to arrive at a definition of function. The definitions of the terms form and function (and the related words, performance, behavior, and biological role) as used in this chapter are given in Table 1.1. Form is defined in terms of phenotypic features and their component anatomical parts, and structural analysis describes the topological relationships among features. Structures might be bones, muscles, or amino acids in a protein.

Function is more troublesome to define. As discussed previously (Lauder 1986, 1990), many investigators (especially in ethology) use the term function as synonymous with "selective advantage." The function of a structure under this view is the effect that the structure has on fitness: How did selection act to produce the structure? If selection on the hindlimb, for example, acted to increase the length of the limb due to the fact that longer-limbed individuals were better able to escape from predators, then the function of the hindlimb would be "predator escape." There are two main difficulties with this definition. First, we must know both that selection acted specifically on the structure in the first place, *and* the direction of that selection before we can speak of the function of a structure. This is exceedingly unlikely information to possess, especially in any retrospective comparative study of extinct species



(Lauder et al. in preparation). Second, this definition of function leaves us without a word to describe what morphologists often mean by function: the use or action of a structure (Bock & von Wahlert 1965; Hickman 1991).

In this paper, the function of a structure will be defined as the *mechanical role* or *physical role* that it performs in the organism: that is, how a phenotypic feature is used (Lauder 1990). A bone might have the function or mechanical role of stiffening the limb, or of providing a rigid element on which muscular forces can act. In describing mechanical roles, we might measure kinematic and kinetic variables – force, displacement, velocity, and acceleration – to quantify how a structure is used. Or we might analyze when a structure is used in a particular behavior in comparison to other structures that contribute to the behavior. Experimentally modifying structures is also useful for understanding mechanical roles. Under this definition of function, which is derived from that of Bock and von Wahlert (1965), our ability to measure the occurrence and direction of selection on structures is irrelevant to determining their function. Functional data, then, are measurements of mechanical role and use (Lauder 1990). This definition of function thus does not include structural data that may be given a functional *interpretation* or may assist in defining possible limits to mechanical role: that is, lever arms, muscle masses, allometric relationships, bone shapes, or interconnections of central nervous system nuclei.

While the analysis of structure and function is often at the level of individual features of organisms, the study of animal performance, behavior, or biological role may occur at more integrative levels (Table 1.1). For example, performance (Arnold 1983) is the measured score of an individual on an ecologically relevant task (such as maximal feeding rate or maximum sprint speed). Individuals (or species) that differ in mean performance on a specific task might do so because of changes at many other levels. For example, feeding rates on the same prey in two species might differ because of changes in muscle physiology, muscle lever arms, or nervous system structure in feeding and/or locomotor morphology; many structural and functional features may be involved in causing a difference in performance.

A similar situation holds for behavioral differences among individuals or taxa. If we define behavior as the actions and/or responses of whole organisms (Table 1.1), then it is apparent that behavioral differences among species may also be the result of differences at both structural and functional levels. Different patterns of muscle activity, for example, will generate different locomotor behaviors in two species, even given similar limb morphology (Lauder 1991).

The term *biological role* (Table 1.1) was advanced by Bock & von Wahlert (1965) to indicate the role that a structure plays during behavior in a specific environmental and/or ecological setting. The biological role of a particular hindlimb morphology in a species, for example, might be given as "enhancing escape from predators." Biological role can also be viewed as synonymous with selective advantage. Given the difficulty of measuring selection in comparative studies (especially in extinct taxa), the study of biological roles is likely to be quite difficult in practice.

### THE INFERENCE OF FUNCTION FROM STRUCTURE IN PALEONTOLOGY: METHODS AND THEIR DIFFICULTIES

Two main methods have been used to infer function, behavior, or performance from structure in extinct taxa: the phylogenetic method and the paradigm method.

#### The phylogenetic method

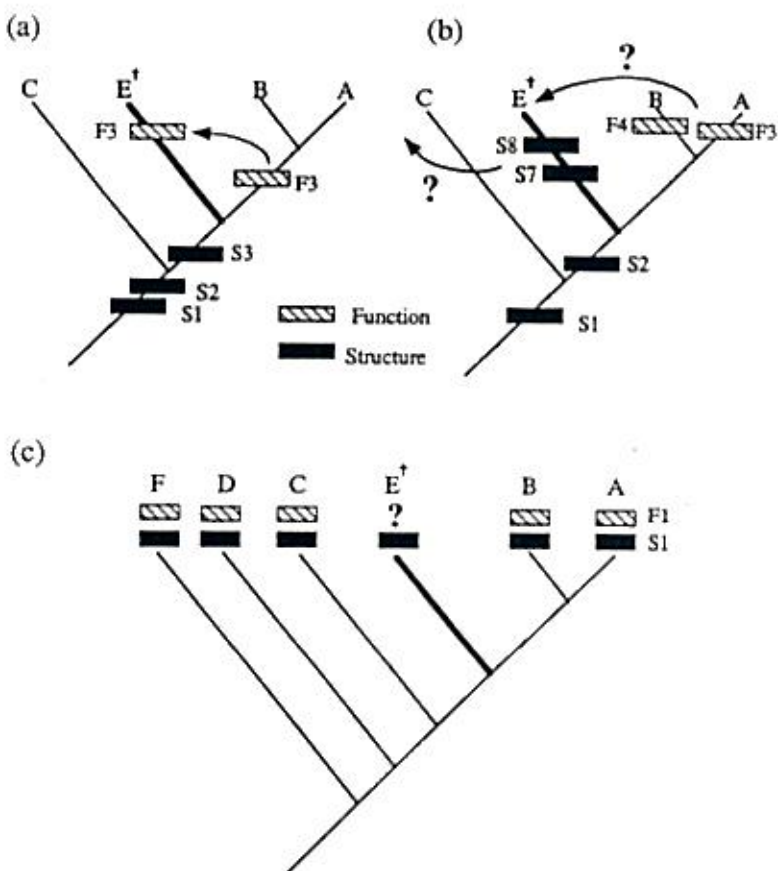
This method relies on comparative studies of related living taxa to estimate the function of a structure. The observed relationship between structure and function in extant species is then applied to extinct taxa of interest. Structures that are homologous among living and extinct taxa are presumed to share homologous functions, allowing the inference of function in a fossil taxon (Stanley 1970). As summarized by Raup and Stanley (1971; p. 166) in their text on principles of paleontology, "Often we can observe the mechanical function of a structure in Recent taxa and, by homology, apply our observations to closely related fossil taxa."

The phylogenetic method as it is often practiced is illustrated in Figure 1.1a. The extinct taxon E can be shown by a study of its morphology to share structure S3 with taxa A and B. Structure S3 is thus a shared derived feature of taxa E, A, and B and provides evidence that these three taxa form a monophyletic group. S3 is thus considered to be homologous in these three taxa (Lauder in press; Patterson 1982). The function of structure S3 may then be studied experimentally in taxa A and B. If similar functions (F3) are found in these two taxa, then one may by inference ascribe function F3 to taxon E. Figure 1.1a also illustrates that taxon E shares as primitive traits (plesiomorphies) structures S2 and S1 with taxa A and B. We could thus also investigate the functional correlates of S2 and S1 in A and B as well as in taxon C to assist in the inference of the functional attributes of taxon E.

The phylogenetic method as illustrated in Figure



**Figure 1.1.** (a) One application of a phylogenetic approach to inferring function from form. Taxon E is extinct and together with taxa A and B possesses structure S3. Inference of the function of this structure in extant taxa A and B provides the basis for inferring the function of structure S3 in taxon E. (b) Potential difficulties with a comparative approach to inferring function from structure. Uniquely derived structures may exist in the taxon of interest, E, such as S7 and S8, and the inference of the function of these structures must then be based on a search for "similar" (analogous) structures in other clades (*left arrow*). Also, if taxa A and B are shown by the experimental measurement of function to possess different functions for S2 (F3 and F4), then the inference of function in taxon E is greatly complicated (*top arrow*). (c) An appropriate use of phylogenetic methods (parsimony) to infer that extinct taxon E possesses function F1.



1.1a for inferring function from structure relies on a crucial assumption: a tight link between structure and function. If homologous structures have similar functions, then the phylogenetic method may work well for characters that are not unique (apomorphic) to extinct taxa. However, two difficulties exist that may severely cripple our ability to infer function using this methodology. First, the extinct taxon E might possess many uniquely derived characters that have no homolog in extant species. Figure 1.1b shows extinct taxon E with two unique structures S7 and S8. If we are interested in understanding the functional significance of these structures, then we must reach outside this clade to find similar (analogous) structures elsewhere. When we do this, however, we have moved beyond comparing homologous structural features to infer function: We are now comparing analogous structural features in the hopes of identifying analogous functions (Lauder in press). This is surely a risky procedure as we no longer have even the assurance of an homologous structural base on which to base our inferences. Even with this caveat, many structures that draw the attention of paleontologists are unique to a clade: It is their very novelty that attracts research in the first place. But novel features pose special problems if

similar structures cannot be found in other clades. Inferring function in this case becomes more a matter of speculation than inference with a firm empirical phylogenetic foundation.

The second problem with the phylogenetic method is the assumption of a close link between structure and function. Figure 1.1b illustrates a situation in which the experimental measurement of the function of structure S2 in taxa A and B results in the discovery of different functions for S2: F3 in clade A, and F4 in clade B. What then can be concluded about the function of S2 in extinct clade E? Furthermore, a similar divergence in function for structure S1 among the terminal extant taxa would leave us in the same position of being unable to infer the functional consequences of S1 in clade E. If the mapping between structure and function, or among structure, function, performance, and behavior is loose, then our ability to predict the appropriate functional or behavioral correlates of structures will be weak. A major aim of this paper is to indicate that the situation illustrated in Figure 1.1b, a phylogenetic divergence or discordance between structure and function, is actually a common situation. This pattern has not been widely recognized because most analyses that follow the method illustrated in Figure



1.1a use structure to infer functions, such as F3 and F4, in extant species. Thus, morphology is used to infer functions in related taxa, and then these inferences are reapplied to the clade and structure of interest: No independent test of function is available.

The difficulties with phylogenetic inferences of function from structure are not inherent in phylogenetic methodology. Functional characters, just like structures and behaviors, may be subjected to phylogenetic analysis and the inference, by parsimony, of states in extinct taxa (Lauder 1990, in press). The methodology for making such inferences is now widely known and has been recently discussed in Brooks and McLennan (1991), Felsenstein (1985), Harvey and Pagel (1991), Maddison and Maddison (1992), and Swofford and Maddison (1992) (also see Witmer, this volume). Figure 1.1c illustrates the reconstruction of function in extinct taxon E using functional data from adjacent extant taxa. Outgroup taxa C, D, and F all possess structure S1 and function F1 as do taxa A and B (Figure 1.1c). Taxon E may be shown by studying its morphology to possess structure S1, and in this case it is simple (by parsimony) to infer that extinct taxon E possessed function F1. But actual cases such as this in which functional characters have been measured for relevant extant outgroup and ingroup taxa in the clade of interest are few in number. Most often, functional characters are inferred, even in extant taxa, and function in outgroup taxa is even more rarely measured. Functions inferred from structures are not independent of those structures, and basing inferences of function in an extinct clade of interest on inferences of function in extant taxa is not likely to lead to robust conclusions.

#### The paradigm method

This is a second method developed to allow the inference of function from structure. Rudwick (1964b) first outlined the paradigm procedure, and indicated that his method was especially useful for structures for which there are no analogs or homologs in extant taxa. This method has been widely discussed in the paleontological literature (Gould 1970; Raup & Stanley 1971; Grant 1972; Thomas 1978; Cowen 1979; McGhee 1980; Hickman 1988; Levinton 1988). According to Rudwick's (1964a,b) procedure, the first step in inferring the function of a novel structure is to develop several mechanical abstractions or models (usually from physical and mechanical first principles) that can be used to predict what a structure should look like, given the constraints and functional goals of the model. This predicted structure is called a paradigm structure. Thus, if a novel bone were discovered in the jaw of a fossil taxon, one might make a mechanical model

of the jaw by assuming a specific pattern of movement, and this model could be used to predict the specific morphology of a bone in the location of the new structure. Rudwick advocated making several alternative models so that the several predicted structures could be compared with the real one. The function of the new structure would then be inferred to be that function whose paradigm most closely matches the real structure.

Overall, the paradigm method may be considered as a variant of the general approach of making mechanical or mathematical models to "deduce" the shapes and types of biological structures that might perform the functions included in the model (Dullemeijer 1974; Gutmann 1981). A priori model-building approaches have not been very successful in functional morphology, due in part to the enormous difficulty in building a model that reflects biological reality from first principles, and to the fact that a given model often does not generate a sufficiently limited set of predicted structures.

The paradigm method makes several important assumptions, one of which is that there is a strong correlation between function and structure at the level of the traits under study: Any model developed from first principles should only allow one paradigm structure. If multiple functions can be associated with a given structure and if a given function can be performed by many structures, then model-building is unlikely to yield successful predictions. A further difficulty is that the structure is known before the model(s) are built, making a truly independent prediction of structure from function impossible. In addition, the "functions" assumed by the paradigm method are often general behaviors or biological roles (Table 1.1), and usually do not lead to specific structural specifications.

A variant on the paradigm method is the use of basic physical principles to predict general functional or behavioral properties of extinct taxa (Alexander 1989; McGowan 1991; also see the papers in Rayner & Wootton 1991). This approach has been more successful (although the predictions can usually only be indirectly tested) because a considerable body of data on extant species may be used to generate the predictions. An example is Alexander's (1989) analysis of the locomotor speeds of dinosaurs: an attempt to predict a functional attribute from structural data. Alexander used fossil trackway data, data on limb length and stride length from living animals, and estimates of leg length in dinosaurs to predict their locomotor speeds. Similarly, Thomason (1991) used the extensive data base on the biophysics of extant horse locomotion to infer functional properties of the limb in two extinct horse taxa (*Mesohippus* and *Merychippus*). Even using biophysical principles to predict function may be difficult, however, as there



may be many possible predictions and interpretations even when these are based on a single morphological system. One example of such a situation is the controversy over the aerodynamic properties of morphological features in pterosaurs and *Archaeopteryx* (Padian 1991; Rayner 1991).

#### LEVELS OF RESOLUTION IN PREDICTIONS FROM STRUCTURE

Given the above caveats regarding our ability to infer function from structure, it is reasonable to ask what conditions are most likely to lead to successful predictions of organismal function, behavior, or performance, and which past investigations have yielded the most success. It is my view that predictions appear to have been most successful at both the most general (ecological/behavioral) and at the finest (within tissue) levels of resolution.

At a general level, success has been obtained in predicting basic ecological categories (such as herbivore vs. carnivore; climbing vs. cursorial) from gross and microscopic features of fossil taxa and from data such as limb proportions (e.g., Van Valkenburgh 1988, 1991; Damuth & MacFadden 1990). Tooth wear patterns as well as general tooth morphology and other aspects of skull structure may be reliable indicators of ecological situation, and are often based on comparative analyses of many extant taxa. Similarly, analyses of performance may be based on measurements from extant taxa and may thus allow estimates of performance in fossils (or extant taxa for which performance cannot be measured). For example, Garland and Janis (1993) tested the ability of measurements of limb proportions in 49 species of cursorial mammals to predict maximal running speed. They did have some success in making predictions of speed from hind limb length, but end on a cautionary note: "Prediction of locomotor performance of extinct forms, based solely on their limb proportions, should be undertaken with caution" (p. 133).

At a specific level, prediction of function from structure within biological tissues also appears to have been relatively successful. Basic principles of mechanical design do allow precise statements about function to be made, or at least the definition of functional limits within which structures must work (Wainwright et al. 1976). One example is the highly predictable relationship between the physiological cross-sectional area of vertebrate skeletal muscle and the maximum tetanic tension developed by that muscle (Powell et al. 1984; also see Gans & Bock 1965 and Alexander 1968). Another example would be the general predictability of muscle contractile performance from a knowledge of myosin ATPase

types, and mitochondrial, glycogen, and capillary density. Unfortunately, this type of prediction is one that is not often of use to paleontologists. Of more use to paleontologists are analyses of bone mechanical properties. At least some of the functional properties of bone tissue appear to be generally predictable from an understanding of structure. For example, Bertram & Biewener (1988) analyzed bone curvature as a response to loading pattern, and Biewener (1982) examined the regularity of the interspecific relationship between bone safety factors and body size (see Thomason, this volume).

However, it is our attempt to understand biological function at an *intermediate* level of generality that causes the greatest difficulties, and unfortunately, this is precisely the area where many workers wish to make inferences. An example of prediction at such an intermediate level might be the inference of specific movement patterns of jaws or limbs from morphology alone (in order to reconstruct feeding or locomotor biomechanics and behavior). While the case studies considered below do not give much cause for optimism in predicting functional characteristics at this level, there are approaches that have proven useful for defining the physical limits to function given a specific morphology. Much progress, for example, has been made by modeling locomotion using well-established biomechanical and hydrodynamic principles, as has been discussed by Briggs et al. (1991) for fossil arthropods. Interspecific measurements of drag and lift forces on models of extinct taxa permit general comparative statements about locomotor habit. At the least, such modeling does assist in delimiting the boundary conditions for organismal function. In addition, tooth wear patterns and striations allow inferences to be made about the movement patterns of jaws in fossil vertebrates, providing some indirect indications of the results of muscle activity (see chapters by Janis, Naples, and Rensberger, this volume).

Much of the difficulty in predicting function from structure by any method stems from the existence of multiple confounding factors that increase the chance that many functions could be performed by a given structure. In the case of muscles and bones, the nervous system serves as an important locus of these difficulties. In fossil taxa we have no access to the motor programs that the nervous system is capable of producing, and yet changes at the level of central nervous structure and function may have a dramatic impact on the function of morphological features (Lauder 1990, 1991). For example, the evolution of a novel pattern of motor output could easily alter stride length by changing patterns of limb-muscle activity (thus compromising predictions of speed), or change jaw mechanics with few visible structural



effects (leading us to incorrectly infer jaw function based on living taxa).

### THREE CASE STUDIES

How closely linked are structure and function? This is the key issue that must be addressed if we are to make progress in developing methods for inferring functional characteristics from morphological data. One way to address this question is to undertake direct experimental studies of function in living species to measure the functional properties of structures. In this way, we can determine empirically just how predictable functional features are from morphology, and we can do so by the measurement of function. It is vital that functional inferences be tested by experimental measurement to obtain an independent assessment of function, and that functional hypotheses themselves not be tested by inference from other morphological features (a circular procedure). The three case studies that follow all address the issue of predicting function from structure, given particular configurations of muscles and bones.

#### Case Study 1: Prey manipulation in osteoglossomorph fishes

The Osteoglossomorpha is a monophyletic clade of fishes that, as presently understood, represents the most primitive living clade of teleost fishes (Figure 1.2a; Lauder & Liem 1983). Outgroup taxa to the Osteoglossomorpha include the bowfin (*Amia*) and the clade including gar (Ginglymodi: *Lepisosteus*). There are approximately 210 species of osteoglossomorphs (Nelson 1984) including such taxa as the knifefishes (Notopteridae), arawana (Osteoglossidae), and elephantfishes (Mormyridae).

The Osteoglossomorpha are of interest for the analysis of structure-function relationships because most members of this clade possess a rather dramatic suite of apomorphic morphological modifications to the feeding apparatus: a bite between the basihyal (BH), or "tongue," and the base of the skull (Figure 1.2b). (In addition, shearing action may take place between the basihyal and lateral teeth on the palate.) This tongue-bite is a significant evolutionary novelty that, if present in an extinct taxon, would provoke functional speculation and hypotheses as to its role in the feeding mechanism. Given that many members of the clade Osteoglossomorpha possess this structural novelty, we may hypothesize that, if structure and function are closely linked (as indicated in Figure 1.1a), these taxa will share a common functional novelty associated with the tongue bite.

The teeth on the tongue of osteoglossomorphs

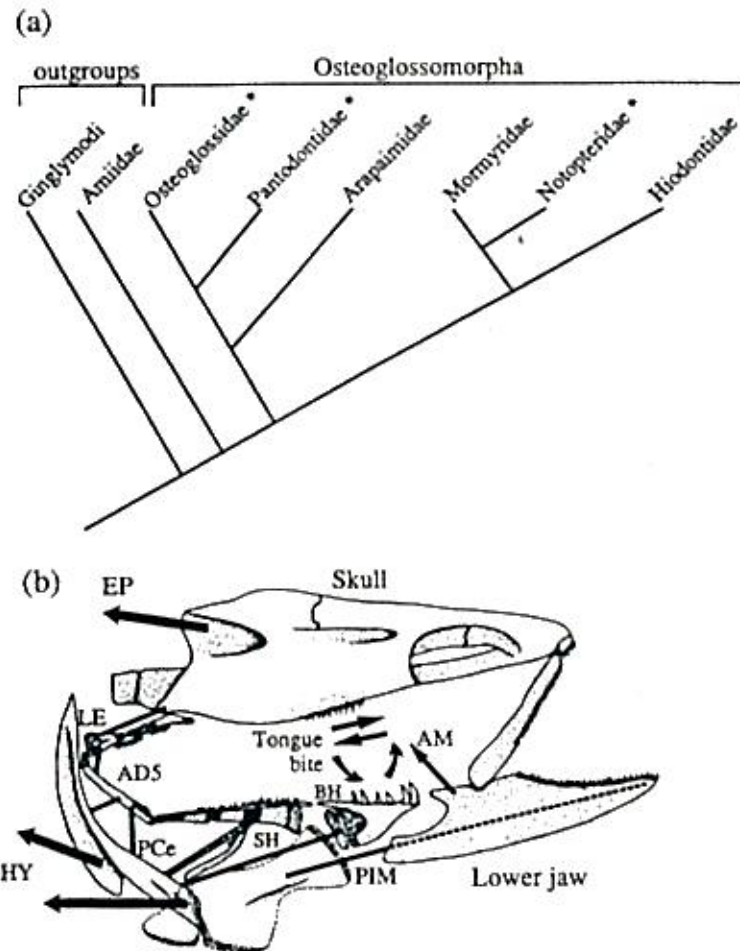
may be quite large (Figure 1.2b), and experimental research has shown that these teeth are used very effectively to puncture and shred prey once they have been trapped within the mouth cavity (Sanford & Lauder 1989). A number of muscles attach to bones surrounding the tongue bite (Figure 1.2b), including the sternohyoideus (SH) which retracts the hyoid (and attached teeth), the posterior intermandibularis (PIM) which protracts the hyoid, and the hypaxial muscles (HY) which retract the pectoral girdle. In addition, the epaxial muscles (EP) insert on the skull and elevate the cranium and the attached teeth on the base of the skull.

By recording the electrical activity pattern of these (and other) muscles in the knifefish *Notopterus* using electromyography, and by analyzing high-speed films of prey manipulation, Sanford and Lauder (1989) documented the use (function) of the tongue-bite apparatus. The pattern of motion of the teeth on the hyoid is shown by black arrows inside the mouth labeled "Tongue-bite" (Figure 1.2b). A key finding of these experiments was that the major movement of the hyoid teeth was anteroposterior (not dorsoventral): The teeth were dragged (raked) posteriorly through the body of the prey while it was clamped in a fixed position by adduction of the mandible and upper jaw. The basihyal teeth were moved posteriorly by extensive posterior rotation of the whole pectoral girdle pulling the hyoid with it. These kinematic results were surprising; such extensive rotation is not seen in outgroup taxa. *Notopterus*, therefore, possesses an extensive suite of functional novelties (including pectoral rotation) correlated with the obvious structural novelty of the teeth on the hyoid and skull (the tongue-bite), which is shared with other osteoglossomorphs. This result begs the question: Do other osteoglossomorph species with a tongue-bite morphology also share the functional novelties identified in *Notopterus*?

Sanford and Lauder (1990) extended this study to a comparative kinematic analysis of two other osteoglossomorph taxa: *Pantodon* (the freshwater "butterfly-fish"), and *Osteoglossum* (the arawana). From high-speed video records of prey manipulation behavior using the tongue-bite, we derived eight kinematic variables that measured various aspects of tongue-bite function (such as the extent of hyoid movement, the relative timing of mouth opening and head lifting, etc.). Statistical analyses (analysis of variance and principal components) were then used to compare the function (pattern of bone movement) of the tongue-bite apparatus among the three taxa. The result of the principal-components analysis is summarized in Figure 1.3a: The taxa differ significantly in the function of the tongue-bite morphology. Each of the three genera cluster in a significantly different portion of multivariate kinematic space, and



**Figure 1.2.** (a) Phylogenetic relationships of the major groups of osteoglossomorph fishes. Asterisks indicate the three osteoglossomorph taxa that have been studied experimentally; outgroup taxa (Ginglymodi and Amiidae) have been investigated also (Lauder & Wainwright 1992). (b) Diagram of the skull of the knife-fish, *Notopterus*, to show the teeth on the basihyal (BH) or "tongue" and on the base of the skull. During intraoral prey manipulation the prey is held in a fixed position by the front jaws, while the basihyal teeth move dorsally into the prey and then posteriorly as indicated by the arrows. Muscles that power the tongue-bite include the epaxial muscles (EP), the sternohyoideus (SH), the posterior intermandibularis (PIM), the adductor mandibulae (AM), and the hypaxial muscles (HY). The pharyngeal jaws are located posteriorly to the tongue-bite and are controlled by several muscles of which three are shown: the pharyngocleithralis externus (PCe), the fifth branchial adductor (ADS), and the levatores externi muscles (LE).



the analysis of variance on the individual variables confirmed that there were extensive differences among the genera.

The conclusion from these experimental results is that, while the three osteoglossomorph taxa all share the common structural novelty of a tongue-bite, they use this morphological adaptation in very different ways. The phylogenetic interpretation (Figure 1.3b) is that, despite the presence of a shared plesiomorphic morphological character, the taxa possess divergently derived functional features. This must be due, at least in part, to novelties in the nervous system that result in changed motor output to the jaw muscles in the three taxa. Differences among taxa in the relative timing and amplitude of activity in homologous muscles (not yet quantified) would test this hypothesis.

The ability to analyze directly the use (function) of the tongue-bite in osteoglossomorph fishes has thus resulted in a pattern similar to that illustrated in Figure 1.1b, where taxa with a common morphology do *not* share common functions. Given these results, I would feel unable to predict functional

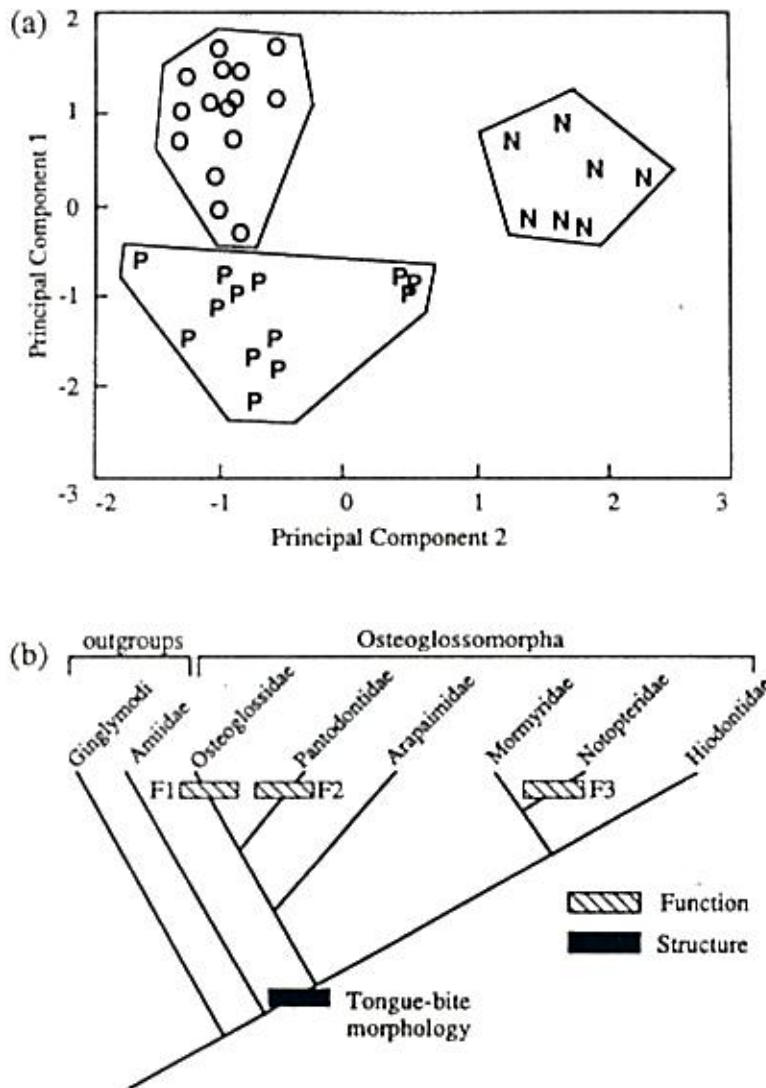
patterns in other osteoglossomorph taxa, and would need to conduct an experimental measurement of function in order to empirically assess how the tongue-bite morphology was being used.

While the specific movement pattern used by osteoglossomorph fishes might be difficult to predict from structure alone, we might wish to infer a general behavioral pattern of intraoral prey maceration using the teeth on the skull and hyoid in all osteoglossomorph taxa. We could be reasonably confident given these results, that a fossil taxon possessing a tongue-bite morphology used these teeth to manipulate and puncture prey. Such a general behavioral prediction would be reasonable, even if we could not venture a specific functional reconstruction.

#### Case Study 2: Aquatic prey capture in salamanders

Aquatic prey capture in salamanders is of interest for the analysis of structure-function relationships because divergent head morphology across families permits an analysis of the extent of functional





**Figure 1.3.** (a) Results of a principal components analysis of kinematic variables measured from high-speed films and video recordings of intraoral prey manipulation (raking) behavior using the tongue-bite in three taxa of osteoglossomorph fishes: *Notopterus* (N), *Pantodon* (P), and *Osteoglossum* (O). (b) Phylogenetic interpretation of the results of the principal components analysis. Each of the three taxa studied possesses a different functional pattern for the common morphology, rendering the inference of function of the tongue-bite in other members of this clade risky.

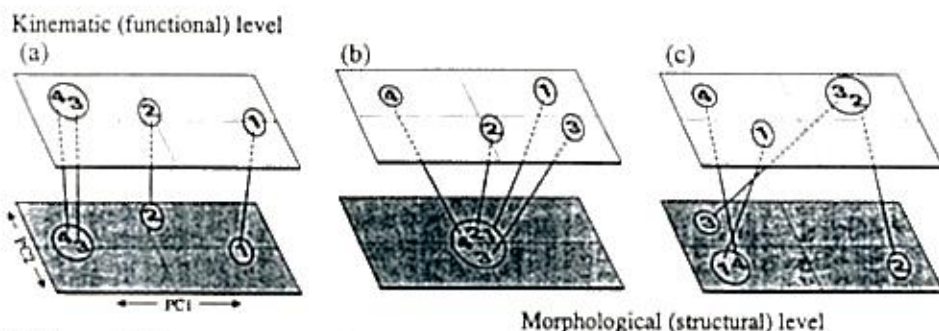
congruence with morphological features. Thus, this case study differs from the previous one in that the salamander families being compared are divergent in morphology, and we wish to examine the extent of functional divergence (if any).

Reilly and Lauder (1992) conducted a comparative analysis of head morphology and aquatic prey capture kinematics in six families of salamanders (Cryptobranchidae, Dicamptodontidae, Ambystomatidae, Amphiumidae, Proteidae, and Sirenidae). The goal of the study was to examine the relationship between morphology and kinematic patterns during prey capture, and the theoretical framework outlined below was used to assess the relationship between morphology and kinematics. Varying numbers of individuals were studied from each of the six families. Morphological variables (e.g., head width and depth, gill slit number) were measured from the

head to capture the size and shape of the feeding apparatus. Seven kinematic variables were derived from a frame-by-frame analysis of high-speed video recordings (200 fields per second) of prey capture. The function of individual head bones was defined as movement contributing to the overall feeding behavior, and was, therefore, quantified directly. All individuals from each family fed in the water on the same type and size of prey (earthworm pieces) dropped in front of the head. Both analysis of variance (ANOVA and MANOVA) and principal components analysis were conducted to examine differences among the taxa.

Before presenting the results of this study, it is useful to consider some of the possible theoretical relationships between structure and function among taxa. Figure 1.4 illustrates one way of visualizing these data. This format has the advantage of allowing





**Figure 1.4.** Using principal component analysis to compare the congruence of variation in morphological space (lower, shaded planes) with that in kinematic or functional space (upper, clear planes) for four species (numbered 1 to 4). The mean position of a taxon in each plane is indicated by a number, and ellipses around each number indicate the 95 percent confidence interval about the taxon mean. Thus, taxa included in the same ellipse are not significantly different from each other in that principal component plane. Each of the three pairs of planes illustrates a different possible result from a study of morphology and function in a clade of four species. (a) A situation in which function can at least broadly be inferred from structure: the relationships among taxa are the same across planes. (b) Function cannot be predicted from morphology as the four taxa are all similar morphologically but possess divergent functions. (c) A second between-level pattern in which function cannot be predicted from structure. Taxa 1 and 4 share similar morphologies but divergent functions, whereas taxa 2 and 3 are similar functionally but divergent morphologically. Abbreviations: PC1 and PC2, principal component axes 1 and 2.

us simultaneously to see patterns of variation among numerous morphological and kinematic variables, and also to map the degree of congruence between both classes of data. If we combine the individual morphological variables measured from each taxon into a reduced number of variables using a principal components analysis, we can plot the position of each taxon (as the mean of all individuals studied) in a plane representing principal components 1 and 2. This plane represents a multivariate morphological space. Similarly, we may use the kinematic variables for all the taxa in a principal components analysis and plot the mean position of each taxon in multivariate kinematic (functional) space. The mapping of taxon position across the two planes provides an indication of the extent of congruence between structure and function.

In this theoretical example, the position of the number in the plane indicates the mean value for that taxon, and the circle around the number represents the 95 percent confidence interval about the mean. Taxa whose circles do not overlap are considered significantly different from each other in multivariate space. Panel (a) in Figure 1.4 illustrates a situation in which structure and function are closely matched. Taxa 1 and 2, for example, are divergent both in kinematic and morphological space from the other two taxa, while taxa 3 and 4 share similar positions in both morphological and kinematic space. In no case does a taxon share space in the kinematic plane with a morphologically divergent taxon.

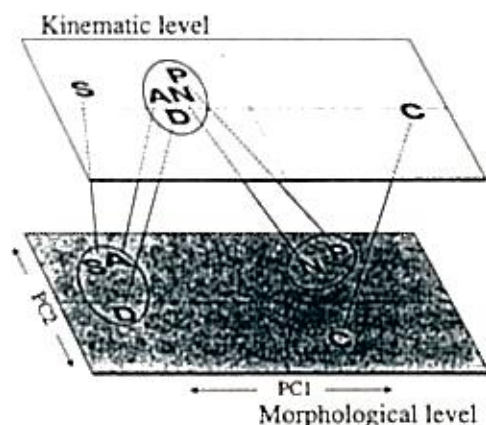
Panel (b) of Figure 1.4 illustrates one possible pattern of incongruence between structure and function where taxa that share a common morphology

possess divergent kinematic patterns (similar to the result of case study 1 above). In such a case, knowledge of the position of a taxon in the morphological plane tells us nothing about its position in the kinematic plane. Panel (c) shows a pattern of incongruence in which there is no clear relationship between morphological variation and functional variation among taxa. Taxa 1 and 4 share a common morphology but are divergent kinematically, while taxa 2 and 3 show the reverse pattern.

The results of the salamander study are presented in Figure 1.5 (Reilly & Lauder 1992). One pair of taxa (*A. Ambystoma* and *D. Dicamptodon*) are grouped together in both morphological and kinematic space, indicating that shared structure of the feeding mechanism is associated with a common kinematic pattern. *Cryptobranchus*, which is divergent morphologically, also possesses a divergent kinematic pattern. However, *Siren* (Figure 1.5; *S*), which groups with *Ambystoma* and *Dicamptodon* in the morphological plane, possesses a divergent pattern of feeding kinematics. Thus, the kinematic pattern of *Siren* feeding is not predictable from its morphology. The genera *Necturus* and *Amphiuma* (Figure 1.5; *N, P*) do share common morphological and kinematic patterns. However, together they are divergent from the other salamander taxa morphologically and yet similar in kinematics to *Ambystoma* and *Dicamptodon*. The morphological data do not allow prediction of this similarity in feeding behavior.

The overall conclusion from this experimental study of structure and function in the salamander feeding mechanism is that, for some taxa, there is evidence of congruence between the structural and





**Figure 1.5.** Results of an analysis of head morphology (shaded plane) and functional or kinematic variation in aquatic feeding (top plane) in six families of aquatic salamanders: A, Ambystomatidae, *Ambystoma*; C, Cryptobranchidae, *Cryptobranchius*; D, Dicamptodontidae, *Dicamptodon*; N, Proteidae, *Necturus*; P, Amphiumidae, *Amphiuma*; and S, Sirenidae, *Siren*. Note that taxa such as *Ambystoma* and *Necturus* are divergent morphologically but share a common region of kinematic space, while *Siren* and *Dicamptodon* are similar morphologically but divergent kinematically. A pattern such as this makes prediction of function from structure difficult. Other conventions and abbreviations match those of Figure 1.4.

functional levels, but for others there is not. Perhaps most disturbing is the lack of any clear a priori indication of the taxa in which one might find congruence, and the taxa in which one might not find congruence. If these six salamander families are in any way representative of other animal taxa, then empirical investigations of both structure and function will be the only way to determine their relationship; this prevents the formulation of a broad, general framework of congruence to use in making functional predictions from structure.

### Case Study 3: Snail crushing in pumpkinseed sunfish

The North American sunfish family Centrarchidae contains about 35 species, including a well-known piscivore, the bass *Micropterus*. Also included in this clade are two sister species that eat snails: the pumpkinseed sunfish (*Lepomis gibbosus*) and the redear sunfish (*Lepomis microlophus*). In previous work I have studied interspecific morphological and functional differentiation among sunfish species in their feeding mechanisms (Lauder 1983a,b), but (as is the case with most research in functional morphology) little work has been done at the popula-

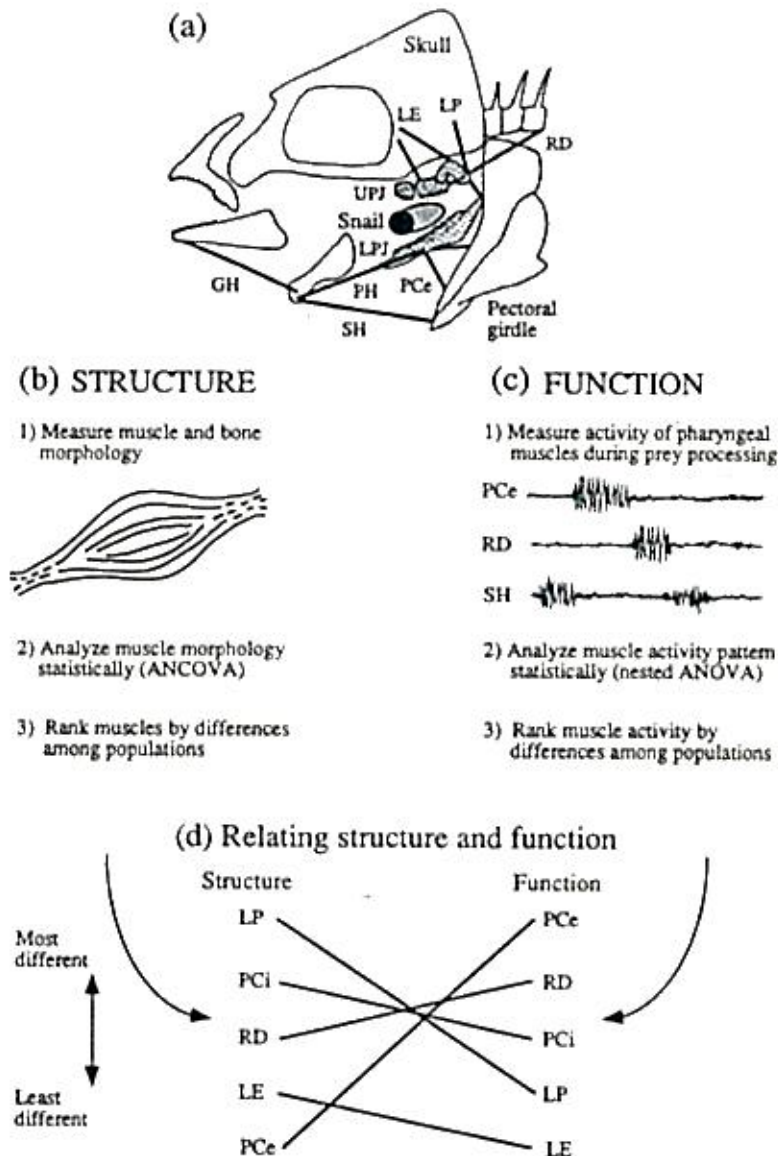
tion level within a species. The pumpkinseed sunfish populations in lakes of southern Michigan are of special interest in this regard because there is considerable interlake variation in prey abundance. For example, Wintergreen Lake contains few snails, while a nearby lake, Three Lakes II, possesses a very large snail population (Wainwright et al. 1991a,b). Both lakes contain pumpkinseed sunfishes, and both populations of sunfishes will readily feed on snails in the laboratory. Wainwright et al. (1991b) discovered that the populations of pumpkinseed sunfishes in these two lakes possessed a distinctive trophic polymorphism: Individuals from Three Lakes II (with abundant snails) possess hypertrophied pharyngeal muscles relative to individuals in Wintergreen Lake. (The morphological differences between sunfish populations appear to be an ecophenotypic response to prey differences.) In this section I describe the results of the morphological analyses of Wainwright et al. (1991b) and our subsequent functional analyses of the patterns of muscle activity during snail crushing (Wainwright et al. 1991a).

The mechanism of snail crushing in pumpkinseed sunfish is of interest for the analysis of structure-function relationships because intraspecific comparisons (i.e., among populations) should provide us with one of the strongest possible tests of the correlation between structure and function. There is little possibility of confounding phylogenetic factors as there has not been much time for differentiation among taxa. Thus, it would be difficult to argue that demonstrating a lack of congruence between structure and function is really due to uncontrolled phylogenetic differences among the taxa. In this case, the difference among pumpkinseed populations appears to be very recent, the result of a winter snail die-off after 1977 (Wainwright et al. 1991a). The key question in this case study is: Do interpopulational differences in morphology of the trophic musculature correlate with functional differences in those muscles?

Figure 1.6a illustrates the morphology of the part of the feeding mechanism involved in eating snails. Pumpkinseed sunfishes capture snails by suction feeding and transport them back to the pharyngeal jaw apparatus just anterior to the esophagus by creating a current of water through the oral cavity (Lauder 1983a). Once the snail reaches the pharyngeal region it is positioned in between the upper and lower pharyngeal jaws (Fig 1.6a; UPJ, LPJ). Activation of many of the pharyngeal jaw muscles in a distinctive motor pattern (Lauder 1983a,b) results in forces which crush the snail's shell. Shell pieces are separated from the body of the snail by the pharyngeal jaws and by water currents created by head-bone movements. The pharyngeal jaws then move the snail body posteriorly into the esophagus.



**Figure 1.6.** (a) Schematic lateral view of head of a percomorph teleost fish such as a pumpkinseed sunfish (Centrarchidae) illustrating position of the pharyngeal jaws (stippled), some of the muscles that control the pharyngeal jaw apparatus, and position of a snail prey item between upper pharyngeal jaw (UPJ) and lower pharyngeal jaw (LPJ). Pharyngeal jaws are used to crack the snail's shell and to separate it from the snail's body which is then swallowed. (b) Procedure followed to analyze the morphology of pharyngeal jaw apparatus in two populations of sunfishes (*Lepomis gibbosus*) that live in two lakes differing greatly in the number of snail prey available. (c) Procedure followed to analyze the function of PJA muscles during feeding on snail prey. (d) The result of both procedures was a ranking of muscles by significance of the difference in either structure or function between lake populations. Note that there is little correlation between structure and function even in this intraspecific case study. Muscle abbreviations: GH, geniohyoideus; LE, levatores externi; LP, levator posterior; PCe, pharyngocleithralis externus; PCi, pharyngocleithralis internus; RD, retractor dorsalis; SH, sternohyoideus.



**ANALYZING THE STRUCTURE OF THE PHARYNGEAL JAWS (FIGURE 1.6B).** Pharyngeal morphology was measured in a series of individuals from each lake that ranged in size from 40 to 132 mm standard length: ten muscles and five bones from the pharyngeal jaw apparatus were dissected out and weighed (Wainwright et al. 1991a). Previous interspecific work (Lauder 1983a) had shown that the mass of several pharyngeal jaw muscles is correlated with the proportion of snails in the diet, but no comprehensive analysis of both the bones and muscles between populations had previously been undertaken. Second, an analysis of covariance (ANCOVA) was used to assess significant interpopulational differences in muscle and bone mass. Three of the five bone masses differed between lakes, with the masses of three

pharyngeal bones mechanically involved in snail crushing being on average 1.5 times greater in the Three Lakes fish. In addition, six of the ten pharyngeal muscle masses were significantly greater in the Three Lakes fish, with one muscle (the levator posterior) possessing a mass 2.3 times greater than that of a fish of similar size from Wintergreen Lake. Third, the muscles were ranked using the degree of statistical difference between lakes as the criterion. Thus, the levator posterior muscle is at the top of the list of muscles (Figure 1.6b; LP) because it exhibited the most significant differences in mass between the lake populations.

**ANALYZING THE FUNCTION OF THE PHARYNGEAL JAWS (FIGURE 1.6C).** Electrical activity patterns were



recorded (using the electromyographic procedures described in Lauder [1983a,b]) from five pharyngeal jaw muscles during snail crushing. This allowed the timing of muscle activity to be quantified. We measured 16 statistical variables from each feeding on each of six individuals from each lake to capture variation in relative timing of muscle activity, duration of activity, and intensity of activity. These data were then analyzed using a nested ANOVA (individuals were nested within each lake), and the significance of the "lake effect" tested. Four of the 16 variables showed a significant lake effect, and the muscle that showed the greatest differentiation between lakes in function was the pharyngocleithralis externus (PCe). The five muscles were then ranked by the extent of functional differentiation between lake populations using the statistical difference between populations as the criterion. The pharyngocleithralis externus muscle is at the top of the list (Figure 1.6c; PCe) because it showed the most significant difference in function between lake populations.

**ASSESSING THE STRUCTURE-FUNCTION RELATIONSHIP IN THE PHARYNGEAL JAW APPARATUS.** By connecting homologous muscles in the two lists (Figure 1.6d) we can see that there is little relationship between structure and function in the pharyngeal jaw apparatus of pumpkinseed sunfishes. The levator posterior muscle (LP) shows the greatest differences between lakes in mass, but almost the least difference in function. Conversely, the pharyngocleithralis externus (PCe) is functionally the most differentiated between lake populations but is the least differentiated structurally.

This case study of sunfishes is of special concern because the relative sizes of muscles and bones often are used as functional or behavioral indicators. A massive muscle (by implication, one of large physiological cross-sectional area) will exert greater maximal force than a similarly designed muscle of smaller cross-sectional area. But such comparative physiological facts, while true, say little about how a muscle is used during behaviors such as locomotion and feeding. The use of muscles is a critical determinant of organismal behavior, and different morphological substrates may produce very similar behaviors, given an appropriate pattern of muscle activity (Lauder & Shaffer 1986; Lauder 1991; Reilly & Lauder 1992). The finding of considerable discordance in patterns of structure and function even at an intraspecific level indicates that interspecific predictions of function based on structure alone should be treated with caution.

It is nonetheless true, that if prediction at a general level is desired, one could accurately infer the difference among populations in diet and ecological

situation based on morphological differences measured in the pharyngeal jaws. Snail-eating populations do possess hypertrophied bones and muscles relative to outgroup populations. Such general inferences are valuable, especially if we wish to understand the life habits of extinct taxa, even if we cannot accurately infer function.

## DISCUSSION

### On the importance of functional inference

The desire to infer function, performance, or behavior from morphological data is common to many fields. Ecologists, ethologists, systematists, and population biologists, in addition to morphologists and paleontologists, have used structural data on organisms as a basis for inferences about the movements and actions of living animals (Hopson & Radinsky 1980; Fisher 1985; Grant 1986; Boucot 1990; Wainwright & Reilly in press). While the urge to make such inferences is a natural one (after all, the goal of gathering morphological data in the first place is usually to contribute to our understanding of what animals do and how they live), it is also reasonable to ask just how accurate such inferences are likely to be.

The primary means of evaluating the accuracy of inferences of function from structure should be a comparison of functional predictions based on form to measured functions in living taxa. Only in a situation where we can measure actual movements, actions, and experimentally evaluate alternative functional hypotheses can we test predictions from structure. The conceptual methods proposed to date as aids to the inference of function from structure contain no means of verifying or testing the functional predictions independent of morphological data. I have argued elsewhere (Lauder 1990) that using only morphological data to test hypotheses of function that have themselves been predicted from morphological data is circular. Functional data are of a fundamentally different character than morphological data (Lauder 1990, 1991), and a further examination of morphological characteristics (or a manipulation of morphological characters alone) is not likely to provide a strong test of a hypothesized function. Functional data need to be generated by direct observation, measurement, and experimentation. Methods such as the paradigm approach serve only to provide a mechanical model based on initial morphological inputs: they do not provide data on actual performance or function.

This is not to say that the extensive studies to date on the biomechanics and functional morphology of fossil taxa have no value. Quite the contrary. Research (much of it experimental in character) on



how structures in fossils *might* have been used and the ecological roles that might have resulted from use of these structures (e.g., Stanley 1970; Fisher 1977; LaBarbera 1981; contributions in Rayner & Wootton 1991) is an important component in the analysis of organismal design. These studies may allow rejection of certain classes of functional hypotheses, or may provide an indication that a given structure may have had other functions than those currently under consideration. Biomechanical research on fossils helps to define the realm of the possible. But, given the results from experimental work on extant taxa, we must be extremely cautious in drawing the conclusion that these types of studies definitively show how structures were used.

One reason that the inference of function is so widespread may be that organismal function and performance are difficult things to measure. Even most extant taxa do not lend themselves to experimental work and may be located in inaccessible habitats. Individual species in a clade of interest may not adjust well to laboratory conditions or to experimental protocols. Finally, conducting experimental work such as a description of limb movements, an analysis of muscle function, an analysis of ground reaction forces, and the related biophysical calculations on a clade of even a few species is a time-consuming task. It is often easier to generate a model or make general inferences of function from structure.

In addition to satisfying our natural urge to understand the actions and movements of living organisms, functional inferences are beginning to play an increasingly important role in many aspects of comparative biology (e.g., Brooks & McLennan 1991; Harvey & Purvis 1991). For instance, Greene (1986), Coddington (1988), and Baum and Larson (1991), all advocate a method for recognizing adaptive characters in organisms that depends in part on our ability to measure organismal function and/or performance. Coddington (1988; p. 3) even defines the term *adaptation* in terms of organismal function: an adaptation is "apomorphic function promoted by natural selection." Baum and Larson (1991; p. 1) note that in order for a character to be an adaptation it must "provide current utility to the organism" and that "the criterion of current utility is applied by comparing the performance of a derived trait to that of its phylogenetically antecedent state." Measurement of function and performance is one aspect of identifying adaptations in organisms.

But how are such analyses of function or performance carried out in practice? Baum and Larson (1991; pp. 12-13) recommend use of the paradigm method so that "performance is assessed by comparing a character state with an abstract model, or 'para-

digm,'" and "the closer the observed character comes to the paradigm, the higher is its inferred performance." However, as indicated above, inferences of function or performance from morphology via the paradigm method do not provide a reliable means of estimating how organisms function. In fact, in working out the example of adaptation in the limbs of plethodontid salamanders, Baum and Larson (1991; p. 13) simply assert that the derived state is "mechanically superior"; no model is presented that allows such predictions for primitive and derived limb morphologies, nor do functional data to support such a statement exist in the literature. Demonstration of mechanical "superiority" in limb function by experimental functional analysis would be a difficult task indeed, and identifying the precise morphological basis for relative performance differences among species would be even more laborious. In fact, a signal difficulty in comparative performance analyses of organismal function is identifying the underlying morphological bases of those differences (Arnold 1986; Jayne & Bennett 1989). Unfortunately, without such experimental data, historical or retrospective methods for the analysis of adaptation cannot be applied.

### The case studies

The three case studies presented earlier were chosen to indicate the difficulty of inferring function from structure even in extant species on which we can perform experimental functional analyses. These examples show that functional characteristics may not be easily correlated with (apparently) associated morphological features, and that structure and function may be relatively uncorrelated phylogenetically. These case studies are not an isolated body of data. Numerous examples, especially in the musculoskeletal system, exist to corroborate the main conclusion of each case study: Function is often not predictable from structure.

One excellent example from the mammalian literature further illustrates the difficulty in predicting function even in the best of circumstances. O'Donovan et al. (1982) conducted a comprehensive experimental functional study of two muscles in cats: the flexor digitorum longus (FDL) and an anatomical synergist, the flexor hallucis longus (FHL). Based on morphological evidence, one would predict that the two muscles should show very similar activity patterns. Both muscles extend in parallel around the ankle joint, and their tendons join together on the plantar surface of the foot to insert together onto the distal phalanges. From morphology alone and from simple manipulative experiments (such as muscle stimulation), it was predicted that



the two muscles would show similar activity patterns: "For a variety of reasons the FDL and FHL muscles in the cat have been considered as more-or-less interchangeable 'extensor' muscles" (O'Donovan et al. 1982; p. 1140).

The function of these muscles was assessed experimentally by recording electromyographic activity of each muscle during a variety of locomotor behaviors as well as by directly measuring muscle force (using implanted strain transducers on the muscle tendon) and taking simultaneous video images of each behavior. O'Donovan et al. (1982; p. 1127) described their results as "surprising in that the functional activity of the FDL muscle during locomotion proved to be complex, including stereotyped flexor behavior and facultative activity that appeared to respond to perturbations in the step cycle. Neither aspect was present in the activity of the FHL, which instead behaved as a stereotyped antigravity extensor." The authors conclude that these two muscles, defined by anatomists as synergists, have fundamentally different activity patterns (O'Donovan et al. 1982).

The feeding mechanism in terrestrial salamanders illustrates another point. The subarcualis rectus 1 (SAR) muscle in salamanders is a muscle that has been predicted to cause projection of the hyobranchial apparatus since turn of the century morphologists began to study salamander structure (Drüner 1902, 1904). This muscle, based on anatomical analyses (Severtsov 1971; Lombard & Wake 1976) should protract the hyobranchial apparatus thus extending the tongue toward the prey during feeding. Reilly and Lauder (1989, 1990; 1991a) conducted morphological, functional, and experimental investigations of the role of this muscle during initial prey capture in the tiger salamander, *Ambystoma tigrinum*, and confirmed that this was indeed the case, although the electrical activity pattern for the SAR showed an interesting pattern with two peaks: one during mouth opening, and the other during the mouth closing phase of the gape cycle.

Reilly and Lauder (1991b) then investigated the function of the SAR muscle during prey transport. One would have predicted that, because the tongue is not projected from the mouth when previously captured prey are transported from within the buccal cavity posteriorly to the esophagus, the SAR muscle would not be active during prey transport. Quite unexpectedly, we found that the SAR muscle is indeed active during prey transport behavior, with a single sharp peak in activity during mouth opening, a time when the hyoid is moving posteroventrally. The mechanical role of this muscle during prey transport is still unknown. The SAR muscle thus functions during two different behaviors with different

kinematics, although activity in just one behavior was expected from a priori anatomical analyses.

This last example illustrates yet another problem with inferences of function from structure, and one that has long been recognized (Darwin 1859; Gans 1974; Levinton 1988; Raup & Stanley 1971): Structures may have many functions. Although this idea is well known, the serious consequences of this fact for specific inferences of function from structure have not hindered functional speculation based on morphology. In practice, even in extant taxa on which functional studies can be performed, organisms exhibit constant surprises: Structures are used in novel and unexpected ways. There is hardly a paper in the literature that contains measurements of the function or functions of a structure or complex of structures, in which unexpected and surprising results about the use of those structures are not found. Given this track record, it is perhaps unwise to place much faith in detailed predictions of function from structure, especially those predictions involving taxa and structures in which no experimental test can be conducted to test function independently.

#### Why is function not predictable from structure?

A key reason for the discordance described above between structure and function in the musculoskeletal system is the nervous system. The nervous system is the "wildcard" in comparative and historical analyses of musculoskeletal systems. Changes in central nervous structure and function alone have the capability of radically altering the accuracy of predictions based only on musculoskeletal morphology (Lauder 1990, 1991). Alterations in the output of central neuronal circuits can (and do) thoroughly alter the function of structures, the effect of structures on organismal performance, and the behavioral pattern of the whole organism. In addition, changes in sensory feedback pathways from peripheral morphological structures may also have a profound influence on movement patterns, even in the absence of changes in central motor circuits. Where nervous system structure and function can be investigated along with musculoskeletal function, analysis has often shown that unexpected functional patterns may have a basis in neuronal reorganization (O'Donovan et al. 1982; Vilensky 1989; Vilensky & Larson 1989; Arbas, Meinertzhagen & Shaw 1991; Katz 1991; Paul 1991). Unfortunately, methods of assessing changes in neural circuitry for fossils are extremely circumscribed (Giffin, this volume) and permit only broad inferences of behavior, not of specific functional patterns (Table 1.1).



### PROSPECTUS: LIMITS TO COMPARATIVE METHODS

Our desire to understand the biological significance of newly discovered structures (in both fossils and extant organisms), and the lack of a clear understanding of the difficulties that even experimental functional morphologists have in elucidating the function of structures in extant taxa, have provided much of the basis for optimism regarding the prediction of function from structure. Functions of structures, the mechanical roles or properties of structures, and the effect of structure on performance can best be studied by direct measurement in extant taxa. Even in extant taxa, functional morphologists have been constantly surprised by unexpected functions and mechanical roles for structures.

Perhaps the best case scenario for functional inference would be one in which a clade contains mostly extant species that can be subjected to experimental studies of function. If we can verify by experimental analysis that a certain structure has a specific function in extant taxa, and if a newly discovered taxon in this clade (either a fossil or living species that is not accessible for functional study) shares homologous morphology, then it is most parsimonious to infer that the new taxon shares the function for that structure (Figure 1.1c). Unfortunately, this will not be a case of much interest to most workers, as it is the truly novel structures, or at least structures that have no obvious known counterparts, that evoke the greatest interest.

But it is exactly this latter situation in which the limits to comparative and retrospective investigation are the greatest and in which our inferences are weakest. The results of the case studies presented above provide arguments indicating that the inferences may be so weak that it might be best to limit the extent of functional inference and speculation.

Perhaps now is a good time, as we gather increasing amounts of functional data from living organisms and as functional morphologists make progress in understanding the functional consequences of organismal design, to step back from extensive functional inference based on morphology alone, and recognize the limits that exist on the inference of both functional and evolutionary mechanisms from comparative and historical data. Comparative data on morphology have numerous valuable uses which are subject to fewer limitations than functional inference, including the study of ontogenetic and evolutionary trends to size and shape, and the testing of models of morphological change through time (Gould 1985). Similarly, neontological data on organismal structure contribute in many ways to some of the most important questions in evolution-

ary biology, contributions that do not depend on our ability to infer function from structure.

If there are limits on the ability of comparative and retrospective investigations to infer mechanistic processes, then perhaps more overt recognition of these limits in studies of structure-function relationships will act as a positive force, and stimulate the discovery of new directions and methods for understanding how organisms work.

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