

The Argument From Design

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I. Introduction

Let us suppose that one day, while out for a walk, I have the good fortune to come upon a Rolex watch lying on the ground. At first I am pleased at the prospect of possessing an improvement to the inexpensive plastic watch that I am currently wearing. But as I continue my walk and examine the Rolex more closely, I begin to suspect that this watch may not be all that it seems. The gold on the casing has started to flake off, and the band has a suspiciously flimsy feel to it. I come to suspect that the watch I have found might be a counterfeit, discarded by an embarrassed purchaser who uncovered the deception. Just how good is the watch that I have found? How does this "Rolex" compare to my inexpensive digital watch in timekeeping and resistance to shock? How does a Rolex keep time in comparison to the U.S. National Bureau of Standards atomic clock? The watch I have found may run slow due to lack of a precise fit among the parts. The watch may not run at all due to a broken spring. Or the watch may actually be a counterfeit Rolex, made by a clever watchmaker, which looks well made but only runs a few days before breaking. We can only discover the quality of a watch we have found by taking it apart, examining its mechanics, and testing its performance against alternative designs.

The central theme of this chapter is that we have been too assumptive in the study of organismal design. Too often we have been willing to assume, like the purchaser of a counterfeit Rolex, that the watchmaker has done a good job as a result of looking at the external features of the watch instead of focusing on mechanical and performance evaluation. We also have been assumptive in presuming that some features of organismal design are accidental by-products of the method of construction, without a design analysis. This is not so much the fault of the watchmaker as it is a case of "buyer beware." Evolutionary biologists interested in organismal design must experimentally assess the mechanical quality of a watch they have discovered in comparison to other designs, and not restrict themselves to an analysis of the face alone.

This chapter addresses two specific issues. First, I suggest that in our desire to draw conclusions about biological design and to support theoretical views of how organisms are built, we have been too willing to make assumptions about the relationship between structure and mechanical function, about the patterns of selection that have acted on components of design, and about the process of design construction itself. Second, I argue that we have not often conducted the mechanical and performance tests needed to assess the average quality of organismal design. Perhaps we have been blinded by a few exemplary cases, but if the variance in quality is high, these few best cases will give a misleading picture of the range and variation in design. Additionally, conclusions that specific phenotypic features may be accidental by-products of the design process may also suffer from the lack of a rigorous design analysis.

I begin by reviewing the argument from design in its classical and modern formulations. I then consider four reasons why we might be cautious about accepting an argument from design as *prima facie* evidence of the past action of selection in generating adaptive traits. My analysis of the argument from design will use primarily concepts and examples from the study of animal morphology and physiology. The investigation of animal design is the focus of research in the disciplines of functional morphology, biomechanics, and comparative physiology, and many issues relevant to the argument from design can be seen with special clarity via the study of specific features of animal structure. Two major means by which we recognize design in organisms are by applying engineering and mechanical principles, and by analogies to man-made devices. In addition, both the original formulations of the argument from design and their modern counterparts often rely heavily on anatomical examples and analogies. While the argument from design is certainly much broader than this and has been applied to numerous other phenotypic features, such as behaviors and host-parasite relationships (e.g., Cronin, 1991; Dawkins, 1987; Williams, 1966, 1992), this chapter will focus on the application of the argument from design as it relates to the specific areas of anatomical structure and physiological function.

One advantage of restricting the analysis to this area is that the mechanistic emphasis of biomechanics and physiology allows explicit specification of performance metrics such as efficiency, force output, and velocity of motion (Lauder, 1991b, 1994). Also, structural configuration can be quantified with considerable precision, and the physiological function of these structures can be measured directly to permit a direct evaluation of design performance. It is often more difficult to conduct comparative analyses of behavioral or ecological designs and their relative efficiencies. In addition, the causal implications of differences in design among species are often easier to determine in a mechanical system (where lever arms, masses, etc. can be measured precisely) than in ecological or behavioral comparisons, and we can thus minimize the problem of correlative results not possessing causal information.

II. The Argument From Design

A. The Classical Argument

The charm of the argument from design (or AFD) is considerable, and in its classical formulation, the logic of the AFD is as follows. The very existence of any object of complex structure or function implies the existence of a purposeful maker of that object. Hence, Paley (1836), in an oft-cited example, explained that finding a watch on the ground implies directly the existence of a watchmaker. It would be inconceivable to attribute the presence of a watch on the ground to the spontaneous assembly of materials into the exact configuration needed to make a working watch. However, should we happen to find a stone on the ground, we need not invoke any maker of the stone as it is common for stones to arise as a result of numerous geological processes. In the case of the stone, we can clearly identify a mechanical causal agent that could place the stone in the position that

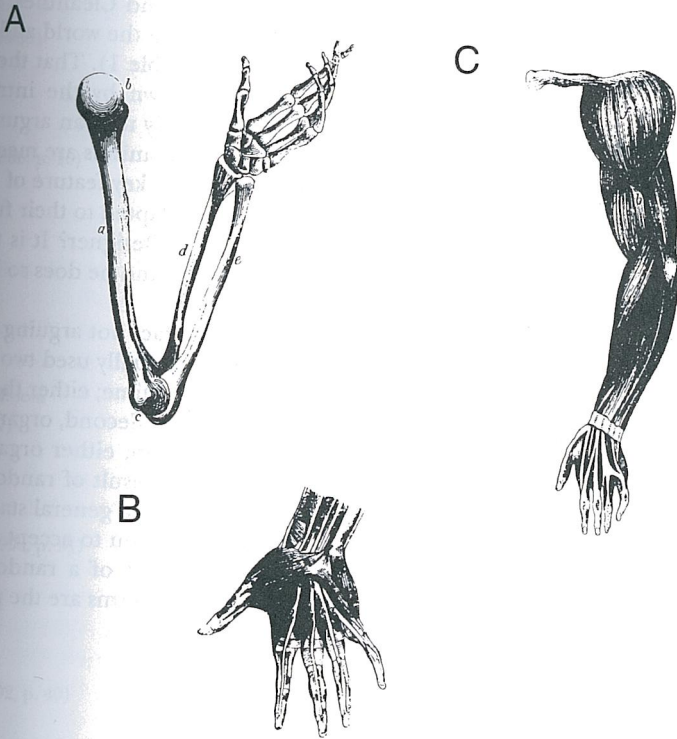


Figure 1 Representative plates from Paley (1836) who used the mammalian forelimb to illustrate biological design. (A): Human arm bones, including the humerus (a), radius (d), ulna (e), and hand. (B): Human hand showing the superficial musculature and flexor tendons to the fingers. (C): Human arm with skin removed to show the musculature.

we happen to find it, without the need to resort to a “designer” to construct the stone. A watch is considerably more complex and intricate than a stone, and Paley argues that it is this complexity that requires the invocation of a maker or “designer” of the watch.

Paley then compares the complexity of the watch to the complexity of organisms (Fig. 1; Table 1). He argues that just as the intricate watch required a designer, so does a complex organism. Organisms, then, provide evidence of a Creator and are one manifestation of His work.

There are differing interpretations of the logic of Paley’s argument from design. If one accepts that Paley was constructing an argument by analogy, suggesting an analogy between how we conceive of the intricacy a watch and how we perceive the complexity of organisms, then Hume (1779) is often held to have demolished this argument more than 50 years prior to Paley. Thus, Hurlbutt, (1985, p. 169) was able to remark that “... I shall assume what I feel to be quite evident: the proposition that Hume’s analysis destroyed the rational foundations of the design argument as it was commonly presented in the seventeenth and eighteenth centuries.” In fact, Hume’s “Dialogues Concerning Natural Religion” (1779) are valuable reading for modern biologists interested in the logical foundation of the argument from design. In his Dialogues, Hume describes a conversation among three individuals: Philo, Demea, and Cleanthes. Cleanthes argues in favor of the proposition that God is manifest in the world and that such manifestation is evident in the design of organisms (Table 1). That the Designer of the world is intelligent and magnanimous is shown by the intricacy and harmonious nature of organic design. Cleanthes directly uses an argument from analogy: human designers built a mechanical world, organisms are mechanical in design, so a Creator must have constructed organisms. A key feature of Cleanthes’ argument is that the parts of organisms appear to be adapted to their functions as “means to ends”; how else could this occur without a Designer? It is the role of Philo in the Dialogues to destroy Cleanthes’ argument, and he does so by showing that the argument from analogy is logically flawed.

Sober (1993, pp. 30-36) argues that Paley was in fact not arguing by analogy (hence Hume’s critique has no force) and that Paley actually used two arguments as follows. First, a watch is a complex design for keeping time; either the watch was produced by a designer or by a random physical process. Second, organisms are of complex design which aids in survival and reproduction; either organisms have been constructed by a Designer or organisms are the result of random physical processes. Sober suggests that the Paley AFD amounts to a general statement that if you accept the first argument then it is plausible for you to accept the second. Since no one believes that the watch was the product of a random physical process, then you should be inclined to accept that organisms are the product of a Creator.

B. The Darwinian Argument

This dispute over the logical nature of Paley’s AFD notwithstanding, it is clear that publication of the *Origin of Species* (Darwin, 1859) ushered in a new way of thinking about the design of organisms. Richard Dawkins has most clearly

TABLE I

Selected Statements from the Literature Illustrating Both the Teleological and Modern Argument from Design

Reference	Comment on the argument from design
1. Hume (1779, p. 109), writing as Cleanthes	<p>“Look around the world: contemplate the whole and every part of it: you will find it to be nothing but one great machine, subdivided into an infinite number of lesser machines...”</p> <p>“All these various machines, and even their most minute parts, are adjusted to each other with an accuracy, which ravishes into admiration all men, who have ever contemplated them.”</p> <p>“The curious adapting of means to ends, throughout all nature, resembles exactly ... the productions of human contrivance...”</p>
2. Paley (1836, p. 18)	<p>“...for, in the watch which we are examining, are seen contrivance, design, and end, a purpose, means for the end, adaptation to the purpose.”</p>
3. Rudwick (1964, pp. 34-35)	<p>“...the detection of any adaptation in a fossil organism must be based on a perception of the machine-like character of its parts, and on an appreciation of their mechanical fitness to perform some function in the presumed interest of the organism.”</p>
4. Williams (1966, p. 10)	<p>“A frequently helpful but not infallible rule is to recognize adaptation in organic systems that show a clear analogy with human implements.”</p> <p>“At other times the purpose of a mechanism may not be apparent initially, and the search for the goal becomes a motivation for further study. Adaptation is assumed in such cases...on the indirect evidence of complexity and constancy.”</p>
5. Pinker and Bloom (1990, p. 707)	<p>“Evolutionary theory offers clear criteria for when a trait should be attributed to natural selection: complex design for some function, and the absence of alternative processes capable of explaining such complexity.”</p>
6. Thornhill (1990, p. 31)	<p>“...adaptations are the long-term consequences of evolution by selection and thus understanding the functional design of an adaptation is synonymous with understanding how evolution by directional selection worked ...”</p>
7. Williams (1992, p. 40)	<p>“Adaptation is demonstrated by observed conformity to <i>a priori</i> design specifications.”</p> <p>“The hand is an adaptation for manipulation because it conforms in many ways to what an engineer would expect, <i>a priori</i>, of manipulative machinery...”</p>

expressed the Darwinian formulation of the argument from design in his book entitled "The Blind Watchmaker" (Dawkins, 1987). Dawkins argues cogently in favor of the view that the process of evolution by natural selection may act like a blind watchmaker. Basic biological principles of variation, heredity, and selection operate to generate biological design and complexity of structure without requiring a purposive guiding hand or a Designer with a view to the end product. Biological design arises as a result of selection and is modified in succeeding generations as selection acts on those designs that result from previous episodes of selection. Although mutation, which generates new variation, may be random with respect to currently available variation within populations, natural selection is not random. Selection acts on existing variation within the context of the current environment to build up biological design, modifying what has come before and not acting to generate design *de novo* in each generation. The potential transformation of any biological design is thus constrained by its past history of variation and selection. The role of Paley's purposive Creator/Designer/watchmaker has been replaced by selection acting on heritable variation. Darwin's mechanistic explanation of organic design was surely a great intellectual achievement.

One might suppose that the presence of a mechanistic explanation for biological design such as that proposed by Darwin would have marked the end of the argument from design in modern biology. After all, given the sufficiency of a purely statistical/mechanical explanation for design, it would seem unnecessary to even present arguments derived from the way organisms are constructed.

C. The Modern Application

But in fact the AFD is alive and well, although certainly different in its particulars, if not in character, from what Paley invoked. In its modern formulation, the AFD centers around the recognition of adaptive characters and the inference that these traits have been produced by the process of natural selection. Instead of attempting to infer the action of a Creator from the manifest complexity of organisms, many evolutionary biologists seek instead to infer the action of selection from organismal design. Often it is the complexity of design itself that is held to provide evidence of the past action of selection (Table 1; Pinker and Bloom, 1990). A second criterion for the inference of adaptation is the resemblance of organic design to man-made design. The selection of comments from Rudwick (1964) and Williams (1966, 1992) presented in Table 1 illustrates this widespread view. If we can recognize in organisms a configuration reminiscent of how a human engineer might have designed a structure (enabling us to call the structure a "design"), then according to the modern AFD we can reasonably infer that selection acted to produce the structure and that the structure serves an adaptive function, aiding survival and reproduction.

There are many conceptual similarities between the modern AFD and the classical version presented by Paley. Indeed, some modern advocates of the AFD use Paley explicitly as a suggested guide for the study of adaptation. Thus, Williams (1992, p. 190) suggests that the works of Paley be studied as a means of understanding how adaptation may be recognized, and he approvingly reproduces

portions of Paley's Natural Theology as a methodological guide for comparing biological design to man-made structures. A significant overall similarity in all arguments from design is the inference of a process (either natural selection or the action of a Designer) from a pattern (organismal design, however recognized). Indeed, the validity and the utility of the modern AFD depend critically on the extent to which one can reliably make such an inference.

Not all evolutionary biologists have accepted the modern version of the AFD or even use the term "design" to reflect the result of a mechanistic process that generates complex structure (whether by a Designer or by natural selection). Dawkins (1987) subtitled his book "why the evidence of evolution reveals a universe without design," implying that the very concept of "design" has been made obsolete for biological systems. Continued use of the argument from design in ethology prompted Ollason (1987) to proclaim in frustration that "...the idea that animals are designed is dead, killed by Hume, buried, perhaps unwittingly, by Darwin, but however comprehensively it is disposed of, like the walking dead it haunts us still."

Far more than simply haunting us, the modern version of the AFD is so pervasive that in many ways it may be said to be the most commonly used means of inferring the past action of selection (Table 1; Thornhill, 1990, 1996; Williams, 1966, 1992). And far from abandoning the use of the term "design," evolutionary biologists have instead relied heavily on this concept as a means of inferring selective forces.

In order to understand the logical structure of the modern AFD, it is necessary to consider what is meant by three key terms: adaptation, function, and design. Because each of these is used in many different ways in the literature, clarifying these concepts will be critical to understanding both the promise and the difficulties inherent in the modern formulation of the AFD.

1. Adaptation

While it has been widely noted that the term "adaptation" may refer to both a trait (an adaptation) and the process of becoming adapted (Brandon, 1990; Futuyma, 1986), this distinction is necessarily conflated in most discussions of adaptation (see Lauder *et al.*, 1993; Leroi *et al.*, 1994; Sober, 1984). Many workers accept some variation of the following historical definition of adaptation, and this is the definition I will use here: an adaptation is a trait that enhances fitness and that arose historically as a result of natural selection for its current biological role (Arnold, 1994b; Baum and Larson, 1991; Brooks and McLennan, 1991; Coddington, 1988; Gould and Vrba, 1982; Greene, 1986; Harvey and Pagel, 1991; Lauder *et al.*, 1993; Mishler, 1988; Sober, 1984). Thus, adaptation as a state is defined in part by the action of a mechanistic process, natural selection, acting directly on that trait currently deemed to be an adaptation. One implication of this definition is that neither a trait that resulted from correlated responses to selection on a *different* character nor a trait that results from random genetic drift would be considered as adaptations. Such traits might have fitness effects and they might even form an integral part of the phenotype, but they would not be adaptations. [A number of other terms have been proposed to describe traits of this type (Baum and Larson, 1991; Gould and Vrba, 1982; Griffiths, 1992), some of which will be considered later in this chapter]. To be an adaptation a trait must

have resulted from direct selection for that trait. Not all workers accept this approach, however: other definitions of adaptation emphasize that an adaptive trait is one that enhances current fitness without regard to the mechanism that gave rise to the trait (Fisher, 1985; Reeve and Sherman, 1993) and consider the comparative fitness of extant variation in a trait as the means to identifying adaptation.

2. Function

The term "function" has an equally confused history in the literature, with biologists in different research areas using this term with very different meanings. Recently, a number of authors have attempted to sort out some of this conceptual confusion and clarify the multiple uses of this term (Allen and Bekoff, 1995; Amundson and Lauder, 1994; Bekoff and Allen, 1995; Griffiths, 1992; Lauder, 1994). Most evolutionary biologists use the term function as synonymous with selective advantage, suggesting that the function of a trait is that property of the trait that resulted in the trait having been selected for. Thus, the function of long limbs in ungulates might be given as "escape from predators." By this definition, a function is recognized as an effect of the process of selection [and hence may be referred to as the selected-effect (SE) definition of function (Amundson and Lauder, 1994)] and by the performance/fitness advantage incurred by the trait. Implicit in this definition is that the history of selection needs to be known in order to make an informed statement about function, and hence the SE definition of function is inherently historical.

On the other hand, functional morphologists and physiologists often use the term function to mean the use, action, or mechanical role of phenotypic features (Amundson and Lauder, 1994; Bock and von Wahlert, 1965; Lauder, 1994). Thus, a bone might have the mechanical function of stiffening the limb against gravity even though this may not be the effect or performance advantage on which selection acted during the origin of the bone. (For example, the bony components of the limb could have originated in an aquatic ancestor of the terrestrial taxon now under consideration.) This is a nonhistorical use of the term "function" that does not depend on identifying selection forces. The concept of anatomical function is essential to our discussion of the argument from design because it is the measurement (or estimate) of how structures are used by animals that most often is the basis by which inferences about adaptation and selection are made. The biomechanical analysis of anatomical structure and function provides the basis for comparing biological phenotypes with man-made devices, and thus is a tool by which one could possibly detect adaptation in biological design. It is analysis of the "machine-like character" of traits (Rudwick, 1964), "complex design for some function" (Pinker and Bloom, 1990), and "conformity to *a priori* design specifications" (Williams, 1992) that encourages the inference of adaptation and selection, and hence constitutes a key component of the modern argument from design (Table 1).

This chapter uses the phrase "mechanical function," "anatomical function," or "physiological function" to distinguish this nonhistorical meaning from the selected-effect use more common in evolutionary biology ("evolutionary function" or "adaptive function"). This will be a convenient way to describe the action of complex morphology in our analysis of the AFD below, without making any

assumptions about selected functions of those structures. The biological context of structure and function is referred to as the "biological role" of a structure or mechanical function (Bock and von Wahlert, 1965; Lauder, 1994).

3. Design and the Argument from Design

The concept of design as used in the fields of biomechanics and functional morphology refers to an organized biological system which performs one or more mechanical functions (Lauder, 1982, 1995; Amundson and Lauder, 1994). Design in this sense is not necessarily equivalent to structure, but is a more general concept of structure in relation to function. However, the term design is often also used as shorthand for complex structure that appears to have some, possibly yet to be determined, function.

In evolutionary biology, the notion of function often has a teleological connotation that is closely related to the concept of "design" (Allen and Bekoff, 1995; Ayala, 1970; Griffiths, 1992). The "design" of an organism in evolutionary parlance often includes the adaptive (selected-effect) function of those traits that we wish to call a "design" (Dennett, 1995). Although the purposive connotations of design have engendered some controversy (e.g., Ollason, 1987), in general there is widespread recognition of the fact that natural selection acts to alter biological organization based on currently available variation and not with anticipation of an endpoint in the future.

The modern evolutionary incarnation of the argument from design is based either directly or indirectly on several propositions that are required to perform the research program suggested by the AFD. At its core, the AFD is an inference of process from pattern: the process and the action of natural selection are inferred from the complexity and configuration of structure. Most of the discussion about the AFD concerns allied research programs, as there are several means of analyzing biological design. How, empirically, do we recognize biological adaptation? How can we analyze complexity of organization and the relationship between biological and human design? What can we infer about the action of selection from an analysis of the phenotype alone? If the argument from design is to be more than a theoretical construct, we must be able to successfully conduct an empirical research program.

There are four critical components to the analysis of biological design. Not all of these will be present in any one analysis, and any given investigation may use aspects of more than one of these components.

First, we must be able to make accurate inferences of mechanical function from structure. Many authors writing about the AFD have stressed the relevance of understanding how organisms function as machines (Table 1). It is through such biomechanical analyses that we come to understand how organisms are constructed and how various components of the phenotype interact to generate behavior. And it is via an understanding of the relationships between mechanical function and structure that we propose hypotheses about evolutionary function, adaptation, and selection, key elements of the modern AFD.

Second, if organic design is to be compared to man-made implements as a means of inferring evolutionary function, then we must be able to specify design criteria. That is, given a mechanical function such as "detect prey in the water at a distance of 10 cm" as a goal, we must be able to abstract from the desired

mechanical function basic elements of design that will meet that goal. Then we need to evaluate the extent to which one or more biological designs match those design criteria and thus are likely to have performed the hypothesized function. In addition, it would be enormously helpful in formulating AFD hypotheses to construct alternative designs and to assess the relative performance of those configurations. Are there several designs with equivalent performance that could perform the needed function?

Third, we must be able to infer evolutionary function from analysis of the phenotype alone. Many AFDs are based exclusively on a phenotypic analysis of a few individuals or a few groups of related taxa. Central to the modern AFD is the ability to make inferences of patterns of selection on traits so that we can say that a given trait is an adaptation for some specific evolutionary function. Indeed, we must be able to go further than this and distinguish between *direct* selection for a trait and alternative explanations for that trait: correlated response to selection on another character, drift, unmodified inheritance from the ancestral condition, and the like.

Fourth, a key to the successful implementation of the AFD is the ability to atomize complex collections of phenotypic features into relevant component parts. This is necessary in order to analyze individual components of design. If all parts of an organism function in such an interconnected and integrated manner that we cannot consider components in isolation, then we cannot apply the AFD to less than the entirety of the organism, the latter not normally being a feasible research program.

III. Problems With Applying The Argument From Design

This section treats the four issues discussed above in detail and evaluates the empirical sufficiency of each issue as it might relate to our ability to apply the AFD to a specific case. The general theme of this section is that there are considerable difficulties associated with all four empirical components of the AFD, and that these difficulties place considerable constraints on applying this argument in practice.

A. Structure And Mechanical Function Are Not Tightly Matched

The notion that structure and function are closely linked has a long history in biology dating from at least the time of Aristotle (Russell, 1916). Indeed, some of the leading figures in the history of biology, such as Cuvier, have been strong believers in the matching of structure to function, and this view is held by many to this day [(Arber, 1950; Dullemeijer, 1974; Rudwick, 1964); also see papers in Thomason (1995)]. Certainly the ability to predict the mechanical function of a structure from an analysis of the structure alone has a strong appeal, if only because we could then avoid having to measure the physiological function of structures directly.

Unfortunately, as functional morphologists have begun experimental investigation of the relationship between structure and function, a large number of complexities have been discovered that render the structure-function relationship more obscure than previously supposed (Gans, 1983; Lauder, 1995).

Much of the discussion of structure-function relationships tends to be highly qualitative and assumptive in character, drawing on expected patterns of function or on hypothetical relationships that appear likely to be true based on knowledge from human engineers. In order to evaluate the precision of the relationship between structure and function it is vital to conduct experimental analyses and directly test predicted relationships.

I have previously argued that the predictability of mechanical function from structure may be scale dependent (Lauder, 1995). At a histological level of analysis, the relationship between cellular structure and function appears to be reasonably predictable. For example, myofibrillar cross-sectional area can be used with a high degree of accuracy to predict maximal muscle contractile tension; changes in membrane surface area have predictable effects on diffusion rates. At the general level of behavior and ecology, numerous examples exist of well-founded general inferences of traits such as habitat (arboreal or aquatic) or diet (hard or soft prey) based on organismal structure. Although we may in fact be ignorant of many ecological complexities when we make such broad comparisons, good success has been obtained in inferring general dietary characteristics. It is at an intermediate level, of which musculoskeletal function acting to generate behavior is one good example, where the relationship between structure and function becomes much more obscure. Yet it is at this level where anatomical structures may be studied with relative ease in both living and fossil taxa and predictability is most often desired. It is also at this gross anatomical level where the argument from design, from Paley (1836) to Williams (1992), has often been made.

Here I briefly present two case studies from the experimental functional morphology of vertebrates that exemplify the complex character of structure-function relationships.

1. Intraspecific Differentiation in Structure and Function

Many vertebrates that eat hard prey possess molariform teeth which act as crushing surfaces for the application of forces from the (usually) hypertrophied jaw muscles. Sunfishes (Centrarchidae) provide a nice example of durophagy (consumption of hard prey) as several species are known to eat snails and to possess both molariform teeth and hypertrophied pharyngeal muscles. In addition, we know from experimental studies of muscle function in which direct electromyographic recordings were made of the relevant jaw muscles, as both hard and soft prey were being eaten, just when the muscles are activated by the nervous system during the crushing behavior (Lauder, 1983a, b). In addition to measuring the structures associated with durophagy, we also quantified the pattern of muscle activity used by fishes in different populations to discover if there was differentiation in the mechanical function of the muscles that perform the crushing behavior. One might expect to find a good correlation between the presence of hard prey in the diet (in this case, snails), hypertrophy of jaw muscles, and changes in function of the hypertrophied muscles across populations that vary in the proportion of hard prey in the diet. Is there, at this interpopulational level, a positive relationship between structure and function?

There is indeed a clear relationship between the morphology of the teeth and muscles and the ecological character of the presence of snails in the diet in

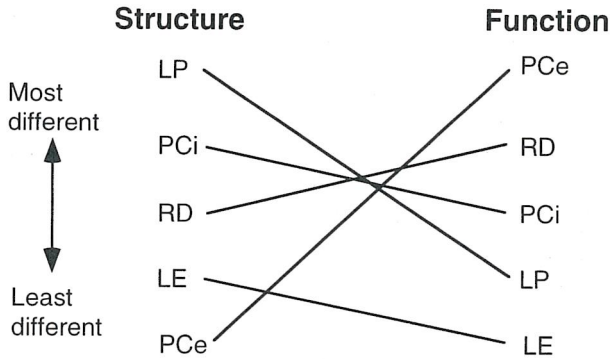


Figure 2 Comparison of structure and function in the pharyngeal jaw bones and muscles of the pumpkinseed sunfish (*Lepomis gibbosus*). The left column lists several different muscles that control the crushing behavior of the pharyngeal jaws. Two populations were compared that differ in the extent to which snails are an important part of the diet, and the muscles are ranked within each column by the magnitude of the difference among populations. Thus, the LP muscle differed most in structure between the snail-eating and the nonsnail-eating populations, while the PCe differed least between these two populations. A similar ranking was performed for muscle function. Note that little correlation exists between structural and functional differentiation in the muscles of these two populations. Muscle abbreviations: LE, levator externus; LP, levator posterior; PCe, pharyngocleithralis externus; PCi, pharyngocleithralis internus; RD, retractor dorsalis.

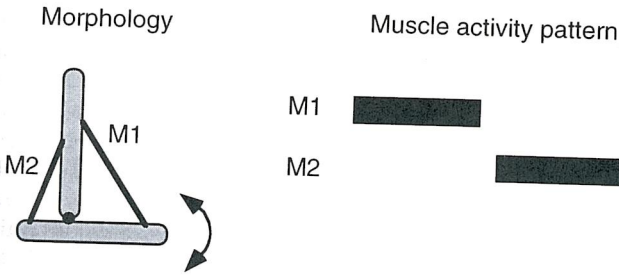
different populations of these fishes (Wainwright *et al.*, 1991a, b). We found that the two populations studied were significantly different in their muscle activity patterns (Wainwright *et al.*, 1991a). However, the surprise was that the pattern of differentiation in structure and function among muscles was not consistent between populations: muscles that were most different in structure were least differentiated in function. This result may be visualized (Fig. 2) by ranking the level of differentiation between populations in muscle structure in one column (from most different at the top to least at the bottom) and comparing it to the level of differentiation in mechanical function ranked similarly in a second column [see Wainwright *et al.* (1991a) for details]. Connecting homologous muscles across columns shows clearly the discordance between structure and function. This result was surprising because it suggests that even in an intraspecific study there is little predictability of function from structure at the level of gross anatomical muscle and bone function.

2. Musculoskeletal Design and the Causes of Behavior

Behavior results from patterned output from the central nervous system to musculature. This output, in conjunction with physiological properties of the musculature and the mechanics of the arrangement of muscles and bones, determines the observed pattern of movement that we call behavior. The analysis of musculoskeletal function provides one way of addressing the causal

A

Primitive behavior: flexion then extension



B

Derived behavior: extension then flexion

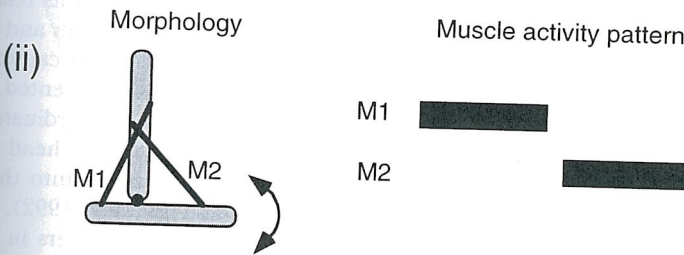
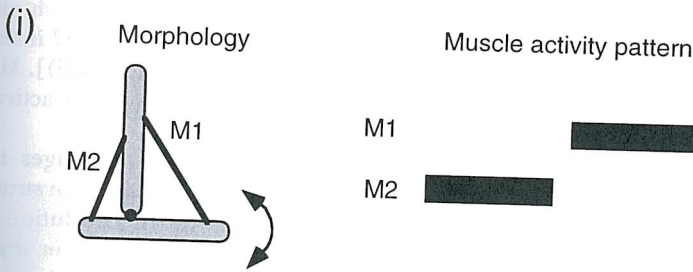


Figure 3 The relationship among structure, function, and behavior. Within a hypothetical clade, both primitive (A) and derived (B) behaviors are observed. The behavior primitive for this clade is “flexion then extension” which is achieved by the activation of muscles (M1 and M2). Muscle M1 is activated first (indicated by the black bar) to effect the flexion movement of the arm, and then muscle M2 becomes active to extend the arm. The upper arrow indicates flexion movement and the lower arrow indicates extension. The derived behavior shown in B is “extension then flexion” which may be achieved by novelty in either (i) the function (timing) of muscle activity or (ii) the topology of muscles. In B(ii), activation of muscle M1 now causes extension while activation of muscle M2 results in flexion. Modified from Lauder and Reilly (1996).

(mechanistic) bases of evolutionary changes in behavior and of illustrating the complexity of the relationship among structure, function, and behavior.

If two species differ in some aspect of their behavior, then these differences might have resulted from changes in either musculoskeletal structure (topology) or in neural output to the muscles that produce the behavior. Figure 3 illustrates this concept using a simplified vertebrate forelimb (humerus and forelimb bones and associated muscles). Given a monophyletic clade, we might investigate the pattern of movement (behavior) in each of the species and determine that the primitive condition in the clade is the behavior "flexion then extension": that is, the forearm flexes by moving dorsally (up) and then extends by moving ventrally (down). Thus, the forelimb in most species in this clade moves dorsally around its articulation with the humerus in a flexion motion, followed by ventral rotation in an extension movement (Fig. 3A). This behavior is caused by the activation of two muscles (M1 and M2) in sequence. Now imagine that within this clade we discover a new species that exhibits the novel behavior of "extension then flexion." This novel behavior could be produced by either of two possible mechanisms. Changes in muscle *function* (the timing of activation) certainly could generate the new behavior by altering the sequence in which each muscle is activated and hence generate the novel behavior [Fig. 3B(i)]. But changes in musculoskeletal *structure* could also produce the same new behavior. The primitive pattern of muscle activity in conjunction with a new arrangement of muscles (in which muscle M1 now attaches to the posterior of the forearm, while the muscle M2 insertion has moved anteriorly) also could generate the new behavior [Fig. 3B(ii)]. Muscle M1 now acts to move the forearm ventrally in a flexion motion and is activated first, while muscle M2 elevates the forearm and is activated next.

This theoretical example illustrates the point that changes in either musculoskeletal structure or function may occur and that changes in structure and function may be dissociated from each other during the evolution of novel behaviors. *There is no obligatory historical coupling between novelty in structure and function; there is no reason why structure and function at any one level must evolve in concert.*

Here I provide a case study of musculoskeletal function and its relationship to behavior by summarizing the results of a study of the jaw muscles and bones of salamanders and their physiological function during aquatic prey capture. Some background is needed before the major conclusions can be presented. Aquatic feeding occurs in several salamander families and involves the coordinated action of many cranial muscles to cause a rapid expansion of the head and the subsequent creation of a current of water (carrying the prey) into the mouth (Lauder, 1985; Lauder and Shaffer, 1985; Reilly and Lauder, 1992). There is considerable diversity in the structure of the head of salamanders in different clades that exhibit aquatic feeding, and the goal of this analysis was to study four taxa to determine if interspecific patterns of variation in mechanical function and feeding behavior matched structural differentiation [details are provided in (Lauder, 1995) and (Reilly and Lauder, 1992)]. We quantified the structure of the musculoskeletal system of the head, the function of the head muscles (by recording muscle activity electromyographically), and behavior (by obtaining high-speed video recordings of prey capture); each class of traits was quantified by measurement of a number of variables. We were thus able to make a multivariate assessment of behavior, function, and structure and to assess the extent to which

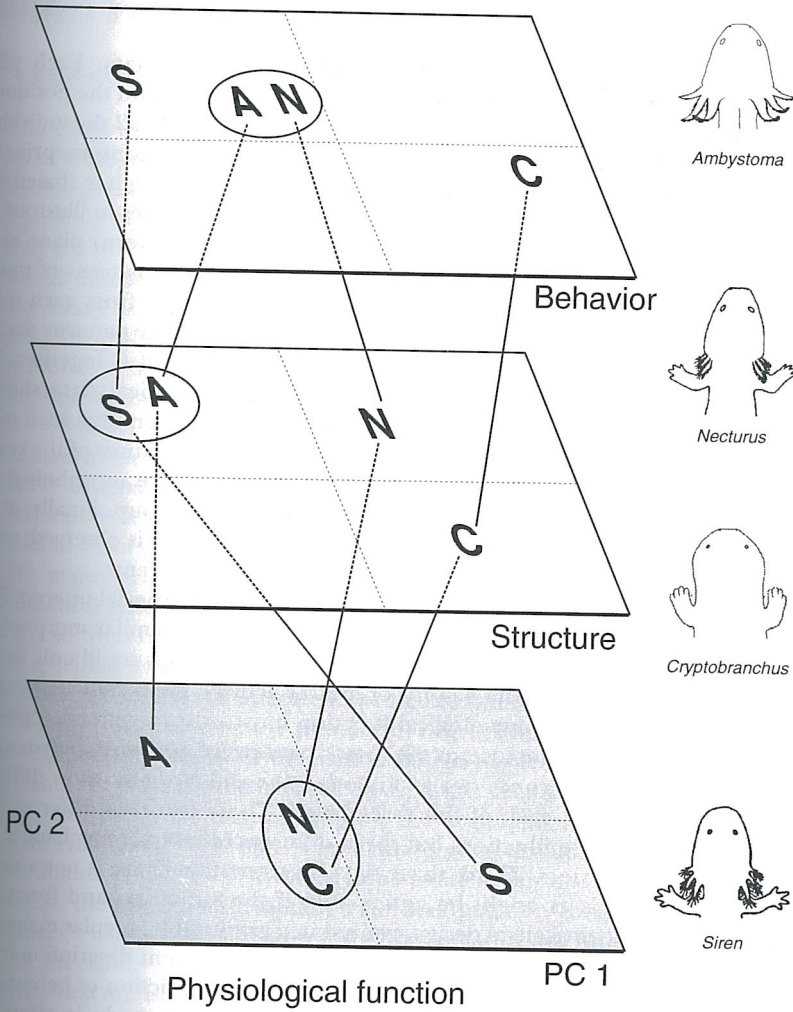


Figure 4 The results of three principal components analyses of physiological, structural, and behavioral data on four taxa of salamanders: A, *Ambystoma*, C, *Cryptobranchus*, N, *Necturus*, and S, *Siren*. The principal component plots of PC 2 versus PC 1 summarize the pattern of variation for each data set. Dorsal views of the head of each taxon are shown on the right. The symbol plotted on each plane for each taxon represents the mean for all the individuals studied in that taxon. Lines connect taxa on adjacent planes to show the mapping across levels of analysis. Note that there is no clear relationship among the positions of taxa in a single plane to their positions on other planes, making the prediction of function and behavior from structure alone difficult. Modified from Lauder and Reilly (1996).

structure and function coevolve in these salamander taxa. To enable visualization of the relationships among characters and taxa, the relationships among characters at any one level (function, structure, or behavior) have been reduced to two dimensions by conducting a principal components analysis on each class of data separately.

Figure 4 illustrates the pattern obtained from these data. Each plane represents the results of the analysis of one class of characters, and the position of the four taxa in each plane is determined by the mean value for all the individuals studied for that taxon. Taxa that are circled occupy positions in principal component space that are not significantly different from each other (based on a MANOVA of PC scores), and lines connect taxa in adjacent planes to illustrate the mapping across levels. Thus, in the muscle activity (motor pattern) plane at the bottom of Fig. 4, *Necturus* (N) and *Cryptobranchus* (C) possess patterns of muscle activity during prey capture that are not significantly different from each other. *Siren* (S) and *Ambystoma* (A) both possess novel muscle activity patterns that are significantly different from each other as well as from N and C together. The principal component analysis summarizing the morphological data shows a different pattern of interspecific differentiation in structure from that seen in the function plane. Here, *Siren* and *Ambystoma* possess similar structures of the cranial musculoskeletal system, while *Necturus* and *Cryptobranchus* are morphologically different from both each other and the *Siren*-*Ambystoma* group. Finally, at the behavioral level, a third pattern of interspecific differentiation is observed, where *Ambystoma* and *Necturus* show similar patterns of feeding movements.

The data summarized in Fig. 4 illustrate three results of special interest. First, *Ambystoma* and *Siren* possess different feeding behaviors but similar morphology. Due to the mechanistic nature of musculoskeletal function, this could only be true if these two taxa differed in the pattern of muscle activity: given similar structure, differences at the level of physiological function must exist to generate different behaviors. This is indeed the case, as the motor patterns of *Siren* and *Ambystoma* are significantly different. Second, two taxa, *Ambystoma* and *Necturus*, show different patterns of grouping in each of the three levels. These two taxa differ in both morphology and muscle function, but these differences interact mechanically to produce similar behaviors. Third, these data illustrate that there is not a simple mapping across levels as might be anticipated if the structural and functional components of musculoskeletal design evolved in a predictable, regular manner. It is clear that an analysis of any one level alone is an insufficient description of the design of the feeding system in salamanders, and that prediction of behavior or physiological function from structure alone in this case study is effectively impossible.

3. Conclusion

Numerous other examples could have been chosen to illustrate the point that structure and function exhibit a complex relationship that makes prediction of function from structure a very hazardous proposition (e.g., Gans, 1983, 1988; Lauder, 1991a, 1994, 1995; Vermeij and Zipser, 1986). Without an assessment of mechanical function independent of structure, we cannot hope to avoid circularity in our efforts to understand organismal design. And yet, what structures actually do, how they are used, and how they perform is an integral component of

arguments about the history of organismal design and about the mechanistic causes of design.

B. Relevant *a Priori* Design Criteria are Rarely Identified

1. Engineering Models and Mechanical Function

The claim that relevant design criteria can be specified *a priori* to allow the analysis of biological design amounts to a claim that we can specify in advance the problem or problems that the design is supposed to solve. Although it is almost always possible to specify *some* design criterion, the more complex the design, the less likely is it that we will be able to determine what the relevant performance and mechanical functions are that any given structure needs to solve. And furthermore the less likely is it that we will be able to meaningfully weigh alternative performance goals. Models of optimal foraging, sex ratio proportions, and life history evolution have used a few carefully chosen design criteria such as minimal foraging time as the performance goal to evaluate ecological design (Beatty, 1980; Orzack and Sober, 1994a, b; Parker and Maynard Smith, 1990), and analyses of plant biomechanics have been successful in using engineering criteria to evaluate alternative designs (Niklas, 1986, 1992). While even some of these efforts have been criticized (e.g., Rose *et al.*, 1987), such endeavors have been still less successful in other arenas (Lauder, 1995).

The major problem facing an anatomist in specifying design criteria is that the anatomical system of interest is often so complex and the “degrees of design freedom” so high that a virtually infinite number of possible performance goals may be specified to explain the very large number of anatomical traits. In cases where biological structures operate in primarily two dimensions and the number of elements is low (reducing the number of degrees of freedom), it will be easier to use engineering theory to determine design criteria and hence to evaluate performance. In practice, the necessary design specifications are most often simply assumed, and based on this assumption the argument from design is used to suggest an evolutionary function. A particularly good example of this is the human hand. Williams (1992, p. 40), for example, with reference to human anatomy, asserts that “the hand is an adaptation for manipulation” because it conforms to an engineer’s *a priori* specification for a manipulative machine (Table 1). Let us examine this claim.

First, what are the structural components of human hand design that call for explanation? The human hand possesses 26 separate bones (Fig. 5; for our purposes I define hand structure as those elements distal to the radius and ulna, although there are of course structures such as nerves, blood vessels, and tendons that pass from the forearm into the hand). Some of these bones articulate with each other to form five separate fingers, elongate combinations of phalangeal skeletal elements that articulate with each other in ball and socket joints and which are capable of some independent movement. Five other bones, the metacarpals, articulate both with the phalanges and a collection of seven carpal bones grouped together at the base of the wrist (Fig. 5). Numerous ligaments restrict motion of the hand bones. For example, the transverse metacarpal

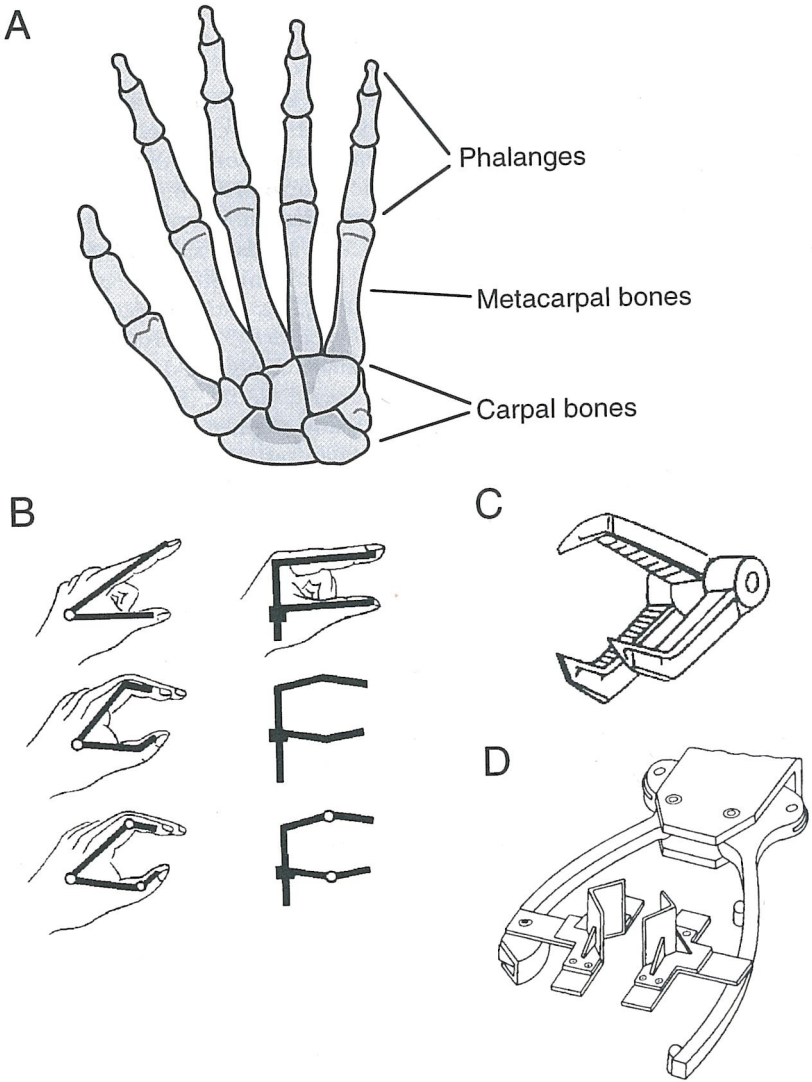


Figure 5 (A): The major osteological components of hand design. This diagram shows the human left hand in ventral view. (B): Diagram of a human hand on the left and a mechanical schematization on the right to show one possible mechanical abstraction of the human hand. (C): Design of a mechanical hand with three fingers. (D): Design of a mechanical hand with two fingers which move to grip cylindrical items in the center. Panels B, C, and D are modified from Kato (1982). Reproduced by permission. All rights reserved.

ligaments tie the distal tips of the metacarpals to each other, while the collateral capsular ligaments of the phalanges restrict motion at the knuckle joints to primarily one plane.

The hand also contains about 18 intrinsic muscles, limited to the hand itself, which interconnect skeletal elements. The various interosseus muscles, for example, act to abduct, adduct, flex, and extend the fingers. The lumbrical muscles of the hand take their origin from tendons of the flexor digitorum profundus (whose belly lies in the forearm) and these muscles both flex and extend the fingers at separate joints. Additional muscles abduct and adduct the thumb and little finger. Finally, the hand contains an extensive network of sinovial sheaths and bursae (fluid-filled sacs) through which tendons run.

Second, exactly which components of hand structure described above are designed specifically for manipulation? Has the hand in its entirety resulted from selection for manipulative function, or, have only some components of this design been selected for manipulation? If only some components were so designed, which ones? Is it perhaps only the muscles, bones, and sinovial sheaths of the thumb that have been designed by selection for manipulation, or is it the combination of the palmar interosseus muscles, the dorsal intercarpal ligament, and the triquetral carpal bone that we should focus on? We cannot gloss over the problem of identifying those elements that were subjected to selection for manipulative function because we must have a biological design to compare to our engineering model: the closer the fit, the more likely our argument from design is correct.

Third, which engineering model are we to choose to represent the function of manipulation? We might choose to develop a specific mechanical model based on a series of rigid elements, articulating with each other, controlled by a series of cables to permit motion of the various "joints," and capable of movement in opposition (such as our thumb and fingers) so that individual objects may be picked up. Or, we might simply specify general engineering principles: that manipulation can be accomplished by any design with independently movable parts connected in a way that permits objects to be grasped and controlled. But surely we must go farther than this and specify the model precisely enough to generate a predicted design that one would expect *a priori* to exist when manipulation of objects is a problem to be solved.

Fourth, we must ask if there are other ways of designing a manipulative structure. What is striking about the mechanical engineering literature on manipulative function is the extent to which the engineering solutions themselves have been dictated by existing *human* anatomy and used multiple jointed elements as key features of the design for manipulation (Fig. 5: B, C, D). Everything from remote manipulation arms in deep-sea research submarines to artificial forelimbs appear derived from a human model (Kato, 1982), and it is thus circular to argue that mechanical hands provide evidence of "good" biological design. It could be argued that this similarity is in fact evidence for the engineering design of the human hand itself, as there may only be one "good" design. But if alternative designs for manipulation exist, then this argument fails.

Octopus arms are an excellent manipulation device that embody well-understood engineering design concepts using the principle of a muscular hydrostat and layers of circular and longitudinal muscle (Kier and Smith, 1985). There is little about this manipulative design that can be claimed *a priori* as being

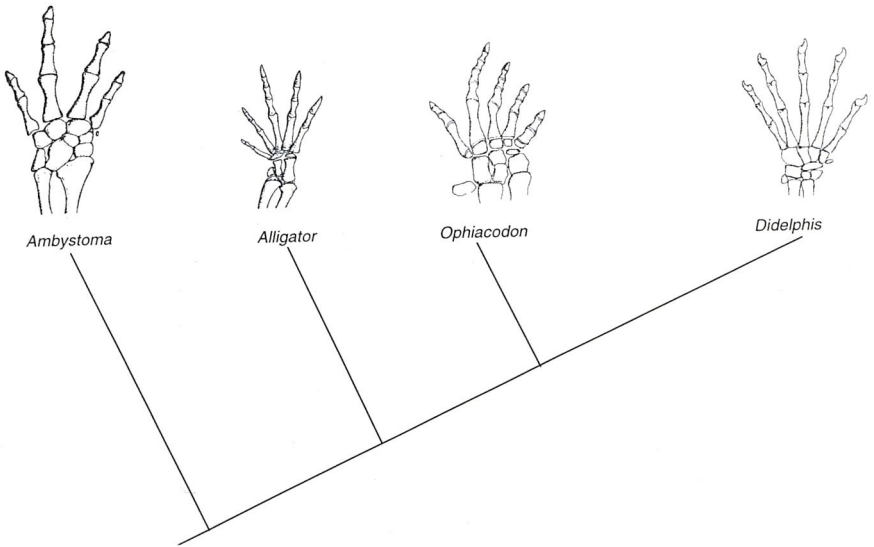


Figure 6 Phylogenetic relationships of several selected hand designs to show that many design elements of the human hand are in fact ancient features of the vertebrate forelimb. Such ancient features (such as multiple jointed digits that are capable of largely independent motion) cannot be used to argue for adaptive design of those features in the human hand. Note that even taxa as phylogenetically disparate as the salamander *Ambystoma*, the pelecosaur *Ophiacodon*, and the opossum *Didelphis* show many similarities in hand design. The diagrams show the left hand in dorsal view [diagrams modified from THE VERTEBRATE BODY, Fifth Edition by Thomas S. Parsons and Alfred S. Romer, copyright © 1977 by Saunders College Publishers, reproduced by permission of the publisher].

irrelevant to the development of a general engineering model for manipulation: octopus arms contain no specialized anatomical elements that could not in theory develop in any multicellular organism. In addition, octopus arms do not contain jointed bony elements and yet are capable of fine manipulative function, especially when several arms are used in concert. If we choose the octopus arm model, then it will indeed be difficult to argue that the human hand is the only possible engineering design for manipulation. If there are alternative designs for manipulative function, then which of the available models will we choose? And how will we ensure that we have not biased our choice of model by the knowledge we already have about the biological design that we are trying to explain?

Fifth, on what basis has it been decided that manipulation is the problem to be solved? Perhaps various components of the human hand have resulted from selection for grasping function (perhaps the grasping of branches during arboreal locomotion). Some of the anatomical features that characterize the design of the human hand today may have been incorporated into hand design to “solve” problems that were experienced by ancestral populations. For example, many of the ligaments that bind hand bones together might be designed to solve problems relating to ancestral locomotor styles. Finally, perhaps certain aspects of current hand structure evolved as a result of selection for more precise communication using hand signals. Generating *a priori* engineering designs that distinguish

between grasping and manipulation will be a challenge, as will ruling out other possible *a priori* functions that might be proposed for the hand.

Despite the manifold difficulties that occur when attempting to specify in advance the engineering problem to which any anatomical design is a solution, there is at least one method that can be used to rule out particular structural features as possible design elements for current function. A phylogenetic analysis of tetrapod hand structure, for example, can at least provide some guidelines as to which structural components of the human hand are *not* likely to be adaptations to manipulative function. A highly simplified phylogeny with representative schematic illustrations of hand osteology is shown in Fig. 6. From this phylogenetic pattern it is clear that possession of independently mobile jointed elements ("fingers") is not a design component that could be linked to any specific function that is unique to the human hand: fingers are an ancient design feature of the vertebrate forelimb (Coates and Clack, 1990) and occur in many animals that do not have the manipulative abilities of the human hand. Neither can the presence of carpal bones be adduced as a design feature of the human hand that arose by selection for manipulative function as these too are ancient elements. Indeed, the basic structure of the tetrapod forelimb predates fully terrestrial vertebrate life (Eaton, 1960; Edwards, 1989) and cannot even be used to support a claim that forelimb design arose as a result of selection for support against gravity and locomotion on land.

With a phylogenetic analysis of hand design in humans and closely related outgroup taxa, we could at least narrow down the possible set of design features for which explanation is required: traits unique to those taxa which share the purported mechanical function. That is, the relevant anatomical structures should possess a concordant phylogenetic distribution with the proposed function. But this would not alleviate the requirement of (1) demonstrating experimentally that the function was in fact present in the relevant taxa, (2) producing an engineering model that demonstrates that the design features actually do solve the functional problem, and (3) rejecting other plausible models of function.

None of these arguments change the fact that the human hand might actually be *used* for manipulation. But our observation that the human hand is currently used for manipulation in no way supports an *a priori* engineering argument that the hand was *designed* for manipulation (or any other function for that matter) as a result of natural selection for that function. In fact, no engineering argument has been presented at all, alternative functions have not been ruled out, and manipulation as the engineering "problem" that must be "solved" by natural selection is simply assumed.

2. *Spandrels and the Assumption of Design Constraints*

The problems in specifying design criteria for biological structure outlined above are not restricted to cases in which we might like to argue that some design resulted from selection for one specific physiological function. A similar difficulty exists in attempting to claim that a particular trait is an accidental by-product of construction and in fact has not arisen as a result of selection for a specific function.

Perhaps the most famous analysis of a design that is held to have arisen as a by-product of construction, one that spawned numerous rebuttals, much soul

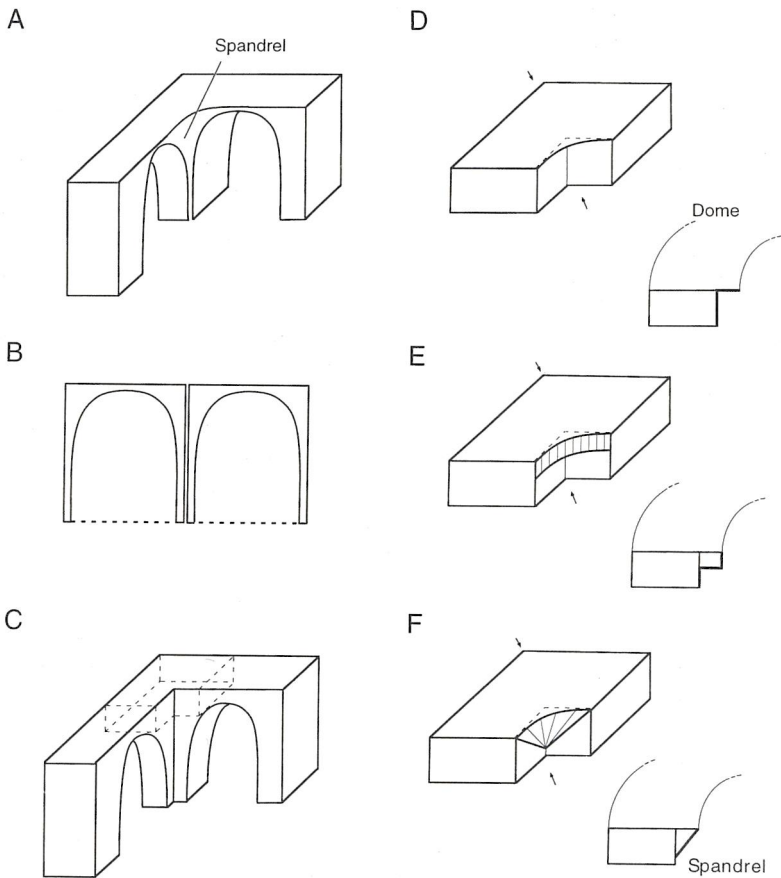


Figure 7 The construction of a spandrel [more properly called a pendentive, Mark (1996)]. In (A) and (C) the domed roof has been omitted for clarity. (A): A spandrel is formed by the space between two perpendicular adjacent arches which is filled in and frequently decorated. These arches arise in walls perpendicular to the floor with a curved dome above forming the roof. (B): Two arches juxtaposed within rectangles in the same plane. (C): Bending the two arches from the previous panel into a right-angle intersection leaves an upper corner space (dotted lines) that does not contain a spandrel. Note that the walls containing the arches meet at a right angle from floor to ceiling. (D), (E), and (F) show three alternative designs for putting a domed roof onto a corner intersection of two walls (whether they contain arches or not). In the cross-sectional views shown in panels D, E, and F thick lines accentuate the surface facing into the room. The portion of the wall illustrated is that outlined by the dashed lines in C; the dome is again not shown for clarity. The inset for each of these panels shows a cross-section through the region supporting the dome (in the plane defined by the two arrows) and one possible configuration of a domed roof. (D): By curving the supporting surface above the corner, a curved dome can be attached above a right-angle junction of two walls. (E): The curved addition onto the corner can be extended toward the floor, increasing the amount of supporting material under the edge of the dome and providing a surface for decoration (vertical lines) that can be seen from the room below. (F): A spandrel may be constructed by adding material in the corner in a cone shape that tapers from the curved interface with the dome above to a point below. This design also allows for decoration. A spandrel is thus not an obligatory element arising necessarily from building two arches at right angles to each other: spandrels are added design elements and do not arise from mechanical necessity.

searching, new analyses (Bock, 1980; Brandon, 1990; Coddington, 1988; Dennett, 1983; Gans, 1988; Garland and Adolph, 1994; Harvey and Purvis, 1991; Lauder *et al.*, 1993; Mayr, 1983; Mitchell and Valone, 1990; Reeve and Sherman, 1993; Ridley, 1983; Wenzel and Carpenter, 1994), and even a book on literary critical analysis of the paper itself (Selzer, 1993), is the engineering case presented by Gould and Lewontin (1979) of the spandrels of the San Marco church in Venice. In brief, Gould and Lewontin use spandrels to argue that the traditional optimization research program in evolutionary biology does not allow for design features that may arise as purely constructional artifacts. These design features may indeed be coopted by organisms (and architects) and subsequently put to some (adaptive) use. But Gould and Lewontin suggest that we need to develop a research program that enables us to recognize that the primary origin of some components of design may have nothing to do with selection for a specific function.

The architectural example used by Gould and Lewontin (1979) to illustrate their point is the spandrel. When two arches are brought together with their bases at right angles, a triangular area is formed between the top of each arch and a domed roof (Fig. 7A). Note that the arches arise perpendicular to the floor, and that the dome sits on top of these vertical walls which contain arches. This triangular space, which is decorated to great effect in the church of San Marco, is the spandrel (or pendentive; Mark, 1996). In addition, note that the surface area of the spandrel is not parallel to either of the walls containing the arches and is at roughly a 45 degree angle to the plane of each arch. The surface of the spandrel faces out into the room, and the spandrel actually occupies a triangular volume extending from the wall behind on each side out to the decorated surface. Gould and Lewontin argue that spandrels arise from architectural or constructional constraints. Spandrels must be formed when two arches are brought together, and it would be incorrect to view them as primary (adaptive) design features of the church: they are a "secondary epiphenomenon" (Gould and Lewontin, 1979, p. 584) that should not receive an adaptive explanation. Any attempt to argue adaptation from spandrels would be erroneous. It is important to realize that Gould and Lewontin's analysis of spandrels is primarily an engineering one: they suggest that there is simply no other way to design a dome mounted on two arches without forming a spandrel. The term spandrel has even passed into the biological literature to mean a trait that arose nonadaptively as a by-product of constructional necessity [see Pinker and Bloom (1990) and the discussion articles that follow].

But the argument that spandrels are secondary by-products of constructional principles is similar to the argument discussed above that the function of the human hand is manipulation. Both rely not on actual engineering models or comparative mechanical analyses which the reader can evaluate, but on the *assumption* of a mechanical function (or the lack thereof). Let us examine the claim that spandrels arise from constructional necessity.

Even a simple design analysis reveals that spandrels are not an obligatory architectural construct associated with two arches [as first pointed out by Dennett (1995) who discusses other architectural implications of the Gould and Lewontin paper]. Figure 7B shows (in two dimensions) two arches aligned in the same plane but with some construction material such as concrete filling in the spaces between

each arch and the edge of a rectangle enclosing the arch. Pushing the two arches together so that one edge of each rectangular area meets results in an expanse of concrete between the two arches [a proper spandrel as defined by Mark (1996)]. If we now bend the two arches so that they form a right angle to each other and view the result in three dimensions (Fig. 7C), we can see that the two walls containing arches can meet at a right angle with no necessary triangular space being formed. The narrower the arches, the greater the cross-sectional area of the column supporting the roof and thus the less stress (force per unit area) on that column. Widening each arch to reduce the surface area of concrete between the arches (and hence the cross-sectional area of the column) does not produce a necessary triangular space, but rather a smaller corner.

Now consider the ways in which a domed roof might be added above the walls by focusing on the region of the corner marked in dotted outline in Fig. 7C. We might simply add a dome-shaped roof by curving the region where the dome meets the walls, leaving a small ledge in the corner (Fig. 7D). This would create a dark area of shadow (if light emanated from lights or skylights in the dome) under the curved region above the corner. Alternatively, we could design the dome to curve around the corner with a supporting shelf (Fig. 7E). This too leaves a ledge in the corner, but now at least there is a curved surface facing out that could be used for decoration. There is still an area under the ledge that might be dark and unsuitable for decoration. Finally, we could fashion a decorative spandrel-shaped region in the corner (by adding material below the dome) with the base of the dome forming the curved top of the spandrel (Fig. 7F). To orient the surface of the spandrel so that the decorated surface might be seen from below, we might taper the lateral edges of the spandrel so that they meet at the junction of the two walls (Fig. 7F).

Each of these designs will have engineering strengths and weaknesses, but they do represent valid alternative designs to the “problem” of designing the space formed by a roof and two walls. It is hardly true that a spandrel *must* be an incidental artifact of construction (Dennett, 1995). Indeed, as Fig. 7F shows, construction of a spandrel requires deliberately *adding* material to the corner to build up a surface that faces down and into the room. In fact, Mark (1996) argues that this additional material behind the curving face of the pendentive is functionally significant in supporting the dome itself. Hence, a spandrel could be a structure designed to allow decoration of what would otherwise be a dark corner, and might be a functional necessity for dome support. The spandrel would in this case be an “adaptation”. Dennett (1995, p. 273) even suggests that the spandrel might represent the minimal surface area that could be stretched across the corner space, and hence represent an optimal solution (using minimal added material) to a decorative problem.

I have discussed both the spandrel and hand examples at some length to illustrate a general feature of the design literature from two perspectives: *a priori* design specifications are usually assumed and rarely defined and analyzed. This is not surprising, as deriving an appropriate engineering model, even if one can divine the functional problems to be solved, is no easy task given the complexity of biological design. Even in the relatively simple case of the spandrels, where there are few structural elements, we have not exhausted the range of possible configurations, nor have we conducted any mechanical analyses of force transmission from the dome to the supporting columns. It may well be that the

configurations illustrated in Fig. 7 (panels D, E, and F) have differing performance under load and that the performance ranking of the designs might change as we change testing parameters (such as altering the configuration or weight of the roof).

In practice, using the criterion of *a priori* design specification is likely to be applicable under only certain restricted circumstances. Even Williams (1992, p. 41), who strongly advocates the construction of *a priori* designs as a key method for analyzing adaptation, admits that "...those who wish to ascertain whether some attribute of an organism does or does not conform to design specifications are left largely to their own intuitions..." This is hardly a desirable situation for a key methodological underpinning of the argument from design.

C. Inferring the Retrospective Action of Selection from the Phenotype Alone is Difficult

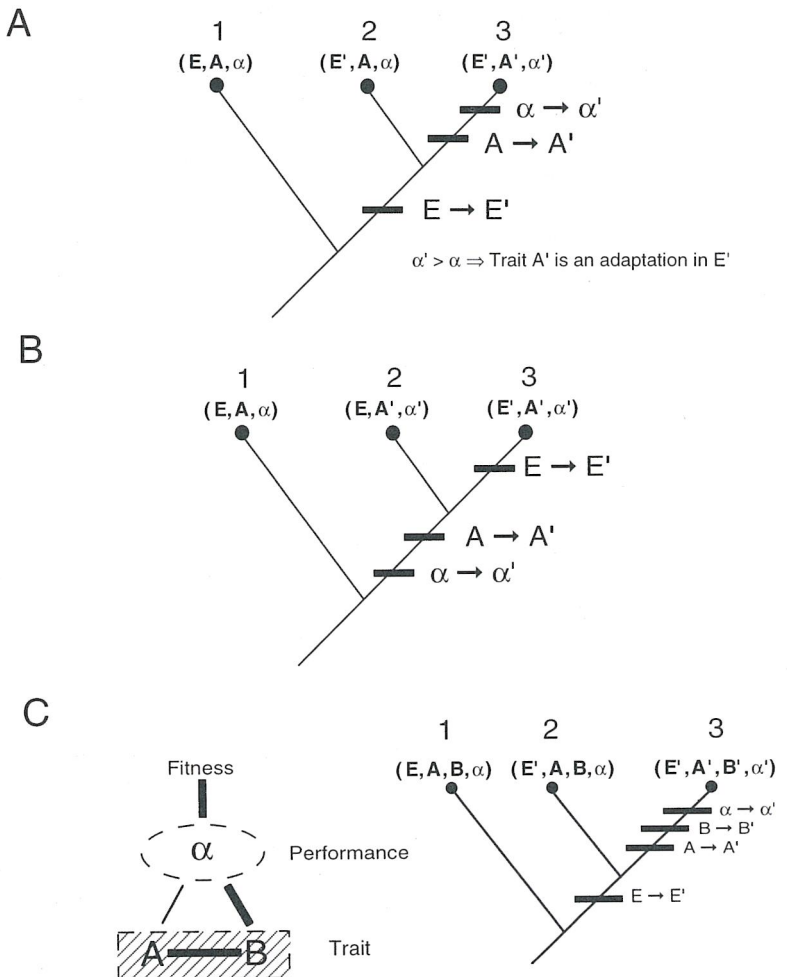
Successful application of the argument from design requires us to be able to make accurate inferences about the process of selection from an analysis of the phenotype. After all, a component of design is an adaptation only if it enhances fitness and arose historically as a result of natural selection on that trait for its current function. Hence, if we are to recognize design by selection we must be able to determine if the process of selection acted on the trait of interest.

Under the best of circumstances, evolutionary biologists can indeed make strong inferences about the action of selection. The best of circumstances include the availability of longitudinal data on extant populations (Arnold, 1983, 1986; Endler, 1986), study of selection in laboratory evolution coupled with genetic analysis of intertrait correlations (Lande, 1978, 1979; Rose, 1984a, b), and the execution of replicated field evolution experiments (Reznick, 1989; Reznick and Bryga, 1987). These conditions do not often hold when the argument from design is made. In fact, the AFD is often applied retrospectively and to taxa in which genetic data and manipulative laboratory and field experiments cannot be done. Imagine, for example, that we have discovered a new species of fish in a geological formation of Mesozoic age and wish to ascertain if a particular structure (such as a conspicuously enlarged caudal fin) is an adaptation or not. How are we ever to know if selection acted directly on the caudal fin? Specifically, there are four major reasons why such retrospective analyses of selection pressures present difficulties for the inference of selection.

First, if the trait of interest is novel, with few available analogs in extant taxa, then we will have considerable difficulty in designing mechanical/engineering models to guide us in estimating the mechanical or evolutionary function of that trait. In cases where structural analogies can be made with extant taxa, then alternative hypotheses of mechanical function can at least be developed by using engineering approaches. But even such analyses are fraught with difficulty because of the large number of assumptions that must be made about the nature of the functional "problem" to be solved. Many structures may have been designed for such problems as signaling during courtship which do not permit easy mechanical modeling. Also, argument by analogy to extant taxa has conceptual problems: we are forced to rely on structures that are analogous to infer analogous functions, which assumes that structure and function are closely linked. I have argued above

that this is a hazardous proposition [also see Lauder (1995)]. We cannot reason from the stronger base of homology of structure.

Second, many structures have more than one mechanical function and may have been subjected to multiple selection pressures in the past. If we can demonstrate using an engineering model that a given structure might have had several mechanical functions, then how are we to choose which function (or functions) should be the one(s) to which we ascribe evolutionary significance by labeling the structure an adaptation? For example, let us say that we wish to investigate the potential significance of the enlarged caudal fin of our fossil fish and propose two likely mechanical explanations: large fin area might increase maneuverability during slow speed swimming (by allowing longer wavelength undulations of the fin rays) or it might enhance escape performance by increasing surface area and hence thrust. If a design analysis shows that both are possible mechanical functions, how can we choose which problem or problems the structure was designed by selection to solve and which was the incidental function?



Third, selection may not have been responsible for the structures of interest in the first place, and if so we cannot assume that these structures are adaptations. Lande (1976, p. 333), for example, examined the extent of phenotypic change in tooth traits of Tertiary mammals and concluded that, "Using statistical tests, it is found that the observed evolution of these mammalian tooth characters could have occurred by random genetic drift in rather large populations, with effective sizes in the tens or hundreds of thousands." If a statistical model of drift cannot be ruled out as an explanation of a trait, then claiming that the trait is an adaptation will require a substantial body of ancillary evidence to justify adducing selection as the causal agent of design.

Fourth, even if we can with some confidence estimate a set of possible mechanical functions of a trait, how are we to know that selection acted on *that* trait and not on some other character with which the trait of interest is correlated. Thus, the enlarged caudal fin might have been purely a correlated response to selection for increased body size, selection for increased pectoral fin size, selection for reduced vertebral number, or a response to selection on any one of a myriad of other characters correlated either positively or negatively with caudal fin area. If so, the large caudal fin cannot be called an adaptation for either locomotor escape performance or for maneuverability, *even if* a biomechanical analysis shows the large caudal fin to have performance benefits. The issue of correlated characters is not merely of academic interest. There is increasing evidence that even traits with major fitness effects can evolve as a correlated response to selection on other characters (Price and Langen, 1992).

One possible means of avoiding some of these difficulties is to use comparative phylogenetic analysis to evaluate the adaptive significance of characters, and in recent years a great many comparative methods have been

Figure 8 The comparative historical approach to studying adaptation and one difficulty with that approach. This clade contains three taxa, 1, 2, and 3, and character states for each taxon are listed beneath in parentheses. (A): The comparative method for uncovering adaptation suggests that by studying the phylogenetic distributions of traits (A and A'), environments or selective regimes (E and E'), and the performance of traits (α and α') one can determine if a trait is an adaptation. If a derived trait (A') is phylogenetically correlated with derived performance (α') and both occur within derived selective regime (E'), then A' is held to be an adaptation that resulted from natural selection for improved performance within the new environment. (B): Phylogenetic methods may also be used to reject hypotheses of adaptation. A study of taxon 3 may suggest that trait A' is an adaptation that resulted from selection for increased performance (α') in environment E'. But a broader comparative perspective would show that trait A' arose prior to the derived selective regime (E') and hence could not be an adaptation in E'. (C): Character correlations pose problems for comparative methods. The diagram on the left shows that traits A and B are both positively correlated with each other (indicated by the thick line connecting the two traits) and that only trait B has a positive correlation with performance and fitness. Thin lines connect genetically uncorrelated traits such as trait A and performance. Trait A' might be deemed an adaptation in the absence of knowledge about trait B because trait A' occurs phylogenetically in correlation with α' and within the derived selective regime E'. But trait A' only occurs at this position phylogenetically due to its correlation with B and B'. Selection acted on B and not on A; trait A' cannot then be viewed as an adaptation. Panels A and C modified from Lauder *et al.* (1993).

advocated as providing data on the adaptive significance of traits (Arnold, 1994b, 1995; Baum and Larson, 1991; Brooks and McLennan, 1991; Coddington, 1988; Garland and Adolph, 1994; Harvey and Pagel, 1991; Harvey and Purvis, 1991; Losos and Miles, 1994; Miles and Dunham, 1993; Pagel and Harvey, 1989; Wenzel and Carpenter, 1994). These methods all require comparative data for at least three taxa on the environment (or problem to be solved), the trait of interest, and performance of that trait in each taxon. These methods do not then alleviate all of the problems described above, but they promise improved inferential ability in some cases where selection cannot be measured directly.

In brief, phylogenetic methods operate by developing a historical view of the pattern of acquisition of traits, performances, and environments (Fig. 8A); arguments about the adaptive character of traits are then made based on the order of appearance of these characters. For example, if trait A' is to be deemed an adaptation for increased performance in climbing trees (α') as a result of selection for escape from terrestrial predators (E'), then to be consistent with this hypothesis trait A' must have evolved in a clade in which both the increased performance is found and in which the environmental shift to a new selective regime has occurred. Also fundamental to a phylogenetic approach to adaptation is the notion that comparisons must be made between the derived states A', α' , and E' and the primitive states of these characters (A, α , and E; Fig. 8A). As described by Baum and Larson (1991, p. 6), "To constitute an adaptation, a trait must have enhanced utility relative to its antecedent state, and the evolutionary transition must be found to have occurred within the selective regime of the focal taxon...." In the example presented in Fig. 8A, the transition from trait A to trait A' is correlated with a performance increase from α to α' , and this transition occurred within the derived selective regime of E' which characterizes taxon 3 (because the transition from E to E' characterizes a larger clade of taxa 2 and 3).

A schema such as that in Fig. 8A can also be used to explain a variety of other terms that have been applied to characters, performance, and environments [see discussions in Arnold (1994a, 1995), Brooks and McLennan (1991), Coddington (1988), Funk and Brooks (1990), Gould and Vrba (1982), Greene (1986), Harvey and Pagel (1991)]. For example, Baum and Larson (1991) term a trait in which performance decreases in the face of a new selective regime ($\alpha' < \alpha$) a "disaptation," while no change in performance ($\alpha' = \alpha$) results in a trait being a "nonaptation." An "exaptation" is a trait which retains its performance advantage despite a change in environment after its origin.

One area in which the phylogenetic approach can be of use is to reject hypotheses of character adaptation by evaluating the expected phylogenetic pattern that must minimally hold if the proposed pattern of selection actually produced the postulated performance advantage (Basolo, 1990; Björklund, 1991; Brooks and McLennan, 1991, 1993; Meyer *et al.*, 1994). Figure 8B shows a situation in which we might wish to reject the hypothesis that trait A' resulted from selection in environment E' for performance advantage α' (making trait A' an adaptation). This hypothesis initially might have resulted from a population-level study of taxon 3 where all three derived traits are present. A broader comparative phylogenetic analysis reveals, however, that trait A' arose prior to the change in environment in correlation with the performance increase (α to α'). This phylogenetic pattern suggests that trait A' might actually have resulted from other patterns of selection in the lineage leading to taxa 2 and 3, but cannot be an adaptation to E'.

Enthusiasm for the phylogenetic approach to adaptation has been considerable but not universal, and several authors have pointed out hidden assumptions and difficulties that may limit the ability of phylogenetic analysis to confirm that a character is indeed an adaptation (Frumhoff and Reeve, 1994; Lauder *et al.*, 1993; Leroi *et al.*, 1994; Wenzel and Carpenter, 1994). While endorsing the general value of a phylogenetic approach to the problem of analyzing character evolution, Lauder *et al.* (1993) and Leroi *et al.* (1994) pointed out several theoretical and practical difficulties of such methods.

Correlations among characters, already noted above as a potential liability for inferences of past selection, also may confound phylogenetic analysis (Fig. 8C). If, for example, trait A is positively genetically correlated with trait B, and selection acted on trait B to effect a transformation to B' (which confers performance advantage α'), then trait A' will be interpreted as an adaptation when it was not in fact the target of selection. As long as correlations among characters are not recognized, errors of this sort are likely to be common. In addition, strong *directional* selection may occur to prevent a trait D (which confers performance advantage and which is genetically correlated with another character E) from changing as a result of selection on character E. Character D will appear to be phylogenetically static, but is so only as a result of directional selection on E.

One practical difficulty that often arises with applications of phylogenetic methodology to the study of adaptation is that data are not often available on patterns of selection and performance for all taxa of interest. Morphological or structural components of design are relatively accessible, and these data are most often the source for hypotheses of adaptive design. But obtaining relative performance data for many taxa is a task not often accomplished (but see Arnold, 1995; Losos, 1990; Losos and Miles, 1994), and obtaining data on the selective regime in relation to the specific trait of interest across a range of taxa is almost never performed. To mitigate this situation, relative performance is often simply assumed, and gross environmental differences (such as arboreal or terrestrial) are substituted for quantified patterns of selection. Baum and Larson (1991) present an analysis of salamander hand morphology that uses environmental surrogates of this type (e.g., scansorial, terrestrial) for a demonstrated selective regime. But as our coding of the environmental character (E in Fig. 8) becomes broad, the number of possible traits and performances that might be associated with such an environment becomes huge, and the possible existence of characters correlated with the trait of interest nearly certain. A final problem with analyses of this sort, discussed in more detail by Lauder *et al.* (1993, p. 296), is the conflation of performance and fitness. Performance is often used as a surrogate of fitness as it is rarely possible to measure fitness directly in comparative phylogenetic studies. But performance and fitness are not the same thing, and measurement of performance, especially the relative performance of two taxa that differ in many traits (not just the one of interest), cannot be equated with the fitness of those taxa.

One implication of the difficulties noted above in inferring retrospectively the action of selection is that much of the terminology so useful for *theoretical* explication of possible patterns of evolution is likely to have limited *practical* utility. For example, if we are to demonstrate empirically that a trait is an exaptation following Gould and Vrba (1982), then we must be able to provide evidence for, and not merely assume, (1) current utility of the trait (a performance advantage),

(2) selection for that specific trait in its current environment, (3) previous utility of the trait in an ancestral taxon or lineage with a *different* performance advantage than the current one, and (4) natural selection for that trait (and not for a genetically correlated trait) in the ancestral environment. To successfully identify an exaptation we must be successful in our retrospective inferences of natural selection and of the trait(s) that it acts on. If an exaptation is claimed to have arisen as a by-product of selection on other aspects of organismal design (perhaps as a correlated character), then we must be able to demonstrate this pattern of selection and not simply assume that selection acted in accordance with our wishes.

D. Complex Features Cannot Easily Be Atomized

The final problem with implementing the argument from design arises when we must decide on those traits and characters that are the subject of selection. Innumerable such traits exist, from the whole arm (Fig. 1) to various parts of the hand (Figs. 5 and 6). Is the finger a trait? Is the terminal phalanx a trait? Or, are the opponens digiti minimi muscle and the deep transverse metacarpal ligament together one character? Clearly if we cannot meaningfully atomize design in some way then it will be difficult to characterize those components of the organism that are the target of the hypothesized selection pattern, and difficult to conduct performance tests on alternative designs.

The problem of how we dissect the organism into component parts has been widely recognized (e.g., Beatty, 1980; Cronin, 1991; Lewontin, 1978; Sober, 1990), and it is useful to view the problem of atomism as arising from couplings among characters at two (related) levels: phylogenetic, and genetic/developmental.

Phylogenetically, characters arise and are integrated into organisms so that our *a posteriori* phylogenetic reconstructions show nested sets of characters, some of which we interpret as homologies and others of which may arise multiple times convergently across a clade. But the pattern of character evolution is not random, in the sense that on average characters persist after arising, allowing us to use them as synapomorphies to recognize monophyletic clades. Some traits persist for a remarkably long time, such as the jaw-opening mechanical system in fishes which, after its origin, persists to characterize a clade of over 20,000 species (Lauder and Liem, 1989). The jaw-opening system in a fish species that is a member of the derived clade Percomorpha consists of elements that have arisen at various phylogenetic levels, and each element forms one component of the final hierarchical design. Biological designs are built piecemeal (Lauder, 1990, 1991a) and yet we must typically disassemble them to apply the argument from design in ways that do not mirror the pattern of construction.

I view this phylogenetic coupling among traits as a fundamental (and mostly unrecognized) aspect of the problem of atomizing organic design and one that does not correspond well to our mechanical intuitions based on human design. If we remove the spark plugs from a car engine, we do so without caring if in the process of engine assembly at the factory the spark plugs were the last component installed. Although we recognize that different parts of a car engine must work together in order for the engine to perform mechanical work, we do not expect that the order of assembly *per se* will influence our analysis of why any particular

engine does not function. On the other hand, biological design is the result of a historical process of assembly, in which each component was integrated into an existing design prior to the addition of subsequent design elements (Lauder, 1990). Removal of components of such a design in ignorance of the process of assembly is likely to lead to considerable difficulty: experimental manipulation of different components will involve altering nonequivalent historical couplings with other characters. While experimental manipulation will continue to be a valuable tool for the study of function, an increased awareness of the historical pattern of construction will limit the confounding effects of history on experimental interpretation.

Pleiotropy and epigenetic effects may also result in correlations among characters that make it difficult to atomize a complex design. Pleiotropic effects are well known and give rise to complex patterns of character intercorrelation (Price and Langen, 1992) which greatly complicate any attempt to isolate any one feature of design for analysis. As noted in the previous section, the widespread effects of pleiotropy make it difficult to assert that any trait could be the single target of selection and to dissociate features into meaningful independent units. Some progress has been made in attempting to use quantitative genetic methods as a basis for defining independent evolutionary associations of characters (Shaffer, 1986), but the vast majority of cases in which functional design has been studied lack such information.

Epigenetic effects arise in ontogeny as a functional connection among traits due to the action of developmental processes such as induction or the effects of hormones on disparate tissues (Atchley and Hall, 1991). For example, if the release of thyroid hormone into the bloodstream affects growth in both bone and muscle cells of the hindlimb, then to what extent are we justified in considering the ontogeny of bone and muscle to be independent of each other (or in analyzing just muscle ontogeny as though muscle were an isolated biological tissue)? As summarized by Atchley and Hall (1991, p. 143), "If an epigenetic factor (hormone, maternal effect, etc.) has a significant impact on development of a morphological structure, then a non-zero covariance results between the epigenetic factor and the morphological structure." Note that a significant evolutionary association between two traits may also arise via epigenetic mechanisms even if the associated structures share no genes in common.

Despite the many difficulties involved in discerning the linkages among characters and the natural biological units into which we might divide morphology, several excellent analyses have shown that progress can be made by combining morphological, developmental, and genetic analyses. For example, Atchley and Hall (1991) summarize current understanding of mouse mandible ontogeny and have managed to identify five developmental units of the lower jaw skeleton. Comparison of the mouse mandible to that of other mouse strains and other species of rodents holds the promise of providing a relatively complete understanding of mandible structure and how intraspecific and interspecific variation in design has been achieved by the transformation of fundamental developmental units.

While the practical consequences of the atomism problem have often been ignored or dismissed (e.g., Cronin, 1991), Sober (1990) suggests that instead of worrying about such difficulties we focus on the properties of traits and ask which of those properties might have resulted from selection. Under this view, there may

be many ways of analyzing any given design, and any one of these ways will be adequate for a specific analysis. Perhaps what really matters are the properties of a specific atomization, regardless of whether or not the dissection into component parts falls along genetic or phylogenetically meaningful lines. However, only the analysis of designs in which phylogenetic and developmental genetic correlations are known will permit us to evaluate empirically the consequences of alternative views of organismal components. At present we are largely operating blind in most comparative studies, with little idea of the historical or genetic patterns that underlie chosen sets of characters.

IV. The Future of the Argument from Design

We have been far too assumptive about the design of organisms. All too often we have been willing to make assumptions about the process of design from the fact of complexity alone. The literature is filled with statements about the mechanical function of this or that trait, or about the "superiority" of this or that design without a single experiment to back up the claim. In addition, facile claims that particular traits cannot have had some specific function (or any function at all) often rest on equally thin ice, a lack of function simply having been assumed. Further, numerous papers elaborate on the evolutionary function of some design without even the pretense of performance analysis, a methodology for breaking down the design into biologically relevant component parts, data on genetically correlated characters, or a quantitative estimate of patterns of selection. It is one thing to simply assume that any complex aspect of the phenotype *must* have resulted from natural selection in its entirety and in its present configuration, but it is quite another (more interesting) thing to demonstrate the complexity of current design, the stepwise historical acquisition of components of that design, and the diverse evolutionary and developmental processes that likely have contributed to any complex phenotypic trait.

As we have seen, the empirical application of the argument from design does not rest on very solid ground. However, the AFD is not without theoretical support: most evolutionary biologists believe that complex organic designs are either partially or largely built by patterns of selection acting on various components of existing designs because there is extensive evidence demonstrating the power of selection to alter biological design in response to environmental demands. Rather, the point of this chapter is that the experiments and analyses necessary to demonstrate specific patterns of selection, especially on gross aspects of the phenotype, are rarely conducted: complexity of design alone is simply assumed to be sufficient evidence. To my mind, assumptive approaches are undesirable largely because they do not promote further research: if we are willing to assume that the hand is designed for manipulation, then we are unlikely to embark on the interesting research program of discovering the historical origin and phylogenetic pattern to hand structure, testing possible models of hand design and their performance on various tasks such as grasping or manipulation, or examining genetic or phylogenetic correlations among components of hand design.

Perhaps empirical standards could be raised if, when we encounter an "argument from design" in research papers or seminar presentations, we ask one

or more of the following questions.

- Where are the physiological or biomechanical experiments to support the interpretation that a structure has the proposed mechanical function? For a comparative phylogenetic analysis, such experiments should be conducted for all members of the clade and outgroups relevant to the interpretation of traits of interest.

- Have alternative designs been compared for performance on a common criterion? It is all too easy to conduct experiments on one design and then simply assert that this design is better than alternatives.

- Do analyses of traits as adaptations or exaptations provide supporting data on (1) patterns of selection (either in the present or past, as appropriate), (2) character correlations to demonstrate that selection either did or did not act directly on the trait of interest, and (3) comparative performance tests to demonstrate the utility or lack thereof of the trait? In short, what evidence supports the inferred evolutionary function claimed for a trait?

- Has the author of an analysis of design explained the criteria by which a design was atomized into component parts and justified the analysis of only a few components of that design?

Let us refashion the argument from design. Instead of aiming to infer processes retrospectively from a design endpoint, we could choose to focus on the process of building the design: an *argument of construction*. How are complex biological designs constructed from the combination of direct selection for certain components, the correlated transformation of others, drift and historical contingency, with each stage in the process of construction influenced by the history of past design? This argument of construction points to a multifaceted research program in which biomechanics, population biology, quantitative genetics, and phylogenetic analysis all have roles to play in research to reveal the process of Darwinian fabrication. The extent to which such research will contribute to our understanding of biological design will be a function of how willing we are to abandon assumptive practices about evolutionary mechanisms to focus instead on patterns of biological design and the many possible mechanisms by which such patterns may have arisen.

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References

- Allen, C., and Bekoff, M. (1995). Function, natural design, and animal behavior: philosophical and ethological considerations. *In*: "Perspectives in Ethology, Vol. 11. Behavioral Design" (N. S. Thompson, ed.), pp. 1-46. Plenum Press, New York.
- Amundson, R., and Lauder, G. V. (1994). Function without purpose: the uses of causal role function in evolutionary biology. *Biology and Philosophy* 9, 443-469.
- Arber, A. (1950). "The Natural Philosophy of Plant Form." Cambridge Univ. Press, Cambridge.

- Arnold, E. N. (1994a). Investigating the evolutionary effects of one feature on another: does muscle spread suppress caudal autotomy in lizards? *J. Zool., London* 232, 505-523.
- Arnold, E. N. (1994b). Investigating the origins of performance advantage: adaptation, exaptation and lineage effects. *In: "Phylogenetics and Ecology"* (P. Eggleton and R. I. Vane-Wright, eds.), pp. 123-168. Academic Press, London.
- Arnold, E. N. (1995). Identifying the effects of history on adaptation: origins of different sand-diving techniques in lizards. *J. Zool., London* 235, 351-388.
- Arnold, S. J. (1983). Morphology, performance, and fitness. *Am. Zool.* 23, 347-361.
- Arnold, S. J. (1986). Laboratory and field approaches to the study of adaptation. *In: "Predator-Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates"* (M. E. Feder and G. V. Lauder, eds.), pp. 157-179. Univ. of Chicago Press, Chicago.
- Atchley, W. R., and Hall, B. K. (1991). A model for development and evolution of complex morphological structures. *Biological Reviews* 66, 101-157.
- Ayala, F. J. (1970). Teleological explanations in evolutionary biology. *Philosophy of Science* 37, 1-15.
- Basolo, A. (1990). Female preference predates the evolution of the sword in swordtail fish. *Science* 250, 808-810.
- Baum, D. A., and Larson, A. (1991). Adaptation reviewed: a phylogenetic methodology for studying character macroevolution. *Systematic Zoology* 40, 1-18.
- Beatty, J. (1980). Optimal-design models and the strategy of model building in evolutionary biology. *Philosophy of Science* 47, 532-561.
- Bekoff, M., and Allen, C. (1995). Teleology, function, design, and the evolution of animal behavior. *Trends in Ecology and Evolution* 10, 253-255.
- Björklund, M. (1991). Evolution, phylogeny, sexual dimorphism and mating system in the grackles (*Quiscalus* spp.: Icterinae). *Evolution* 45, 608-621.
- Bock, W., and von Wahlert, G. (1965). Adaptation and the form-function complex. *Evolution* 19, 269-299.
- Bock, W. J. (1980). The definition and recognition of biological adaptation. *Am. Zool.* 20, 217-227.
- Brandon, R. N. (1990). "Adaptation and Environment." Princeton Univ. Press, Princeton.
- Brooks, D. R., and McLennan, D. A. (1991). "Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology." Univ. of Chicago Press, Chicago.
- Brooks, D. R., and McLennan, D. A. (1993). "Parascript: Parasites and the Language of Evolution." Smithsonian Institution Press, Washington.
- Coates, M. I., and Clack, J. A. (1990). Polydactyly in the earliest known tetrapod limbs. *Nature* 347, 66-69.
- Coddington, J. A. (1988). Cladistic tests of adaptational hypotheses. *Cladistics* 4, 3-22.
- Cronin, H. (1991). "The Ant and the Peacock." Cambridge Univ. Press, Cambridge.
- Darwin, C. (1859). "On the Origin of Species by Means of Natural Selection, or, the Preservation of Favored Races in the Struggle for Life." John Murray, London.
- Dawkins, R. (1987). "The Blind Watchmaker." W. W. Norton, New York.
- Dennett, D. C. (1983). Intentional systems in cognitive ethology: the "Panglossian paradigm" defended. *Behavioral and Brain Sciences* 6, 343-390.
- Dennett, D. C. (1995). "Darwin's Dangerous Idea: Evolution and the Meanings of Life." Simon and Schuster, New York.
- Dullemeijer, P. (1974). "Concepts and Approaches in Animal Morphology." Van Gorcum, The Netherlands.
- Eaton, T. H. (1960). The aquatic origin of tetrapods. *Trans. Kans. Acad. Sci.* 63, 115-120.
- Edwards, J. L. (1989). Two perspectives on the evolution of the tetrapod limb. *Am. Zool.* 29, 235-254.
- Endler, J. (1986). "Natural Selection in the Wild." Princeton Univ. Press, Princeton.
- Fisher, D. C. (1985). Evolutionary morphology: beyond the analogous, the anecdotal, and the ad hoc. *Paleobiology* 11, 120-138.
- Frumhoff, P. C., and Reeve, H. K. (1994). Using phylogenies to test hypotheses of adaptation: a critique of some current proposals. *Evolution* 48, 172-180.
- Funk, V. A., and Brooks, D. R. (1990). "Phylogenetic Systematics as the Basis of Comparative Biology." Smithsonian Institution Press, Washington, D. C.
- Futuyma, D. J. (1986). "Evolutionary Biology." (2nd ed.) Sinauer, Sunderland, MA.
- Gans, C. (1983). On the fallacy of perfection. *In: "Perspectives on Modern Auditory Research: Papers in Honor of E. G. Wever"* (R. R. Fay and G. Gourevitch, eds.), pp. 101-112. Amphora Press, Groton, CT.

- Gans, C. (1988). Adaptation and the form-function relation. *American Zoologist* 28, 681-697.
- Garland, T., and Adolph, S. C. (1994). Why not to do 2-species comparisons: limitations on inferring adaptation. *Physiological Zoology* 67, 797-828.
- Gould, S. J., and Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London. Series B.* 205, 581-598.
- Gould, S. J., and Vrba, E. S. (1982). Exaptation - a missing term in the science of form. *Paleobiology* 8, 4-15.
- Greene, H. W. (1986). Diet and arboreality in the Emerald Monitor, *Varanus prasinus* with comments on the study of adaptation. *Fieldiana: Zoology n.s.* 31, 1-12.
- Griffiths, P. (1992). Adaptive explanation and the concept of a vestige. In: "Trees of Life" (P. Griffiths, ed.), pp. 111-131. Kluwer Academic, Dordrecht.
- Harvey, P. H., and Pagel, M. D. (1991). "The Comparative Method in Evolutionary Biology." Oxford Univ. Press, Oxford, U.K.
- Harvey, P. H., and Purvis, A. (1991). Comparative methods for explaining adaptations. *Nature* 351, 619-624.
- Hume, D. (1779). "Dialogues Concerning Natural Religion." 1991. Routledge, edited by S. Tweyman, London.
- Hurlbutt, R. H. (1985). "Hume, Newton, and the Design Argument." Univ. of Nebraska Press, Lincoln.
- Kato, I. (Ed.). (1982). "Mechanical Hands Illustrated." Hemisphere Publishing Corp., New York.
- Kier, W. M., and Smith, K. K. (1985). Tongues, tentacles, and trunks: the biomechanics of movement in muscular hydrostats. *Zool. J. Linn. Soc. Lond.* 83, 307-324.
- Lande, R. (1976). Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30, 314-334.
- Lande, R. (1978). Evolutionary mechanisms of limb loss in tetrapods. *Evolution* 32, 73-92.
- Lande, R. (1979). Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution* 33, 402-416.
- Lauder, G. V. (1982). Historical biology and the problem of design. *Journal of Theoretical Biology* 97, 57-67.
- Lauder, G. V. (1983a). Functional and morphological bases of trophic specialization in sunfishes. *J. Morph.* 178, 1-21.
- Lauder, G. V. (1983b). Neuromuscular patterns and the origin of trophic specialization in fishes. *Science* 219, 1235-1237.
- Lauder, G. V. (1985). Aquatic feeding in lower vertebrates. In: "Functional Vertebrate Morphology" (M. Hildebrand, D. M. Bramble, K. F. Liem, and D. Wake, eds.), pp. 210-229. Harvard Univ. Press, Cambridge.
- Lauder, G. V. (1990). Functional morphology and systematics: studying functional patterns in an historical context. *Annual Review of Ecology and Systematics* 21, 317-340.
- Lauder, G. V. (1991a). Biomechanics and evolution: integrating physical and historical biology in the study of complex systems. In: "Biomechanics in Evolution" (J. M. V. Rayner and R. J. Wootton, eds.), pp. 1-19. Cambridge Univ. Press, Cambridge.
- Lauder, G. V. (1991b). An evolutionary perspective on the concept of efficiency: how does function evolve? In: "Efficiency and Economy in Animal Physiology" (R. W. Blake, ed.), pp. 169-184. Cambridge Univ. Press, Cambridge.
- Lauder, G. V. (1994). Homology, form, and function. In: "Homology: The Hierarchical Basis of Comparative Biology" (B. K. Hall, ed.), pp. 151-196. Academic Press, San Diego.
- Lauder, G. V. (1995). On the inference of function from structure. In: "Functional Morphology in Vertebrate Paleontology" (J. J. Thomason, ed.), pp. 1-18. Cambridge Univ. Press, Cambridge.
- Lauder, G. V., Leroi, A., and Rose, M. (1993). Adaptations and history. *Trends in Ecology and Evolution* 8, 294-297.
- Lauder, G. V., and Liem, K. F. (1989). The role of historical factors in the evolution of complex organismal functions. In: "Complex Organismal Functions: Integration and Evolution in Vertebrates" (D. B. Wake and G. Roth, eds.), pp. 63-78. John Wiley and Sons, Chichester.
- Lauder, G. V., and Reilly, S. M. (1996). The mechanistic bases of behavioral evolution: comparative analysis of musculoskeletal function. In: "Phylogenies and the Comparative Method in Animal Behavior" (E. Martins, ed.). Oxford Univ. Press, Oxford.
- Lauder, G. V., and Shaffer, H. B. (1985). Functional morphology of the feeding mechanism in aquatic ambystomatid salamanders. *J. Morph.* 185, 297-326.

- Leroi, A. M., Rose, M. R., and Lauder, G. V. (1994). What does the comparative method reveal about adaptation? *Am. Nat.* 143, 381-402.
- Lewontin, R. C. (1978). Adaptation. *Sci. Am.* 239, 156-169.
- Losos, J. B. (1990). The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* 44, 1189-1203.
- Losos, J. B., and Miles, D. B. (1994). Adaptation, constraint, and the comparative method: phylogenetic issues and methods. In: "Ecological Morphology: Integrative Organismal Biology" (P. C. Wainwright and S. M. Reilly, eds.), pp. 60-98. Univ. of Chicago Press, Chicago.
- Mark, R. (1996). Architecture and evolution. *American Scientist* 84, 383-389.
- Mayr, E. (1983). How to carry out the adaptationist program? *Am. Nat.* 121, 324-334.
- Meyer, A., Morrissey, J. M., and Schartl, M. (1994). Recurrent origin of a sexually selected trait in *Xiphophorus* fishes inferred from a molecular phylogeny. *Nature* 368, 539-542.
- Miles, D. B., and Dunham, A. E. (1993). Historical perspectives in ecology and evolutionary biology: the use of phylogenetic comparative analyses. *Annual Review of Ecology and Systematics* 24, 587-619.
- Mishler, B. D. (1988). Reproductive ecology of bryophytes. In: "Plant Reproductive Ecology" (J. L. Doust and L. L. Doust, eds.), pp. 285-306. Oxford Univ. Press, Oxford, U.K.
- Mitchell, W. A., and Valone, T. J. (1990). The optimization research program: studying adaptations by their function. *Quarterly Review of Biology* 65, 43-52.
- Niklas, K. J. (1986). Computer simulations of branching patterns and their implication on the evolution of plants. *Lect. Math. Life. Sci.* 18, 1-50.
- Niklas, K. J. (1992). "Plant Biomechanics." Univ. of Chicago Press, Chicago.
- Ollason, J. G. (1987). Artificial design in natural history: why it's so easy to understand animal behavior. In: "Alternatives: Perspectives in Ethology" (P. P. G. Bateson and P. H. Klopfer, eds.), Vol. 7, pp. 233-257. Plenum, New York.
- Orzack, S., and Sober, E. (1994a). How (not) to test an optimality model. *Trends in Ecology and Evolution* 9, 265-267.
- Orzack, S. H., and Sober, E. (1994b). Optimality models and the test of adaptationism. *Am. Nat.* 143, 361-380.
- Page, M. D., and Harvey, P. H. (1989). Comparative methods for examining adaptation depend on evolutionary models. *Folia Primatologica* 53, 203-220.
- Paley, W. (1836). "Natural Theology." American Tract Society, New York.
- Parker, J. A., and Maynard Smith, J. (1990). Optimality theory in evolutionary biology. *Nature* 348, 27-33.
- Pinker, S., and Bloom, P. (1990). Natural language and natural selection. *Behavioral and Brain Sciences* 13, 707-784.
- Price, T., and Langen, T. (1992). Evolution of correlated characters. *Trends in Ecology and Evolution* 7, 307-310.
- Reeve, H. K., and Sherman, P. W. (1993). Adaptation and the goals of evolutionary research. *Quarterly Review of Biology* 68, 1-32.
- Reilly, S. M., and Lauder, G. V. (1992). Morphology, behavior, and evolution: comparative kinematics of aquatic feeding in salamanders. *Brain, Behavior, and Evolution* 40, 182-196.
- Reznick, D. N. (1989). Life-history evolution in guppies. 2. Repeatability of field observations and the effects of season on life histories. *Evolution* 43, 1285-1297.
- Reznick, D. N., and Bryga, H. (1987). Life-history evolution in guppies (*Poecilia reticulata*). 1. Phenotypic and genetic changes in an introduction experiment. *Evolution* 41, 1370-1385.
- Ridley, M. (1983). "The Explanation of Organic Diversity: The Comparative Method and Adaptations for Mating." Clarendon Press, Oxford.
- Romer, A. S., and Parsons, T. S. (1986). "The Vertebrate Body." Saunders, New York.
- Rose, M. R. (1984a). Artificial selection on a fitness component in *Drosophila melanogaster*. *Evolution* 38, 515-526.
- Rose, M. R. (1984b). Laboratory evolution of postponed senescence in *Drosophila melanogaster*. *Evolution* 38, 1004-1010.
- Rose, M. R., Service, P. M., and Hutchinson, E. W. (1987). Three approaches to trade-offs in life history evolution. In "Genetic Constraints on Adaptive Evolution" (V. Loeschcke, ed.), pp. 91-105. Springer-Verlag, Berlin.
- Rudwick, M. J. S. (1964). The inference of function from structure in fossils. *Brit. J. Phil. Sci.* 15, 27-40.
- Russell, E. S. (1916). "Form and Function: A Contribution to the History of Animal Morphology." Reprinted in 1982 with a new Introduction by G. V. Lauder. John Murray, London.

ive method reveal about
 comotor performance in
 ive method: phylogenetic
 inimal Biology" (P. C.
 ago.
 4-334.
 sexually selected trait in
 42.
 and evolutionary biology:
Systematics 24, 587-619.
 roductive Ecology" (J. L.
 K.
 : studying adaptations by
 their implication on the
 derstand animal behavior.
 Klopfer, eds.), Vol. 7, pp.
nds in Ecology and Evolution
 ptationism. *Am. Nat.* 143,
 ng adaptation depend on
 ry biology. *Nature* 348, 27-
behavioral and Brain Sciences
in Ecology and Evolution 7,
 tionary research. *Quarterly*
 n: comparative kinematics
 96.
 field observations and the
 es (*Poecilia reticulata*). 1.
 41, 1370-1385.
 e Method and Adaptations
 ew York.
 a *melanogaster*. *Evolution* 38,
 phila *melanogaster*. *Evolution*
 s to trade-offs in life history
 schcke, ed.), pp. 91-105.
Brit. J. Phil. Sci. 15, 27-40.
 y of Animal Morphology."
 y, London.

- Selzer, J. (ed.) (1993). "Understanding Scientific Prose." Univ. of Wisconsin Press, Madison.
- Shaffer, H. B. (1986). Utility of quantitative genetic parameters in character weighting. *Syst. Zool.* 35, 124-134.
- Sober, E. (1984). "The Nature of Selection: Evolutionary Theory in Philosophical Focus." MIT Press, Cambridge, MA.
- Sober, E. (1990). Atomizing the rhinoceros. *Behavioral and Brain Sciences* 13, 764-765.
- Sober, E. (1993). "Philosophy of Biology." Westview Press, Boulder.
- Thomason, J. J. (ed.) (1995). "Functional Morphology in Vertebrate Paleontology." Cambridge Univ. Press, Cambridge.
- Thornhill, R. (1990). The study of adaptation. In: "Interpretation and Explanation in the Study of Animal Behavior." (M. Bekoff and D. Jamieson, eds.), Vol. II, pp. 31-62. Westview Press, Boulder.
- Thornhill, R., and Gangestad, S. W. (1996). The evolution of human sexuality. *Trends in Ecology and Evolution* 11, 98-102.
- Vermeij, G. J., and Zipser, E. (1986). Burrowing performance of some tropical pacific gastropods. *Veliger* 29, 200-206.
- Wainwright, P. C., Lauder, G. V., Osenberg, C. W., and Mittelbach, G. G. (1991a). The functional basis of intraspecific trophic diversification in sunfishes. In: "The Unity of Evolutionary Biology" (E. C. Dudley, ed.), pp. 515-529. Dioscorides Press, Portland.
- Wainwright, P. C., Osenberg, C. W., and Mittelbach, G. G. (1991b). Trophic polymorphism in the pumpkinseed sunfish (*Lepomis gibbosus*): effects of environment on ontogeny. *Funct. Ecol.* 5, 40-55.
- Wenzel, J. W., and Carpenter, J. M. (1994). Comparing methods: adaptive traits and tests of adaptation. In: "Phylogenetics and Ecology" (P. Eggleton and R. Vane-Wright, eds.), pp. 79-101. Linnean Society of London, London.
- Williams, G. C. (1966). "Adaptation and Natural Selection." Princeton Univ. Press, Princeton.
- Williams, G. C. (1992). "Natural Selection: Domains, Levels, and Challenges." Oxford Univ. Press, Oxford.