

How to Carry Out Functional Morphology

Optima for Animals

By RM Alexander (1996) Princeton: Princeton University Press. 169 p. \$24.95 (cloth). ISBN 0-691-02798-6.

Climbing Mount Improbable

By R Dawkins (1997) New York: WW Norton & Co. 340 p. \$14.95 (paper). ISBN 0-393-03930-7.

Cat's Paws and Catapults: Mechanical Worlds of Nature and People

By S Vogel (1998) New York: WW Norton & Co., Inc. 382 pp. \$27.50 (cloth). ISBN 0-393-04641-9.

Adaptation

By MR Rose and GV Lauder (1996) San Diego: Academic Press. 550 p. \$69.95 (cloth). ISBN 0-125-9642-18.

Principles of Animal Design. The Optimization and Symmorphosis Debate

ER Weibel, CR Taylor, and L Bolis (eds) (1998) New York: Cambridge University Press. 336 p. \$32.95 (cloth). ISBN 0-521-58667-4.

The Pony Fish's Glow and Other Clues to Plan and Purpose in Nature

By GC Williams (1997) New York: Basic Books, A Division of HarperCollins Publishers. viii + 192 p. \$20.00 (cloth). ISBN 0-465-07281-X.

FUNCTIONAL MORPHOLOGY IS THE STUDY OF ADAPTATIONS

Historically speaking, functional morphology has always been concerned with explaining adaptation, the ubiquitous match between biological forms and the functions they perform. Pre-Darwinian morphologists argued about whether explanations of adaptation were separate from explanations of other facets of organismal morphology, as exemplified by the nineteenth century clash between the French zoologists Georges Cuvier and E. Geoffroy Saint-Hilaire over the relationships among function, structure, and the "natural order" of life.¹

Cuvier, like most post-Linnaean naturalists, saw the "natural" taxonomy of life as being central to zoology. Operat-

ing under the assumptions that "natural" meant rational and that rational reflected God's plan, Cuvier sought the principles that God used in creating animals. For Cuvier, these principles obviously had to be functional: When God created animals, He had to give them morphologies that met the "Conditions of Existence." Accordingly, the component parts of each animal must function together so that the animal survives successfully in its environment.² A classification that recreated the "natural," or God's, system would refer to the structures that animals used to function in their environment. Thus, Cuvier provided a functional explanation for the structure of organisms whereby they must be designed to meet their "conditions of existence," and applied functional principles to group animals.

In contrast, E. Geoffroy Saint-Hilaire argued that pattern is primary and that functional considerations are secondary.³ He argued that the "same" structures in different animals could be modified to perform different functions, but what was prior was their structural similarity or homology, their "Unity of Type." (Geoffroy used the word "analogy," but it is clear that his meaning is closer to a pre-evolutionary definition of homology.) He proposed that all four classes of vertebrates (and later, invertebrates) could be reduced to a single common plan, a plan that was determined neither by function or by God. This plan could be modified to perform different functions, but the Unity of Type could not be violated.¹

Darwin's great achievement was the demonstration that both the structuralist Unity of Type and the functionalist concept of adaptation could be explained by evolution. Similarity of plan (homology) was explicable with reference to descent with modification; the match of biological form to function (adaptation) was explicable with reference to natural selection. Evolution by natural selection occurs when there is variation in phenotypic traits among members of a population; this variation is heritable such that offspring are most like their parents with respect to these traits; and the better adapted variants survive

and reproduce better than do the less well adapted.^{4,5} Thus, the task of post-Darwinian functional morphology was to explain relative reproductive success (fitness) by relative adaptedness, or how one organism is better adapted than another.⁴

This is no easy task, for relative adaptedness cannot be defined in terms of any single physical or biological property such as height, weight, or energetic efficiency. Rather, adaptedness is supervenient on the phenotypic properties of organisms; that is, two organisms with the same physical properties are equally well adapted but no a priori set of physical properties can be used to define adaptedness.⁵ In essence, this means that no single physical property is shared by all "well-adapted" organisms. Philosophers of biology have resolved this problem by defining adaptedness as the propensity to survive and reproduce, distinct from actual fitness, which is actual contribution to future generations.^{6,7}

Post-Darwin, it is no longer reasonable to study functional morphology without considering the influence of history on organismal form. History influences the selective process through developmental and architectural constraints imposed by the available materials. Consequently, there is no "natural break" between functional morphology and the rest of evolutionary morphology⁸: One cannot be a successful functional morphologist in a vacuum. How, then, does one proceed toward a functional explanation of organismal form?

HOW TO IDENTIFY ADAPTATIONS

Although most workers agree that adaptations are the products of evolution by natural selection,^{5,9-12} fundamental disagreements remain regarding the role of historical factors in the definition and study of adaptation. According to the historical definition,¹³ adaptations are phenotypic attributes of organisms that have current utility and evolved by natural selection to perform their current function. If a trait's current function differs from its original function, then it is not an adaptation but an exaptation.¹¹

Box 1. Five Components of Complete Adaptation Explanations (From Brandon 1990)

(1) Evidence that selection has occurred; i.e., that some types are better adapted than others in a specific environment and that this has resulted in differential reproduction.

(2) An ecological explanation of why selection occurred.

(3) Evidence that the trait is heritable.

(4) Information on population structure and gene flow.

(5) Phylogenetic information on trait polarity. Adaptations evolve because their possessors are better adapted to a particular selective environment than are possessors of other traits. Thus, we need to know what evolved from what.

Adaptations are derived features evolved to perform new functions.

In contrast, under the nonhistorical definition,¹³ an adaptation is a trait with current utility, regardless of how it arose. Some advocates of the nonhistorical definition see adaptations as any trait that increases the adaptedness of its possessor.^{8,14,15} Others demand that a trait conform to a priori design specifications.¹² In either case, one does not need to know the historical genesis of a trait to say that it is an adaptation.

The nonhistorical definition seems formally to be nihilistic, saying nothing about the causal history of a trait, and with no obvious connection to natural selection. Yet advocates of the nonhistorical definition view adaptations as the products of natural selection and recognize the importance of historical factors in evolution.^{12,16} The difference between these views of adaptation inheres not in what an adaptation actually is, but in the practicalities of identifying them.

Advocates of the nonhistorical definition of adaptation reject the historical definition primarily because it is difficult, if not impossible, to operationalize.^{12,16} Consider the kinds of information that one philosopher of biology regards as necessary to identify an adaptation according to the historical definition (see Box 1).⁴ Other workers also require evidence regarding past selective regimes and trait polarity.^{17,18}

If we accept these as the necessary components of an adaptation explanation (an explanation that a given feature exists because it is as an adapta-

tion), the study of adaptation becomes very difficult indeed. Of the five components listed in Box 1, evidence of differential reproduction, trait heritability, population structure, and gene flow can be obtained only from studies of living animals. That leaves an enormous number of organisms and an even larger number of adaptations that cannot be studied at all!

The nonhistorical definition of adaptation gets around these problems by waiving the need to document that natural selection produced a given trait. For some, it is assumed that a trait was crafted by natural selection if it contributes to current adaptedness.¹⁵ For others, the trait must match a priori design criteria to be designated an adaptation.¹² Still others make no assumption regarding the process whereby the trait was fixed in a population.⁸

These, then, are the Scylla and Charybdis of functional morphology: a practical nonhistorical definition of adaptation that assumes the past action of natural selection on the basis of current utility and an impractical historical definition, with its impossible requirement that phylogenies be known and that past selection events be demonstrable. Both definitions are in use today.

The historical definition is concerned with questions of evolutionary history¹⁶ and studies of transformation through time.¹⁹ This definition rapidly gained ground among philosophers of biology and biologists in the late 1970s. Philosophers arrived at it through consideration of the logical relationship between selection and ad-

aptation.^{6,7} Biologists adopted it in part because of Gould and Lewontin's influential paper "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme."²⁰ Gould and Lewontin sought to redress the deficiencies in a research program that "regards natural selection as so powerful and the constraints upon it so few that direct production of adaptation through its operation becomes the primary cause of nearly all organic form, function and behaviour" (ref. 20, p. 584–5). They advocated more consideration of phyletic and developmental constraints, aspects of an animal's Bauplan that might be as or more important than natural selection in determining the course of evolution.

Despite Mayr's²¹ reasonable retort

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that Gould and Lewontin ignited a straw man, a new adaptationism is claimed, a post-Darwinian structuralism in which history has taken on the role of the Unity of Plan and the underlying pattern or Bauplan of any group constitutes the pervasive effect of inherited ancestral morphology, manifested as phylogenetic and developmental constraint. Studies using this historical definition of adaptation fall under the rubric of "Post-Spandrel adaptationism," a term coined by Rose and Lauder to introduce their edited volume, *Adaptation*. This "Post-Spandrel" collection of papers on various aspects of adaptation includes a nice history of the concept of adaptation by Ron Amundson, in which he provides

a balanced summary of the development of current thinking about adaptation. (Earlier, I borrowed Amundson's conceptions of historical and nonhistorical definitions of adaptation.)

One important aspect of Post-Spandrel adaptationism is the use of rigorous techniques for developing and evaluating functional hypotheses in the context of phylogenetic hypotheses. Quibbling over the appropriate techniques for phylogeny reconstruction died down in the late 1970s, yielding a methodological and theoretical milieu ripe for the integration of phylogenetic systematics and functional morphology. Larson and Losos, in their contribution to *Adaptation*, discuss and update previous attempts to devise such integrative methodologies.^{17,18} In a "Post-Spandrel" world, integration of phylogeny and adaptation involves using phylogenetic data to test the hypothesis that a trait evolved as an adaptation. A phylogeny is developed, the selective regime and the trait are mapped onto it, then the congruence or incongruence of the two are used to classify the trait as an adaptation, exaptation, disaptation, or nonadaptation. The underlying tests are the predictions of the hypothesis that a trait is an adaptation: that the trait evolved in the context of a specified selective regime and that it is more advantageous than its phylogenetic predecessor.

This methodology demands a well-corroborated phylogeny; adaptation cannot actually be studied without one. Indeed, one needs to be so sure of one's phylogeny that when it suggests that a given trait became "demonstrably inferior" to its phylogenetic predecessor, one can comfortably label the trait a "disaptation" rather than questioning the phylogeny! One wonders whether a phylogeny with more disaptations than adaptations is "functionally" parsimonious. How many disaptations does it take to change a phylogeny?

The fundamental problem with this approach is one of scale. Adaptations that are fixed in a population by natural selection (i.e., by microevolutionary processes) are not amenable to study via macroevolutionary-level or suprapopulation analyses. Comparisons between the functional efficiency

of ancestral and descendent taxa (or between sister taxa or between nodes and tips) are of dubious value for testing hypotheses of adaptation because they do not compare organisms that ever functioned in the same environment. For example, what use are comparisons of *Ardipithecus ramidus* and *Australopithecus afarensis* for hypotheses regarding the adaptive value of bipedality if these taxa never lived at the same time, let alone in the same population?

Alongside the historical tradition, and largely independent of it, the "adaptationist program" has continued to flourish. This tradition is primarily concerned with questions of phenotype or trait existence¹⁶ (p. 2) and does not explicitly consider questions of trait history in the formulation and testing of adaptive hypotheses. Elegant and sophisticated biomechanical analyses of the kind presented in recent years contribute to our under-

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standing of organismal evolution even without detailed knowledge of phylogenetic history. If one can judge the validity of an approach by its results and its productivity, this nonhistorical tradition has explained more than has its historical counterpart.¹²

Under the nonhistorical approach, the environment poses specific problems that traits evolve to solve. By precisely defining both the problem and trait design in mechanical terms, the degree to which design matches problem can be determined. A good match corroborates the hypothesis that the trait is an adaptation, whereas a poor match suggests that the hypothesis is incorrect. There are two obvious questions: How well-designed does a trait have to be to corroborate the hypothesis? And how is poor design explained? GC Williams has long advocated that "[a]daptation is demonstrated by observed conformity to a

priori design specifications"¹² (p. 40), an argument he reiterates in *The Pony Fish's Glow and Other Clues to Plan and Purpose in Nature*. The pony fish possesses a light-emitting organ inside its abdomen, the light from which shines through to its soft underbelly. The apparent advantage of this is that it makes the underside of the fish light, camouflaging it against the background of down-welling light and thereby improving its chances against predation from below. Experimental work demonstrates the fish's ability to regulate the intensity of the light within to match the light without, corroborating the hypothesis that the photophore functions as camouflage.

Williams defends this as a productive example of adaptive story-telling. Rejecting the characterization of such adaptationist theorizing as Kipling-esque "just-so" stories, Williams prefers the detective-story analogy: Adaptationist story telling refers only to "well-established material processes" and includes "a way in which natural selection . . . could maintain the proposed adaptation" (p. 17). Current utility must explain why normalizing selection, or optimization, prevents further evolution of the trait (p. 31).

The argument from design is an old one²² and is at the core of the nonhistorical approach to adaptation: If something appears to have been designed for its purpose, natural selection must have built it, and it must therefore be an adaptation. Lauder's contribution to *Adaptation* enunciates the historical definition's criticism of this perspective: The argument from design requires an inference of process (natural selection) from pattern (design), something which adherents to the historical definition cannot stomach. For them, natural selection must be demonstrable, not assumed. The precise place on the phylogenetic tree that the trait evolved must be specified, and the role of selection in fixing it in the lineage must be tested. Adaptations must therefore be derived traits. Primitive traits cannot be adaptations because they have already been fixed in the lineage. Reductio ad absurdum: The human eye is not an adaptation because one gene involved in its development is also found in flies, its basic retinal structure and extraocular

muscles were inherited from early vertebrates, and its fovea was inherited from the haplorhine ancestor.

Lauder claims that if the argument from design is to function as a research program, if process is to be inferred from pattern, then four criteria must be met: It must be possible to infer mechanical function from structure; We must be able to specify criteria for designs that will solve specific problems; We must be able to infer patterns of selection from analysis of phenotype alone; and we must be able to atomize organisms into relevant component parts. Lauder questions whether any of these criteria can be met, although he presents phylogenetic analysis of adaptation as a partial panacea for the third criterion.

Indeed, the argument from design, like any study of adaptation, is not always going to be possible. However, Kay and Cartmill's²³ four principles for the study of adaptations in fossil organisms attempt to define the circumstances in which function can be inferred from structure. They propose that a trait in a fossil taxon can be said to have had a hypothesized function only if there are some living organisms with the trait and the trait performs the same function in all of them. [In this case, there is no reason to believe that the trait performs a different function in the fossil taxon, addressing Lauder's first criterion.] Kay and Cartmill also specify that there must be no evidence that the trait appeared in the lineage before the function that it performs, supporting, at least in spirit, the kind of phylogenetic consideration specified by Lauder. Finally, all the features used in the definition trait must have some mechanical relationship to the function it performs, a principle addressing Lauder's concern that the organism be appropriately atomized.

As Kay and Cartmill admit, few traits and functions are so perfectly correlated. Those that are present little problem for either a historical or a nonhistorical definition of adaptation. The problems arise when traits have more than one function, or their functions change through time.

In contrast to the historical approach to adaptation, which equates adaptations with shared derived traits and focuses on explaining how traits

originally become fixed in lineages, optimization theory is used by the nonhistorical school to explain how selection can either gradually improve the design of primitive traits or merely maintain primitive traits in lineages. Optimization theory is one of functional morphology's most powerful tools and a cornerstone of the nonhistorical approach to adaptation.

The fundamentals of optimization theory are nicely laid out in Alexander's newly revised *Optima for Animals*. "Optimization is the process of minimizing costs or maximizing benefits, or obtaining the best possible compromise between the two. Evolution by natural selection is a process of optimization" (p. 2). Implicit in the application of optimization theory to zoology is the notion that optimization, like natural selection, is a process whereby the best design is continually preferred over the available alternatives until it predominates in the population. When the best design is fixed in the population, optimization is a "corrective tendency," a point also made by Williams (p. 31).

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Implicit in the optimization approach is the notion of constraints. Optimization only works on the available alternatives. It makes the best of what is available, not necessarily the best possible. As Alexander points out (p. 149); the claim that the adaptationist program ignores phylogenetic or developmental constraints²⁰ reflects a fundamental misunderstanding of the optimization approach. That approach defines not only the best way of solving a particular problem (a global maximum), but also other good ways of solving it (local maxima). There are always several ways to solve a problem posed by the environment; the solution that any animal possesses will be

that which was immediately accessible at the time selection acted. Only by carrying out an optimization analysis can these local and global maxima be identified, allowing hypotheses to be derived for why each animal solves the problem in the way it does. Sometimes developmental constraints can be invoked and sometimes there are constraints due to the materials available, both of which are related to the phylogenetic history of the animals concerned. Sometimes the assumptions underlying the model are incorrect.

Few concepts in the adaptationist program have received as much attention as symmorphosis, introduced by Ewald Weibel and the late Richard Taylor.²⁴ Symmorphosis is all about optimization. It is the "state of structural design commensurate to functional needs resulting from regulated morphogenesis, whereby the formation of structural elements is regulated to satisfy but not exceed the requirements of the functional systems."²⁴ The concept of symmorphosis presented in this book emphasizes the need to study functional systems rather than atomized traits²¹ and the importance of safety factors in the study of animal design. The degree of integration of various functional systems (skeletal, muscular, pulmonary, and nervous) is examined with various degrees of attention to the ways in which changes in one part of the system are accompanied by changes in others. Of particular interest in the current context is the discussion on safety factors. If a functional system evinces overdesign (e.g. more bone than required, as in the browridges of macaques and baboons²⁵), is this evidence that the system is not optimally designed or that it is a different system that is optimized? How supra-optimal must something be before it is no longer optimized? *Principles of Animal Design* provides tantalizing glimpses of possible answers to these questions, but the brevity of the contributions limits the scope of those glimpses. Moreover, the book's esoteric presentation, with no "in-text" references, prevents one from following up on specifics mentioned by each author without searching through the "Further Readings" appended to each chapter. Despite these difficulties, *Principles of Animal*

Design is rich in examples of how functionally integrated systems provide evidence for or against the theory of symmorphosis. It is, moreover, a useful source of data for those interested in issues of constraint and optimization in animal design.

Historical constraints on adaptation are the subject of the focal analogy in Dawkins' *Climbing Mount Improbable*. Dawkins (p. 77) analogizes "the combination of perfection and improbability," that characterizes well-designed structures to a mountain, Mount Improbable. The peak of the mountain represents the perfection of a particular design, the best possible attainable solution to a specific problem. However, Mount Improbable is actually more like the adaptive landscape of Dobzhansky and Simpson, with many different peaks at various heights or degrees of perfection, representing the various possible solutions to a given problem. Natural selection (optimization) for a better design may not drive a lineage up to the highest peak on the landscape, producing the best structure possible. But it should approach a local optimum. Exactly which peak a lineage ends up on will depend on where the lineage starts, where its phylogeny brings it to before optimization drives it upwards.

Good examples of this can be found in Dawkins' (p. 138ff.) masterful treatment of a well-worn touchstone of adaptation debates: the eye. So closely does the human eye seem to match design specifications that many, including Darwin, doubted that natural selection could have built it. Yet eyes are so useful that they have evolved independently at least forty times and several different designs are evident. Exactly which kind of eye any particular animal ends up with is partly a function of its history. And some eyes are better designed in some ways than others are. For example, in vertebrate eyes the photoreceptors lie behind the cellular wiring that connects them to the brain, whereas the eyes of molluscs have their wiring behind the photoreceptors. The mollusc eye must experience less optical aberration than the vertebrate one, but the way that vertebrate eyes develop means we are stuck with a back-to-front retina.

The strength of the adaptationist program lies in how it explains con-

trasting or suboptimal solutions to a specific problem. The historical approach focuses on the specifics of the origin of an adaptation, with some treatment of the hierarchical transformation of adaptations. The nonhistorical approach focuses on patterns of adaptations and on all instances of an adaptation, whether convergently evolved or homologous, whether primitive retentions or newly derived features. What counts is whether the hypothesized relationship between function and structure holds across taxa.

Whereas the historical approach tests hypotheses about adaptation by attempting to reconstruct the precise causal (mechanical) forces that fixed a trait in a lineage, the nonhistorical approach is concerned with identifying the functional rules and principles that apply broadly across taxa and determining which ones any given trait conforms to. The set of rules it conforms to is determined, in part, by its history.

The strength of the adaptationist program lies in how it explains contrasting or suboptimal solutions to a specific problem.

The most stimulating book in this group discusses precisely these general rules and principles that life adheres to, contrasting them with the rules and principles characterizing human technology. Vogel's *Cat's Paws and Catapults* compares the *Mechanical Worlds of Nature and People*, enlightening both in the comparison. Vogel provides insights on an array of topics. For example, humans tend to make levers that amplify force at the expense of distance, possibly because nature makes levers that amplify distance at the expense of force. Human engines are usually based on rotation or expansion, but nature's engines use sliding and contracting. Human technology operates by storing mechanical work as electrical, kinetic, gravitational, or elastic energy, whereas na-

ture emphasizes the last two, especially elastic energy.

Vogel notes that when looking at the technologies used to make rigid structures, humans make extensive use of metallic structures, while nature completely lacks them. The difficulty of extracting metals from the compounds they occur in may account for the lack of natural metallic structures. The other possibility, which Vogel prefers, is that nature has evolved better rigid materials out of composites such as bone, shell, cuticle, and wood. Composites deter the crack propagation that plagues purely metallic structures. How nature started using composites is not certain, although they appear early in metazoan and plant evolution. They have been retained and modified in numerous ways to serve many functions, and are more easily accessible than the metals humans use. Vogel's work evinces scant concern with phylogeny, but then it does not really need it, being concerned with life in general.

This selection of books on functional morphology is heavy on contributions from the nonhistorical school. Although this is an arbitrary measure of current usage, it nevertheless remains the case that the nonhistorical approach to adaptation is far more productive than the Post-Spandrel approach in explaining the functional design of organisms. Perhaps the nonhistorical approach has been more productive because its goals are more realistic. Instead of focusing on the difficult to know, the contingent and the specific, it emphasizes the general and the predictable. And if explanation involves invoking rules and principles, the nonhistorical approach will always be better at explaining.

Yet surely there must be a way that the two approaches can be merged without giving one kind of knowledge epistemological priority over the other. The incorporation of functional information into phylogeny construction is out of favor, but surely a total-evidence approach to phylogeny reconstruction demands that phylogenies make functional sense, that they are "functionally parsimonious." To draw an analogy with recent work on integrating stratigraphic data into phylogeny reconstruction, phylogenies should also be required to minimize "func-

tional debt," the cost of deriving specific features from specified contexts. It is to be hoped that we will see a revival of interest in the possibility of using functional data to arbitrate between competing phylogenies.^{26,27} Paleoanthropologists who study the biomechanics and function of living primates have an important role to play in phylogeny reconstruction. Their information can be used to evaluate alternative phylogenies advanced by phylogenetic systematists. Similarly, functional morphologists can ask whether their functional models are corroborated by phylogenetic data. For if a well-corroborated phylogeny predicts functional transformations that are at odds with biomechanical theory, it may not be the phylogeny that is incorrect.

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