

Systematics and the Study of Organismal Form and Function

Advances in systematics are defining new directions for functional morphology and comparative physiology

George V. Lauder, Ray B. Huey, Russell K. Monson, and Richard J. Jensen

The study of form and function in organisms has a long and distinguished history, dating at least from the sixth century B.C., the time of the first recorded methodical investigations of animal structure and function (Russell [1916] 1982). Investigations into the design of plants and animals gained increased visibility in the eighteenth and nineteenth centuries with the work of German poet Johann Wolfgang von Goethe, French naturalist Georges L. C. Cuvier, and Swiss zoologist Louis Agassiz. Their investigations of structure captured the attention not only of professional naturalists and scientists but also much of the general public. Physiological investigation also

George V. Lauder is a functional and evolutionary morphologist in the Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92717. He works on vertebrate feeding and locomotor systems. Ray B. Huey is an evolutionary physiologist in the Zoology Department, University of Washington, Seattle, WA 98195. He is interested in the evolution of locomotor performance in lizards and of thermal sensitivity in flies. Russell K. Monson is a physiological ecologist in the Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder, CO 80309. He works on the evolution of photosynthetic mechanisms in plants. Richard J. Jensen is a plant systematist in the Department of Biology, Saint Mary's College, Notre Dame, IN 46556. He uses morphometrics to address problems in oak taxonomy. © 1995 American Institute of Biological Sciences.

A broadly comparative, historical approach to the study of organismal function is just beginning

flourished as the study of the mechanistic basis of animal and plant life began in earnest. A British morphologist of that time, Richard Owen, formulated the concepts of homology and analogy—the central theme underlying all of comparative biology (Hall 1994).

With the start of the twentieth century, the comparative analysis of organismal design expanded into two new areas, while research in historical biology continued to be performed largely by paleontologists, systematists, and comparative anatomists. The first new area emphasized physical principles that govern the structure of plants and animals. This focus on physical biology included mechanistic analyses of developmental patterns by biologists such as T. H. Morgan, E. G. Conklin, and E. B. Wilson (building on the earlier work of German anatomist and zoologist Wilhelm Roux in the late nineteenth century; Allen 1975). There were also general investigations into possible physical determinants of morphological features by workers such as D'Arcy Thompson. Thompson's *On*

Growth and Form (1917) is a classic early attempt to understand physical causes of biological form.

The second new area, an expansion of physiological studies of organismal function, was associated with interest in mechanistic aspects of organismal function. The physiological tradition of mechanistic research on organisms, begun in nineteenth-century Europe, diverged rapidly from morphological and structural work. Morphologists and anatomists were focusing on the use of morphological data for phylogenetic analysis, and mechanistic biologists eschewed phylogenetic goals for experimental and manipulative investigation (Allen 1975, Coleman 1977). The discipline of physiology, even comparative investigations of physiological differences among individuals, populations, or species, remained strangely divorced from systematics and phylogeny for many years.

In the last 30 years, with the rise of integrative research areas such as biomechanics and experimental functional morphology, comparative physiology and comparative anatomy have begun to overlap broadly in their subject matter and techniques of analysis. But even more significant has been the explicit move toward the incorporation of systematic concepts and hypotheses into both comparative physiological and morphological research (Burggren and Bemis 1990, Emerson 1988, Huey 1987, Lauder 1990). Within the last decade, many studies have appeared that integrate compara-

tive morphological and physiological analyses of organismal design with phylogenetic methods and concepts (e.g., Garland and Carter 1994, Huey and Bennett 1987). In many ways, the advances in systematics, phylogeny reconstruction, and comparative methodology are now defining new directions for functional morphology and comparative physiology. In the future, an understanding of phylogenetic principles and practices is likely to be a prerequisite for research in comparative physiology and morphology. This new perspective brings increased precision to the selection of species for structural and physiological analysis, to research on the evolutionary transformation of form and function, and to the statistical analysis of comparative data.

The comparative study of organismal form and function

Research in comparative morphology and physiology lies at the heart of many of the most pressing scientific questions in comparative biology today, and the recent integration of phylogenetics into the conceptual core of these disciplines has redefined many fundamental questions. In this article we consider several examples in which analyses of organismal morphology and physiology (largely separately) have provided new approaches or insights into biological diversity. We also consider the integration of these two disciplines and examples of how a phylogenetic framework and more rigorous systematic underpinnings have shaped current research on both form and function.

Comparative morphology. An important area in which morphological studies contribute to the knowledge of biodiversity is in the discovery of previously unknown organisms. Organismal structure provides much of the record of the history of life and constitutes the most common means by which new species are recognized. Such discoveries often redefine previously accepted limits of organismal design, and they challenge scientists to explain novel structures and evolutionary patterns. These discoveries

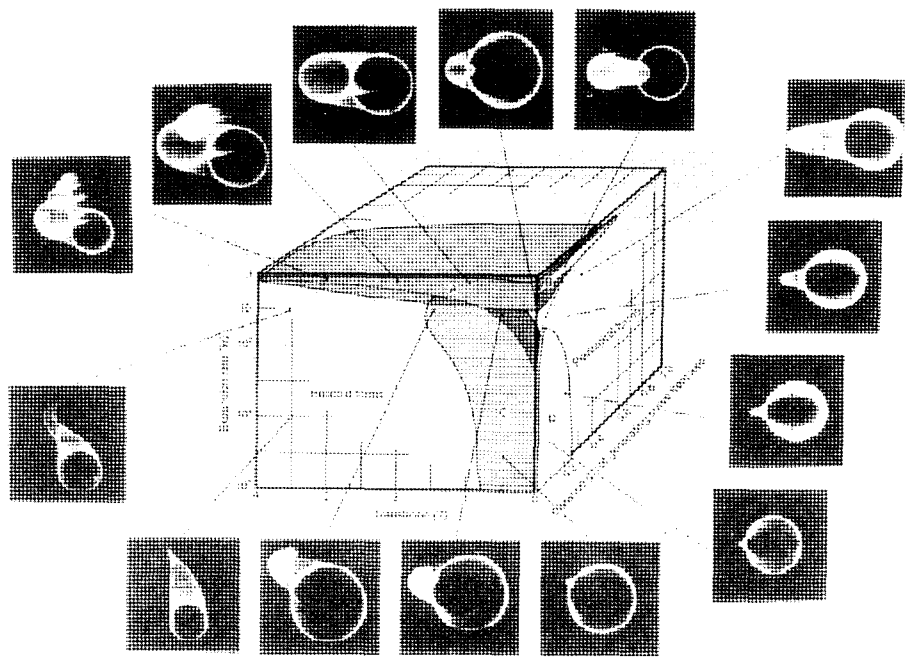


Figure 1. Diagram of the coiled shell morphospace. The central cube shows the volume defined by the three axes used by Raup (1966) to model the geometry of the coiled shell. Regions of the cube labeled A, B, C, and D denote the portion of the morphospace occupied by gastropods, ammonoids, pelecypods, and brachiopods respectively. Representative computer-generated shell shapes from areas of the cube are shown also; note that much of the theoretically possible morphospace is unoccupied by either extant or extinct forms. From: *Principles of Paleontology* by D. M. Raup and S. M. Stanley (1971). © W. H. Freeman and Company. Used with permission.

occur regularly as new geographic areas are explored and as extinct taxa are discovered by paleontologists applying new techniques for recovering fossils from previously studied areas.

The discovery of novel taxa is an important (and yet often undervalued) component of research in quantitative and evolutionary morphology. New discoveries not only contribute to the inventory of biological diversity (as new species) but they also allow current theories about the evolution of form and function to be tested using these fresh data.

Additional discoveries also may overturn previous conceptions of the diversity of life in the past, forcing a reevaluation of models of biological diversification through time. An outstanding recent example of novel structures discovered in fossil taxa is the Burgess Shale fauna, in which a large number of morphologically distinct species have been found (Conway Morris 1992, Gould 1989). The extensive morphological divergence shown by these species has

resulted in new analyses of taxonomic diversity and has engendered a healthy controversy, rooted in systematics, of the extent to which the novel Burgess Shale morphologies represent fundamentally new groups of organisms (Wills et al. 1994). For example, Briggs and colleagues (1992) have argued that the apparent diversity of morphology (often termed *disparity* to avoid confusion with taxonomic diversity) in Burgess Shale taxa is in part an artifact of inadequate phylogenetic knowledge. Taxa are considered to be different when they cannot be placed into extant clades. As structural knowledge of Burgess Shale taxa increases, species previously deemed sufficiently disparate as to constitute new higher taxa (and hence evidence for so-called explosive adaptive radiation early in the Cambrian) are being placed within established monophyletic clades.

Although the discovery of taxa with novel structures provides data on organismal diversity, without a general model of how organisms are constructed one would have little

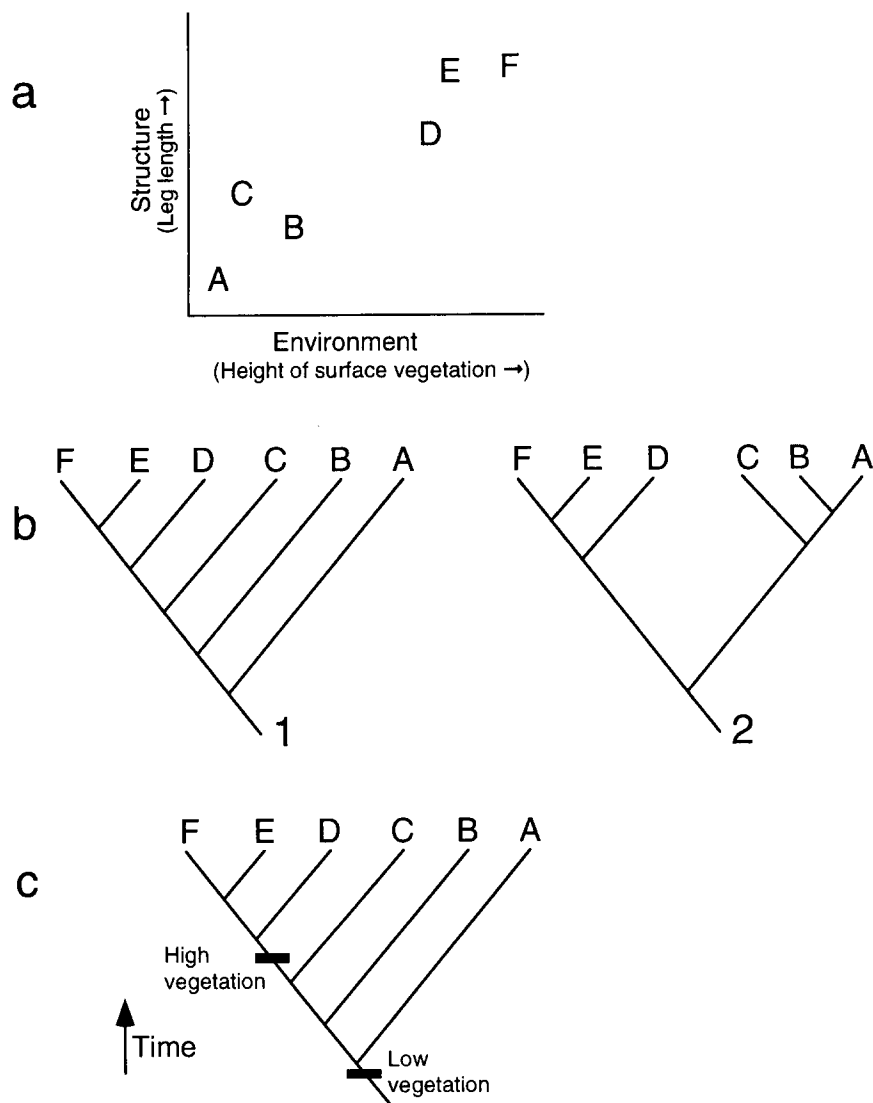


Figure 2. The interpretation of a structure-environment correlation depends on the phylogeny (Lauder 1981). (a) Plot of six theoretical taxa (A-F) illustrating one possible relationship between a structural feature of the taxa (e.g., leg length) and an environmental variable (e.g., vegetation height): Longer length limbs might be found in species that live in habitats with higher surface vegetation. (b) Two possible patterns of genealogical relationship among the taxa. (c) Predicted pattern of environmental change through time if phylogeny 1 correctly depicts the genealogical relationships among taxa A-F. No such prediction can be made if phylogeny 2 is correct.

idea of the range of possible biological designs. Developing a general model into which existing (as well as yet-to-be-discovered) organisms can be placed is of immense value in analyzing the evolution of biological design. Thus, one important contribution of research on organismal form has been the precise definition of a theoretical *morphospace* within which a diversity of forms may be placed. A morphospace defines the

possible range of organismal designs, and one may examine the volume of this morphospace that is actually occupied by living and fossil taxa in an attempt to understand the pattern of structural diversification in a clade.

The classic example of this approach is the work of Raup (1966), in which coiled invertebrate shells were modeled using four parameters. A morphospace can be generated

from three of these parameters by considering x-, y-, and z-axes to be defined, respectively, by the translation rate of the shell coil down the coiling axis, the rate of expansion along the coiling axis, and the distance of the generating curve from the coiling axis (Figure 1). Each point in this three-dimensional space marks a theoretical shape derived from appropriate parameters for each axis. Raup noticed that living taxa occupy a small region of the cube of possible shapes.

Why is so much of the morphospace unoccupied? Perhaps, as suggested by Raup and Stanley (1971), some areas represent biologically impossible morphologies or just regions in which morphologies are inefficient at performing required functions and have thus been selected against. An alternative historical (phylogenetic) explanation might be that the early evolution of shell shape in these clades may have begun in one direction, and once developmental programs and functional relationships among structures became established in the clade, changing to a radically different shell shape was not possible. This type of analysis is important in its use for generating hypotheses about the nature of constraints on morphological evolution and in its definition of potential, not just actual, boundaries to morphological evolution.

More recent analyses have used a phylogeny to determine the historical path that individual clades follow through the morphospace. An advantage of combining phylogenetic analysis with the definition of a morphospace is that a filling of the morphospace may be followed, and the location of primitive clades compared with that of phylogenetically derived taxa. One such example is the definition of a shape morphospace for cottid fishes using multivariate morphometrics by Bookstein and colleagues (1985). A phylogeny was then superimposed onto the positions of taxa in the morphospace.

In addition to allowing generation of a theoretical morphospace, the mathematical modeling of plant and animal structure has additional benefits. For example, the produc-

tion of a mathematical model of organismal design not only abstracts salient features of structure into a precisely defined set of relationships, but the relationships among parts of the model can be manipulated to generate new forms or to simulate change in morphology either in ontogeny or through phylogeny. A good example of mathematical modeling of plant design is the work of Niklas (1992) on plant growth patterns. Plant structure may be defined by branching angles and rotation angles around a central axis and a branching probability function used to generate different plant morphologies. Plant shapes generated using different models may then be compared to see the effect of morphology on performance in tasks such as light interception and fluid conduction within the plant. Niklas (1986) examined major evolutionary trends in plant morphology in the light of results from the modeling and simulation studies and concluded that a number of possible geometric patterns may serve equally well to meet demands of any one environmental task such as light interception.

Comparative physiology. The study of the function of structural features of organisms opens up a new realm in the analysis of biodiversity. Much attention has been focused on the morphological parts of organisms and on the geographic distribution of species, but in comparison relatively little is known about the diversity of function. Although the form-function relationship is one of the oldest areas of concern in biology, relatively little attention has been paid by systematists to the function side of this dichotomy (Lauder 1990). The primary and traditional goals of comparative physiology and biochemistry are to explore the diversity of physiological and biochemical processes and to take advantage of that diversity to elucidate fundamental mechanistic principles (Burggren 1991, Feder 1987, Hochachka and Somero 1984). Accordingly, disciplines analyzing organismal function are traditionally reductionist, mechanistic, and experimental: They seek to understand how organisms work.

In contrast to the paucity of knowledge about the diversity of functional attributes, understanding of the mechanistic aspects of these attributes has increased tremendously over the past 50 years. For example, comparative physiologists have extensively analyzed how physiological processes scale with body size (Calder 1984, Schmidt-Nielsen 1984), and they often interpret residuals from allometric regressions in an ecological context (McNab 1966, Peters 1983). Such analyses have provided insights into many features of organismal design and have been instrumental in the spread of new ways of thinking about how organisms are built. For example, the use of dimensional analysis and scaling to evaluate mechanistic hypotheses about musculoskeletal function has contributed a number of significant insights into how birds fly (Pennycuik 1992).

Also, the now widespread awareness of the importance of fundamental physical relationships such as surface-area-to-volume ratios for understanding organismal design is in large measure due to the contributions of comparative physiologists. Although scaling analyses have in the past usually been conducted outside a phylogenetic framework, several workers (e.g., Heusner 1982) have recognized that the regression slope determined from an analysis of separate monophyletic clades within a larger group may produce a different value than a slope determined from a single overall analysis ignoring phylogenetic structure.

Comparative biochemistry has also contributed important insights into the potential physiological, biochemical, and molecular determinants of biogeographic patterns. Examples include studies by Watt (1983), Koehn (1987), and Powers (1987). An interesting example comes from a study of enzymes (muscle lactate dehydrogenases) from related species of barracuda (*Sphyræna*) found in different thermal environments. Differences in average body temperature of only several degrees apparently favor selection for different enzyme variants that accord with the distribution patterns of the studied species

(Graves and Somero 1982). Minor changes in amino acid sequence underlie the observed differences in kinetic properties and thermal stability of these muscle lactate dehydrogenases. These comparative biochemical-molecular analyses provide information relevant not only to biogeographers and systematists concerned with the factors that might limit species distribution patterns, but also to protein chemists and molecular biologists interested in elucidating protein structure-function relationships. Comparative biochemists thus provide data on so-called natural evolutionary experiments at the molecular level.

Systematics and the analysis of organismal design

The study of organismal form and function may contribute important conceptual tools for the analysis of organismal design. Indeed, such studies are the raw material for historical analyses of evolutionary patterns and processes. But most such analyses, until recently, have lacked an explicitly phylogenetic framework. The increasing use of systematic concepts and methods in comparative morphology and physiology represents more than a minor shift in thinking or research methodology and more than a new and short-lived phase of what might be called phylogenetic correctness. We believe that the integration of phylogenetic methods into disciplines traditionally involved with the mechanistic analysis of organismal design has begun to revolutionize not only the day-to-day analyses conducted on data but also the key conceptual foundations and questions in these disciplines (Huey 1987, Lauder 1991, Wake 1992).

One important problem with many past analyses of organismal design is that species have been treated as statistically independent components of the analysis. Traditional studies of morphological and physiological scaling are particularly subject to this assumption, but the independence of species is an issue that underlies comparative analyses of all kinds. Because organisms are related in a hierarchical fashion, closely related species are more likely

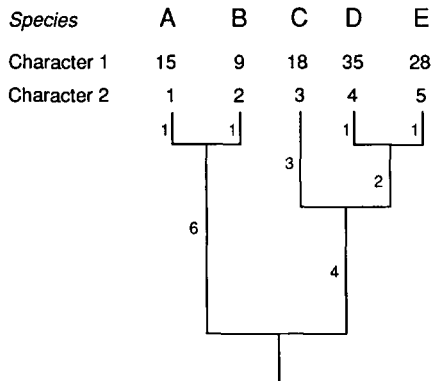


Figure 3. Phylogeny of imaginary species A–E with the numerical values of two physiological characters (1 and 2) shown under each species. Because of the historical (genealogical) relationships among the taxa, a correlation of branch tip values may give a misleading picture of the actual evolutionary transformational relationship between the two characters. The numbers to the left of the branches indicate branch lengths in units of expected variance of change (Felsenstein 1985), which would appropriately be estimated as divergence times (e.g., from fossil information) if characters evolved as by a gradual, clock-like model.

to share aspects of their phenotype than are distantly related species.

An illustration of this point is given in Figure 2, which shows six species (A–F) that show a correlation between some aspect of their design (e.g., leg length) and a feature of their environment (e.g., height of surface vegetation). If one ignores phylogenetic relationships, one might conclude that the species studied show a good correlation between leg length and vegetation height. One might further be inclined to make a causal or efficiency argument that longer leg length could confer a selective advantage in those habitats in which it is found. However (and this point is a key issue in phylogenetic approaches), the interpretation given to the pattern depends critically on the phylogenetic relationships of the taxa studied. Consider two alternative phylogenies for these taxa. The first phylogeny implies that environments with low vegetation heights were the earliest ones inhabited by this group, and speciation subsequently occurred into habitats with higher vegetation. The progressive invasion

of habitats is thus temporally related to structural changes in these taxa, and the phylogeny allows prediction of the sequence of environmental invasion. On the other hand, another possible phylogeny would have closely related taxa corresponding to two major clusters of taxa. In this case, without an outgroup taxa one cannot determine which of the two groups of environments represents the primitive condition. Furthermore, if the six species represent only two major clades, then the individual species clearly are not independent points for regression analysis. Using a computer program such as that described in Martins and Garland (1991), one can compare the correlation observed in the absence of a phylogenetic analysis with a phylogenetically standardized correlation. Ignoring phylogeny, the correlation is 0.935 ($P < 0.01$). Using phylogenetically standardized contrasts for the first phylogeny considered gives a correlation of 0.824 ($P < 0.05$), while the second phylogeny generates a correlation of 0.792 (not significant).

Because species cannot be assumed to represent independent datapoints for statistical analyses, this degrees-of-freedom problem prevents traditional statistical methods from being properly applied to comparative datasets (Clutton-Brock and Harvey 1977, Felsenstein 1985, Harvey and Pagel 1991, Martins and Garland 1991). Computer-simulation studies show that ignoring phylogenetic relatedness, and hence the possibility of resemblance due solely to relationship, leads to inflated Type I error rates (P -values), reduced power to detect significant relationships, and inaccurate estimates of evolutionary relationships (Grafen 1989, Martins and Garland 1991). Several phylogenetically based comparative methods correct for these problems (reviews in Harvey and Pagel 1991, Martins and Garland 1991).

The importance of phylogenetic considerations for statistical analyses may be illustrated by a hypothetical case presented by Martins and Garland (1991) in which a comparative biologist seeks to determine whether two characters are evolutionarily correlated in a set of five

species (Figure 3). The magnitude and significance of a potential evolutionary correlation between the two characters can be tested in several ways. First, a conventional Pearson product-moment correlation, ignoring phylogeny and assuming independence, suggests a strong evolutionary relationship (correlation 0.789) between the characters. Second, Felsenstein's (1985) independent-contrast method, which incorporates phylogenetic information and corrects for nonindependence, suggests instead that the correlation is weak (0.016). Third, a minimal-evolution correlation, which also incorporates phylogenetic information and which assumes gradual character evolution (Martins and Garland 1991), yields an intermediate value (0.498).

Thus, the estimate of the correlation itself depends critically on the phylogeny of the species studied. And the apparent statistical significance of the correlation may depend on the assumed model of evolution (Harvey and Pagel 1991, Pagel and Harvey 1989; see Martins and Garland 1991 for methodology) as well as on the specific test used for estimation and hypothesis testing. Examples of these methods applied to real physiological data are found in Garland and colleagues (1991) and Walton (1993).

Reconstructing historical patterns and sequences of trait differentiation. A major area of interest in comparative biology involves attempts to reconstruct and analyze the historical patterns and sequences of the diversification of traits (Brooks and McLennan 1991, Donoghue 1989, Greene 1986, Huey and Bennett 1987, Monson 1989). A phylogenetic basis is essential for reconstructing the evolution of physiological and biochemical diversity in a lineage and understanding how different types of structural and functional traits evolve. Many studies have focused on evolutionary patterns in one class of traits (e.g., skull structure or the amino acids in a protein). One area of current research is the historical relationship among different types of organismal traits (both structures and functions).

For example, in order to understand why several species of bird differ in the movements of their wings during mating, one might examine several different classes of structural and physiological characters (Table 1)—changes in any one of which could result in a different behavior. Changes in neuronal output patterns in the nervous system, physiological properties of wing muscle fibers, or reorganization of muscle attachments might all (either singly or together) result in a different movement pattern being generated by a species. One can extend the simple hierarchical view of different classes of characters shown in Table 1 to a phylogenetic/historical view of structure and function illustrated in Figure 4. By comparing both the structural design and physiological patterns of several taxa of known phylogenetic relationship, one can begin to examine parallel evolutionary changes in structure and function and hence address questions relating to the evolutionary timing of changes in design. For example, do novelties occur first in neuronal components, or are peripheral musculoskeletal elements altered first? Are some classes of characters (Table 1) more phylogenetically conservative than others? Or do all components of a complex system tend to change together? A phylogenetic approach to reconstructing ancestral characteristics of form and function can help answer these questions.

Major patterns of character evolution. Comparative physiologists sometimes try to reconstruct the origin of major physiological innovations (e.g., origin of endothermy, of anaerobic glycolysis, and of C4 photosynthesis) or the changes in physiological or biochemical traits associated with major evolutionary transitions, such as from water to land (Bennett and Ruben 1986, Burggren and Bemis 1990, Carrier 1987). A phylogenetic and historical perspective is crucial here. For example, although some comparative physiologists had used the frog as a physiological model of amphibians that first invaded the land, Gans (1970) showed in a classic study that frogs are highly specialized animals and thus are hardly appropri-

Table 1. One possible set of structural and physiological classes (or levels) of characters that could be studied using a phylogenetic framework. Evolutionary change might proceed at different rates in each level; change among levels is not necessarily correlated. Thus, a fruitful avenue of research in morphology and physiology is the examination of ontogenetic or phylogenetic transformations among levels.

Class of character (organismal trait)	Sample character
Behavioral	Display behavior during mating
Functional/physiological (at the level of peripheral tissues)	Kinematics of bone movement, physiological properties of muscles, biomechanical tissue properties
Structural (at the level of peripheral tissues)	Topographic arrangement of muscles and bones, tissue histology
Functional/physiological (at the level of the nervous system)	Neuronal spiking patterns, motor patterns, membrane properties, modulation by neurotransmitters
Structural (at the level of the nervous system)	Neuronal morphology, topology of neuronal interconnection, wiring of sensory and motor pathways

ate models of the first amphibians. In effect, "...the frog is a red herring" (Gans 1970).

Similarly, although neurophysiologists have long assumed that heat-sensitive pit organs of the pit vipers (e.g., rattlesnakes) represent adaptations to feeding (i.e., ability to detect warm-blooded prey at night), a recent phylogenetic analysis (Greene 1992) suggests that the origin of facial pits was more likely correlated with the evolution of stationary defensive behavior and only secondarily was used for feeding. Also, although the accumulation of glycinebetaine in response to salinity and water stress was once thought to have evolved widely among plants native to saline habitats, broader comparative studies have shown that not all halophytic species accumulate glycinebetaine. The occurrence of the compound appears to have a strong phylogenetic component (Wyn Jones and Storey 1981).

Another example is provided by Jensen (1992), who demonstrated that failure to consider phylogenetic relationships led to inflated estimates of the correlation between morphological and biogeographic parameters. Other workers had reported that oaks with large acorns have broader geographic ranges than those with small acorns. Their analyses, conducted by treating all eastern North American oaks as a single

group, revealed highly significant correlations ($p < 0.05$) between acorn volume and geographic range, suggesting a cause-effect relationship. Jensen's reanalysis, in which the two monophyletic groups of species were treated separately, revealed much lower correlations between acorn volume and geographic range ($p > 0.05$) and provided evidence that the two groups have evolved differently with respect to morphological features that might influence breadth of geographic range.

Friedman (1990, 1992) was able to trace the evolutionary origins of polyploid endosperm tissue in the seeds of angiosperms. Endosperm functions as the principal nutritive tissue of angiosperm seeds, supporting the growth and maintenance of the embryo. Polyploid endosperm is a defining trait of the angiosperms and might be one of the advantages allowing angiosperms to dominate most terrestrial habitats. Friedman's studies were conducted in the Gnetales, a group of nonflowering seed plants that have been proposed through several phylogenies to represent the closest extant ancestor to the angiosperms. Using the Gnetales as an outgroup, Friedman demonstrated that endosperm probably evolved its nutritive role from supernumerary embryos. In the Gnetales, such secondary embryos degenerate as they nourish the primary

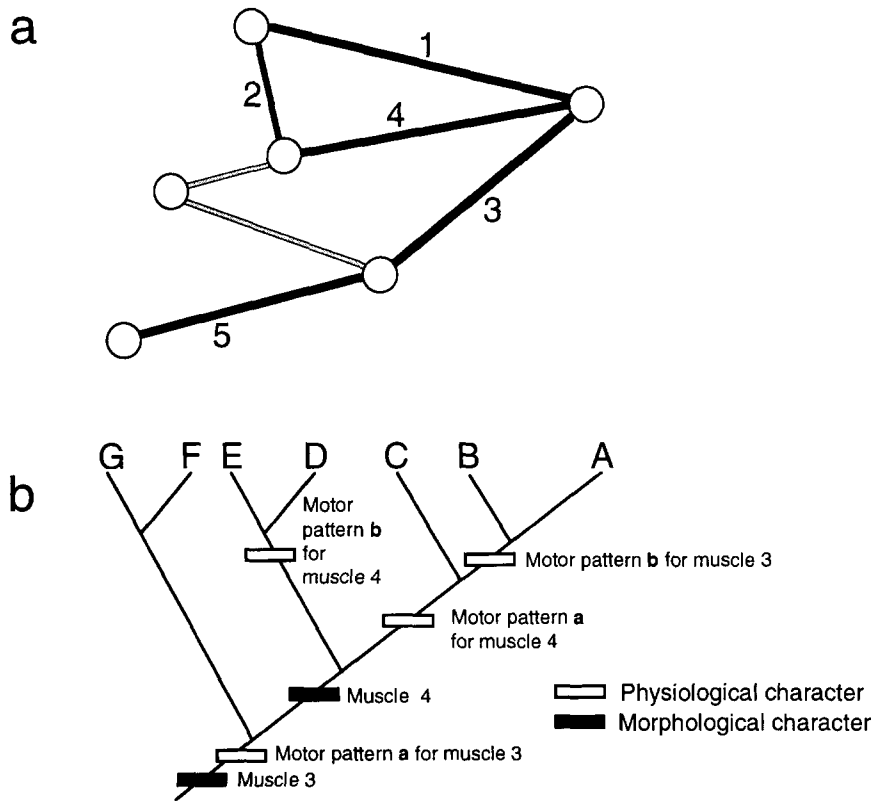


Figure 4. (a) Schematic diagram of a musculoskeletal system in taxon A composed of bones (circles), muscles (black lines), and ligaments (shaded lines) to illustrate the role that a phylogenetic analysis might play in understanding evolutionary patterns of structural and physiological traits. (b) Phylogenetic relationships of seven related taxa showing the origin of morphological and physiological traits of this musculoskeletal system. An analysis of structure and function could be done for each terminal taxon (A–G) and the historical pattern of character change mapped onto a phylogeny. The phylogeny shows the sequence with which physiological and morphological characters have arisen. Note that the structural and functional traits have different evolutionary histories. For example, the presence of muscle 3 is primitive for this clade along with a particular pattern of muscle activation (motor pattern a). The clade A+B is characterized by a novelty in physiology (motor pattern b) for muscle 3 but no change in muscle structure. The presence of muscle 4 characterizes the clade A–E, but two different physiological patterns of activation are present within this clade (motor patterns a and b).

embryo in an apparent act of altruism—a phenomenon that brings to the surface several hypotheses concerning the role of kin selection in the evolution of developmental traits.

Finally, Schwenk (1994) has recently shown how the use of a nonphylogenetically based classification of squamate reptiles, has hindered understanding of the evolution of sensory systems. Schwenk demonstrated that use of a classification that did not reflect genealogical relationships led to incorrect generalizations about squamate vision and chemoreception and their environmental correlates. For example, recognition of nonmono-

phyletic clades of lizards promoted a false dichotomy between taxa purported to use vision for feeding versus taxa that supposedly rely primarily on chemoreception to find food. Had use of these two sensory modalities been mapped onto monophyletic taxa, 40 years of false generalizations about the evolution of sensory systems in lizards could have been avoided. Squamate reptiles provide an excellent case study of the predictive and analytic consequences of phylogenetic hypotheses of organismal design.

Choice of species for comparison. In many comparative studies the choice

of species has been guided by specific features (physiological, morphological, and environmental) of the species or by its tractability and accessibility for physiological studies (the August Krogh Principle—the idea that specific physiological problems can be matched to a species in which that problem can be most easily studied; see Krebs 1975). For example, studies of urine concentration by the mammalian kidney might focus on a species of desert rodent, under the assumption that such a species is likely to be adapted to that environment and will thus show with special clarity the relationship between structure, function, and environment.

However widespread use of the Krogh principle has been in guiding physiological research, it is fundamentally a nonphylogenetic approach to organismal design. The choice of a single species in a single environment does not allow any judgment to be made about the historical origin of the traits under consideration and is in reality an equilibrium (nonhistorical) method for analyzing organisms and their current environments.

A maxim of comparative phylogenetically based research is that at least a three-species comparison is best for clarifying structure-function-environment relationships (Brooks and McLennan 1991, Garland and Adolph 1994, Huey 1987). The use of at least three species allows historical sequences of character change to be reconstructed and is in itself a test of the generality of findings on one taxon alone. Thus, if a second species of rodent closely related to the species studied is examined, one might find that its kidney is modified for urine concentration even though this species does not live in the desert. (An example of supposed physiological adaptations in one species that are later found to be widespread is discussed in Dawson et al. 1977). Furthermore, if a third species of rodent, one that inhabits an arboreal habitat, is studied, one might discover that its kidney is unable to concentrate urine. With these data and a phylogeny, one can reconstruct a historical sequence of physiological and environmental change that is

not possible with a one- or two-taxon study.

In many other comparative studies the explicit intent is to address evolutionary issues such as physiological adaptation to an extreme environment. For such studies, the choice of species for analysis can be guided by systematic information (Burggren 1991, Garland et al. 1991, Huey 1987). A comparison of close relatives reduces, for instance, the probability that observed differences between taxa are an artifact of long-separate phylogenetic history rather than of adaptation to a particular environmental feature.

Detecting evolutionary anachronisms. A systematic and historical perspective also is useful in detecting evolutionary anachronisms (i.e., traits that evolved in response to conditions no longer existing). For example, the giant fruits of some Neotropical trees might have evolved as adaptations for dispersal by Pleistocene megafauna (Janzen and Martin 1982), and the presence of flight motor neurons (currently nonfunctional) in flightless crickets probably reflects the evolution of flightless grasshoppers from ancestors that could fly (Dumont and Robertson 1986).

Thus, an appreciation of phylogenetic history sometimes clarifies the function—or the lack thereof—of an otherwise puzzling physiological trait (Huey 1987). A phylogenetic analysis may reveal that the traits thought to represent novel evolutionary responses to current environments may have been retained from an ancestral condition that had little in common with current environmental conditions.

Morphometrics. Systematics has had considerable influence recently in the quantitative description of morphology. Two distinct avenues of progress are evident. First, many biometricians have developed new methods for archiving the shape of biological structures (and whole organisms). These methods are rigorous, quantitative, and lend themselves to multivariate statistical analysis (reviewed in Rohlf and Bookstein 1990).

Some of these methods deal with organismal shape data presented as

outlines as well as discrete landmarks, and traditional multivariate statistical methods have been extended to deal more effectively with such biological problems as size and shape. In particular, the traditional bivariate approach to allometry has been extended into the multivariate domain, with the benefit that many studies of form today, whatever their purpose, are multivariate in nature.

It would be difficult to overestimate the impact that the development of both data acquisition and statistical tools for the study of morphology has had on research on organismal form; in truth, only in the last decade has the promise of Thompson's approach to structure been realized. Early attempts to study the deformation of one shape into another, for example, were largely qualitative and inaccurate and not readily amenable to statistical study.

Although vigorous debate continues on the assumptions of the analytical methods used to study form, there is no doubt that the recent rapprochement of morphometrics and phylogenetics has opened up a broad array of new questions. It has also raised the standards to which answers will be held (Zelditch et al. 1992, 1995).

Conclusions

Physiological and functional traits of plants and animals are not well-preserved in fossils. Unfortunately, much of the effort toward biodiversity recognition and preservation has focused on biogeographic and taxonomic concerns rather than on the analysis of functional diversity. For most clades, a comparative analysis of physiological traits is in its infancy. In part, perhaps because of the past tendency of physiologists to focus on a few organisms considered to be good models, a broadly comparative historical approach to the study of organismal function is just beginning. This beginning occurs at an opportune time, however, because methodologies for quantitative comparative methods are blossoming, organismal biologists are becoming interested in expanding beyond one-taxon analyses, and the choice of species to be analyzed is

being based increasingly on phylogenetic information. The diversity of organismal function (and its relationship to structure) is a vast area of unexplored biology. With the infusion of historical methods and concepts from systematics, the future promises exciting advances as physiologists and morphologists bring new tools to bear on the analysis of structural and functional diversity.

Acknowledgments

We gratefully acknowledge the contributions of the many members of the original two committees (especially T. Garland) for Systematics Agenda 2000 (Quantitative and Evolutionary Morphology, Comparative Physiology and Biochemistry) who assisted in the preparation of the original reports that formed the basis of this article. This article is a product of the initiative Systematics Agenda 2000, which was generously supported by the National Science Foundation through grant DEB-9396035. Preparation of the manuscript was supported by: NSF IBN-9119502 to George Lauder, NSF DEB-9301151 to Ray Huey, and NSF BSR-8604960 and BSR-8911433 to Russell Monson.

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