



FUNCTION AND ADAPTATION IN PALEONTOLOGY AND PHYLOGENETICS: WHY DO WE OMIT DARWIN?

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ABSTRACT

What phylogeny (but not classification) is has a bearing on how we should try to recover it. Phylogeny is descent with adaptive modifications constrained (and facilitated) by previous stages, largely through natural and sexual selection. This fundamental theorem of the evolutionary process contains a host of post-Darwinian advances in evolutionary biology that relate to it conceptually. Stated simply, this complex bundle of precepts is therefore the theoretical foundation of not only a Darwinian phylogenetic analysis, but also any comprehensive theory of function (in a broad sense) and of structure as well. Darwinian functional biology is also the study of adaptations and the process of their acquisition. Engineering assessments of features are not appropriate substitutes for Darwinian analysis.

Fundamentally structuralist approaches to evolutionary analysis (including those of many phylogenists) consider the goals of adaptational analysis unattainable not only for fossils but for extant organisms as well. Yet adaptations in extinct species are often better understood than their phylogeny, in spite of widely advertised claims that phylogeny reconstruction is more properly scientific than adaptational analysis. Anyone working with bone tissue, bones, joint complexes, and complete skeletal evidence who doubts that these levels are adapted both ontogenetically and phylogenetically either is unaware of the vast body of evidence that supports the adaptedness of the skeleton on all levels or chooses to ignore this area of knowledge in favor of the aesthetics offered by parsimony analysis. Both a strictly functional and an adaptational (ecologically utilitarian) assessment of traits is necessary, in both extant and extinct organisms, in order to reliably (i.e., probabilistically) establish polarities of homologous features that may be used in phylogenetic analysis. Such research, including the culling of homoplasies from a database, yields robust taxonomic properties against which lineage and taxon phylogeny hypotheses may be tested. The pairing of the “causal role function” approach of Lauder and co-authors with parsimony-based cladistics—which is a structuralist perspective, not a Darwinian one—does not advance the aim of reliability in phylogenetic reconstruction. Systematists should attempt to use only ordered and polarized characters in their probabilistic estimation of phylogenies, an approach that provides the most reliable assessment of phylogenetic hypotheses that can also have causal meaning.

An evolutionary explanation (always constrained in its taxonomic expression by heuristics not directly relevant to phylogenetics) involves both the causal and historically mediated components of a particular transformation (an evolutionary becoming). A sharp theoretical distinction between functional and evolutionary explanations should

be replaced by a less dichotomous and hierarchic, as well as a far more “temporally looped” and interrelated, conceptualization of the relationship between the evolution of the function (mechanics or physiology) and biological roles of features. Biostratigraphy and functional analysis (*sensu lato*) provide the theoretically valid bases of the transformational analysis of attributes of populations of organisms in phylogenetics. Transformational analysis of features should be biologically contextualized and kept independent of taxogram-driven parsimony analysis. Transformational analysis and the subsequent understanding of the relationships of lineages is a prerequisite for meaningfully tested taxon phylogenies. Both adaptational and phylogenetic analyses are inferential about events in the past and both are based on theoretical assumptions, never on complete evidential support; therefore neither has theoretical supremacy over the other. The widespread and dogmatically alleged primacy of parsimony-based cladistics as being the foundation of all phylogenetic considerations, with all its truncated and circular assumptions, is more a complex social construct (a Kuhnian paradigm) than a theoretically defensible position.

KEY WORDS: Function, mechanical analysis, adaptational analysis, Darwinian phylogenetic analysis, parsimony cladistics, mosaic evolution.

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INTRODUCTION

Much has been written about the theoretical issues of functional biology, in a broad sense, as these pertain to the study of living organisms, but far less regarding the relevance and significance of function and adaptation for the historical understanding of fossil and living animals. Furthermore, although most ideas of function have always been tied to adaptations (e.g., Pranger 1990), there has also been a tacit general belief that adaptations (or the adaptedness) of fossils cannot really be ascertained. Little attention has been paid to different historical and systemic levels of adaptations within lineages and taxonomic species of these lineages beyond the taxic (and fundamentally punctuationist) conceptualization (e.g., Gould and Vrba 1982). As a result, the usefulness of adaptational analysis and the applicability of ecological inferences for phylogenetic analysis of both fossil and extant taxa has been all but ignored, if not explicitly berated.

The philosopher Amundson (1996, p. 29), in his scholarly account of the history of ideas regarding adaptation, has stated that “Darwin sided with function.” To attribute “siding” to Darwin, however, given his elaborate presentation of the theory of descent based on homology and the paleontological record, is rather problematic. Such an opinion expresses a lack of familiarity with the corpus of Darwin’s work, and misconstrues Darwin, the modern phylogenist. For Darwin to reformulate the structuralist notions of his day into the theory of descent (evolutionary process) required something

entirely different from “siding.” Darwin sublimated both “structuralist” and “adaptationist (functionalist)” views of character equivalence into the cornerstone of the phylogenetic method, practiced in a variety of different forms since 1859.

As a consequence of the modern sidelining of the relevance of function to phylogenetic analysis (and, even worse, a studied misunderstanding of its role in phylogenetics¹), there has been relatively little attention given to the connection between functional biology and transformational analysis to phylogeny estimation in the past three decades of phylogenetics-related literature. Furthermore, judging from the masses of phylogenetic studies published, most of what has been written in the theoretical literature about function is either ignored or misunderstood by most practitioners of numerical cladistics, including stratocladistics. But the functional literature itself is often both equivocal and confused regarding the role of functional biology and its relationship to the estimation of phylogeny. This is peculiar, because what phylogeny is (as we understand it within well-tested Darwinian theory) should have a bearing on the methods we use to reconstruct it. It is for this reason that I undertake the task of briefly drawing attention to some theoretical and methodological relationships (both ontological and epistemological) between functional analysis (*sensu lato*) and phylogenetics (but not the construction of taxograms or classifications). First, I look at the general theoretical issues that relate to the estimation of adaptations in fossils

and their phylogenetics. Second, I examine some of the competing views of what functional biology is supposed to be in relation to functional and evolutionary analyses that include fossils. Third, I specifically make connections between a broad concept of functional biology and Darwinian phylogenetic analysis (but not the taxonomic expression of well-tested phylogenies). Finally, I take a closer look at issues surrounding transformational analysis and attempt to refute arguments leveled against the concept of mosaic evolution based on the taxic conceptualization of phylogeny.

BACKGROUND AND STATEMENT OF THE PROBLEM

For those paleontologists (as well as neontologists) who study vertebrate skeletons, the species-specific microscopic as well as macroscopic attributes of bones are essential information. These are the material foundations of their science within the critical contexts of time and place. Bone tissues and skeletons are complexly imbued, because of descent and adaptation, with both the constraints and adaptive meanings of their past and present at any moment in geological time. This is realized differently at the levels between the bone tissue, the intermediate trabecular structures, and the whole structure of a particular bone as part of a skeleton. Adaptive aspects of skeletal morphology are materially (albeit not conceptually) inseparable from their phylogenetic signals². Theoretical perspectives that ignore contextual, interpretive, and functional analyses of such complexes, and that are used subsequently to test phylogenetic hypotheses, axiomatically deprive themselves of a potentially enormous and relevant material database. Such abiological and ahistorical views about data also potentially deprive phylogenetics of an organism-based causal explanation. Science without causal explanations is a questionable enterprise.

Contrary to such general notions that the concept of adaptation is an onerous one (and should be invoked only with great caution), the adaptive nature of bone tissues, bones, joints, and skeletal systems have proven to be completely adapted within their phyletically constrained limits, both ontogenetically and phylogenetically. This does not mean that given this well-supported generality we can easily understand this or simply accept generalities without rigorous research into the specifics of such adaptations, but that phylogeny is the history of largely adaptive change, within the context of historical peculiarities of all lineages. Attempting to decipher phylogeny without researching the

complex of attributes that can yield these historical peculiarities (the phylogenetic signals) is likely to yield only ephemeral patterns, no matter how rigorous the techniques (usually of fundamentally flawed conceptual methods) are that are used to arrive at them. It should be realized also that macroevolutionary guesswork about paleontological patterns that superimpose random walk models on data do not in any way corroborate notions that certain segments of phylogeny were non-adaptive (contra Gould, 1988; Vrba, 1980).

As a necessary preamble, it should be stated that each organism (a life history) is a complex composite intertwined genetically (i.e., historically) and developmentally (in current and real time). [Note: In sexually reproducing organisms the ovum itself also represents a critical component of the historical heritage beyond genetics.] The evolutionary fate of demes or species (not individuals, but continua in time) is a consequence of the interplay of both the physical world and the Darwinian context (the total environment), and the imperatives affecting the individuals that make up such evolutionary units. The Darwinian components of tested evolutionary theory are obviously not only adaptation or adaptedness through natural selection and modification through sexual selection, but also ancestrally constrained descent with modification. A combination of selectional "forces" (= causes) drives the process of differential survival, and what remains in terms of fitness (differential reproduction) for each organism is its contribution to the proportions of subsequent ontogenies (organisms). Modal patterns of the various frequencies of these variant ontogenies become fixed differently in populations or species, and these variably persist and change in lineages. Therefore, phylogeny is a succession of successful life histories (ontogenies in a broad sense) in the context of ecology. The general statements in this paragraph are a set of assumptions on which the issues discussed later depend.

The specific issues examined in this paper are concerned with neither evolutionary nor cladistic taxonomic expressions of phylogeny. The various caricatures of these schools of classification have been discussed in the partisan literature. As stated by Padian (1999), Darwin's concern was mainly with the expression of phylogeny in formal classifications. But it is a mistake to ignore that it was already just as obvious to Darwin (as it is today) that phylogeny is both constrained and facilitated by ancestry, which guides selectionally-mediated descent. Darwin also fully understood that all information was to be used to test phylogenies and that their taxonomic expression was fraught with the compromises that such heuristic activity must face.

It is just as obvious now, as already noted, as it was to Darwin that what this phylogeny is should direct the construction of methods, our epistemology, in order to recover it.³

Given that a well-tested general understanding of phylogeny (its estimation at best) is a nearly universal goal among modern systematists, the first reaction that comes to mind regarding the adaptedness of past samples of lineages (the fossils) among theoreticians (often neontologists) is that they are dead, so what, if anything, can be said about their adaptations with any degree of corroboration? It should not need repeating here that science is a probabilistic enterprise with equal doses of deductive and inductive activities, contra the Popperian views endlessly defended in the pages of **Cladistics**, and that its various problems can be "solved" or even "resolved" only with varying degrees of success (e.g., see, again, the Popperian and logical-positivist text on cladistics by Schuh 2000.). Yet some of the least "falsifiable" or "provable," but often well-corroborated, answers to questions can be the most important for understanding causes and history (these often being the least logical in a linear sense).

Adaptations in fossil taxa cannot ever be fully understood, but it is also questionable, to a lesser degree, whether they can be completely understood for most living species as well. The reason for the latter is partly theoretical, but primarily because the operational difficulties can be enormous for complex metazoans. These issues are independent of the adaptive nature of the evolutionary process itself. We need to remind ourselves at this point that we should be equally aware of the fact that, although phylogeny also resides in the past, we nevertheless pursue it with zest. And there are very good reasons why we should, therefore, do the same with regard to functional and adaptive analysis for both fossils and living species. There is surely more to adaptational analysis of fossil entities than Novacek's (1996, p. 315) remark that "[t]his situation leaves us looking for something to salvage for the purpose of scientific inquiry." Does this mean that often the litanies of dubious synapomorphies that overwhelm many morphological databases in cladistic analyses of fossils are the proper foundations for a cladogeny that should guide adaptational assessment?

Ontological issues surrounding adaptation as a process, because of the thorny issue of "current utility", cannot be resolved (see later). Such philosophical conundrums, however, do not make the process of adaptation and its results any less real. But it should be realized, because it is not widely appreciated, that the explanation of adaptations in

fossils, as independent of phylogeny as the concept of adaptation can be of phylogeny, is often less of an epistemological problem than the attempts at valid testing (i.e., corroboration) of many phylogenetic hypotheses without independent transformational and functional understanding. The currently dominant view eschews the relevance of adaptational analysis for phylogenetics, if not for so called "scenario building", as I briefly discuss later. According to this view, cladograms, based on parsimony-driven distribution analyses of "synapomorphies" (i.e., untested homology hypotheses of uniquely shared similarities between taxa), represent the foundations (deductive and scientific) of all other historically relevant analysis (e.g., Eldredge and Cracraft 1980; Simmons 1993; Novacek 1996).

FUNCTIONAL BIOLOGY AND TERMINOLOGY

A few concepts should be discussed at the outset before attempting linkage of functional biology with phylogenetics. This is in order to explain and differentiate among issues that have not been uniformly understood, advocated, or espoused by workers in any of the methodological areas related to functional analysis. To most naturalists functional biology has a unifying significance for evolutionary biology. This holistic, and Darwinian, perspective of naturalists should axiomatically apply in the pursuit of phylogenetics; organisms have always represented specific strategies to differentially survive and reproduce, so this fact should have a bearing on any estimation of phylogeny.⁴ A broadly conceived notion of functional biology is certainly not evolutionary biology in toto, but it is at the core of biological as well as macroevolutionary explanations for the history of life. But there are issues related to the term "function" that need to be examined because these relate not only to the clarification of the term but also to phylogeny reconstruction itself.

Bock and von Wahlert on Function

In an attempt to unravel and clarify the several meanings of the term function, a more restrictive use was suggested by Bock and von Wahlert (1965) in a paper on adaptation and the form-function complex. These authors refined the distinction between the mechanical-physiological and behavioral aspects of features of organisms, on the one hand, and the selection-caused (-mediated) biological role (biorole or role; or adaptive or biological function) of these, on the other. Such a conceptual difference was previously well understood by a number of biologists and paleontologists, but it was

not appreciated by many others. The concepts of mechanical and biological functions (i.e., function and biorole) were not only clearly differentiated by Bock and von Wahlert but were presented in a theoretically detailed functional and ecological context. This clarification of terms to cover definitionally well-differentiated (but really only empirically divisible) research domains remains important. But the theoretical relationships between mechanics and adaptation are more complex than normal definitional procedures permit (see later).

I and others have followed the terminology introduced by Bock and von Wahlert (1965) because such practice has the salutary consequence of forcing both an author and his or her reader to think more clearly about the complexity of functional, adaptational, and evolutionary issues. In any meaningful sense, the mechanical and biological functions of organisms in real-time are inseparable (see Szalay, 1999a for discussion of "real-time"). Yet a combination of historical and real-time factors - ontologically but not epistemically distinct - clearly drive evolutionary changes of functioning attributes.⁵ These are wholly interdependent processes and causalities. Note again, however, that many researchers continue to use the single term "function" with a clear meaning where the context renders it obvious that they mean either mechanical or biological (adaptive) function. Others, however, continue to conflate the meanings at the expense of both operational and explanatory clarity.

Lauder (1996), in spite of his attempted endorsement of the functional conceptualization of Bock and von Wahlert (1965) either intentionally or inadvertently confused this approach with "ahistoricity" versus "historicity." When Lauder (1996, p. 63) states that "... a bone might have the mechanical function of stiffening the limb against gravity ..." he is not only referring to mechanical function. In making such a statement that connects an organism (and, needless to say, the size of the animal, and the manner of its locomotor and other positional behaviors) to its specific environmental context, Lauder clearly adds an adaptational, and therefore selectional force-related, component to his characterization, which he refers to as "anatomical function." He obviously believes that there is a difference among the relationships of an anatomical structure, its biological role(s), and what he pursues as the neurologically controlled behaviors of an organism. In making this distinction, he either rejects or misses the universality of meaning attached to the function and biorole dichotomy so well explicated by Bock and von Wahlert. Differ-

ently structured mechanical systems (e.g., his examples of forearm mechanics), although performing the "same" roles, surely have a distinct combination of mechanical factors and resolution of forces acting differently in concert. Such systems certainly do differ in their mechanics. Model-T Ford and late-model BMW automobiles all roll along the same road from point A to B, but no one would seriously entertain the notion that their detailed (progression-related) mechanics are comparable.

This issue of function is further confounded by Lauder (1996, p. 63) when he notes that "[t]he biological context of structure and function is referred to as the 'biological role' of a structure or **mechanical function...**" (emphasis added). In spite of what I believe to be Lauder's misuse of the conceptual and terminological meanings of function, these distinctions continue to serve a significant purpose in comparative biology. When viewed theoretically, both the mechanical and biological functions can change (e.g., from bones to neuronal networks). Both can change independently of one another and have independent historical components. It is important, therefore, not to front-load the historical component (the structural-functional heritage) with fitness considerations within the already enormously complicated theoretical maze regarding function. By not keeping the biological role independent of mechanical explanation, Lauder has done just that.

The "new adaptationism" that has become wedded to a taxic conceptualization of parsimony-based cladistics and has been hailed by many (e.g., Novacek 1996) as the solution to the problem of functional conceptualization has not advanced the cause of either terminological or theoretical clarity. The "causal role function" notion in this "new adaptationism" is an unnecessary and invalid subordination of the adaptational component of phylogeny to a theoretically truncated (= ontologically unrealistic) epistemic paradigm of numerical cladistics. This view of the cladistic component of phylogeny has come to mean not only that taxograms are phylogeny, but that evolutionary explanations (and even theory) should be based on such taxic constructs.

Taxic and Punctuational Perspectives by Gould and Vrba on Adaptation and Function

Gould and Vrba (1982) offered a terminological scheme through which they asserted that one can clarify differences between adaptations due to natural selection for their current role, and various aspects of such features that were not built by selection for their current role, but became useful

for it after their inception. These authors argued that this was partly an effort to replace "preadaptation", a concept they considered teleological. According to Gould and Vrba (1982), "aptation" was the general phenomenon of something being fitted for a role, whereas the term "adaptation" was restricted for traits built by selection for current roles and the term "exaptation" was used for the concept of preadaptation.⁶

The example they used, feathers (without a much-needed clarification of the kind of feathers), has a considerable semantic element to it. The term "feather" covers various kinds of feathers, the expected state of affairs for all evolutionary transformations of attributes through phylogeny, each representing part of a continuous, but at any historical moment possibly distinct, condition of that trait or group of traits. Although feathers are a general developmentally circumscribed group of features, it is obvious that whatever kind of feather came first in a particular lineage (probably the protofeather for improved thermoregulation, from a preexisting condition that we would call a type of scale) was not the same kind of feather that was subsequently developed through selection for flight, or the dazzling variety of display feathers developed through sexual selection in birds. As noted, we could also have begun by calling feathers a particular type of denticulate scale along a continuum of scales (and of bushy phylogenetic patterns), a sequence that undoubtedly was part of the transformation series of scales in general. The same applies for vertebrate limbs, from fins to wings of all sorts. This highly semantic, as well as "lurching" and "jerky," conceptualization, just one of the many possible, played a major role in Gould and Vrba's theoretical presentation.

But the proposed sharp division between "exaptations" and adaptations does reflect two important underlying messages, and the agenda is clearly punctationist. First, and this view is not particularly controversial, lots of features just happen; they are non-adaptive. The second point, however is that the advocated (punctationist and taxic) view of evolutionary change should have a distinct "aptive" component assigned to (punctuated) species taxa (either the first or the second kind of "aptation"). Furthermore, and subsequently, a lineage perspective on evolution - the Darwinian view - should be abandoned in favor of a "stable-taxon"-based notion of punctationism.

This was a very different conceptualization from Simpson's (1953, p. 160-199) expansion on Darwin, namely that the prospective functions in a dynamic overlap of the shifting relationship between a lineage and the environment become

realized functions (including their phenotypic expressions as adaptations). Simpson envisaged the adaptive process as an ongoing seamless relationship between the total environment and the evolutionary unit at a given moment in the history of that lineage. Gould and Vrba (1982), on the other hand, based their discussion on the underlying assumption (never made explicit) of the mysterious and abrupt shifts of speciation. Their conceptualization, and the resultant and ungainly terminology loaded with unacceptable theory, is based on the coded core of punctationism, paleontological species taxa that happen to coincide with the terminal species taxa of cladistics.

The mental imagery offered by the punctationist and taxic terminology is clear: Species give rise to other species with sharply distinctive adaptations, a perspective that studiously underplays the rate-independent gradualism of phyletic continuity and exhorts terminology related to species taxa that serves a speciation theory of evolutionary change.⁷

Causality and Function

An issue of seemingly remote relevance to the theoretical notions embedded in "function" is the dichotomy of "proximate" versus "ultimate" designation of causes in biological explanations. Mayr's (1961) early, popular, and much repeated thesis (Mayr 1982) was that there are both proximate and ultimate causes operating in biology. The former (the mechanics, physiology, etc., of an organism) was pursued by the "functionalists," and the latter (the adaptations and history of species) by the "naturalist-evolutionists." Mayr believed that sharply different conceptual approaches were needed to understand these causes. I take a contrary position. The concept of causality in realtime (Szalay 1999a) should play a fundamental role in any theoretically rigorous connection among the various components of both "nonhistorical" and "historical" causation and explanations in holistic functional biology. (Note that the latter is considered biosystemism by Mahner and Bunge 1997, who maintain the special position of organisms in the various levels of organismic and suborganismic diversity.) Therefore a loose designation of cause can be obfuscating when it comes to either functional or evolutionary analysis, both in the broad and narrower senses (see later). Causes occur in realtime (and that rules out "causal" past history), although obviously the initial and boundary conditions of organisms living at a particular time play a significant constraining and facilitating role throughout their entire life. The initial and boundary conditions together are a rough, if not exact, equiv-

alent of Aristotle's material cause from his "techne" model of causation. I adopt the view of Mahner and Bunge (1997) on causality, except for their insistence that ontogeny is not causal.⁸The arguments of Mahner and Bunge challenge the notion of "ultimate causality" outside of the context of realtime causality in any lineage.

It is important to frame both questions and research strategy not in terms of almost invariably nebulous "ultimate causes" lost in the past, but rather in terms of the knowable but obviously constrained material realities of the organism we study, be it fossil or extant.⁹ It is obvious that any manifestation of the organism throughout its entire life history is deeply functional in the broad sense, and any such functions are as historical as they are adaptive. Furthermore, a phylogeny is tested against these, in contradistinction to the "new adaptationism" paradigm that would map features discovered in these contexts onto a taxogram. Organisms themselves reflect both history and adaptations in an inexorably intertwined manner that should be analyzed to factor out the historically shared (or sequentially related) components of phylogenetics.

Historical narratives are histories of successful and successive ontogenies wastefully managed by ecology,¹⁰ and lineages represent ontologically the past history of evolving populations or species (anywhere along that lineage in time). Therefore, a lineage (a mere record of a species) does not have "causes" acting on it, beyond those that acted on the aggregate of living individuals that made up each segment in the past (a species, or other evolutionary subunits of a species, in an instant in time; such realtime units are not species taxa; see discussions in Bock 1979; Szalay 1999a). Real causes that affect, for example, the becoming of a single organism are demonstrated by the newly emerging "hybrid" fields (e.g., developmental genetics dealing with issues of evolutionary homology, often called "EvoDevo"). These disciplines show with increasing precision how inseparable functional explanations are, not only from history but also from adaptive existence. Mutations and their developmental consequences are inseparable from the context of a particular genotype. This is well beyond the occasionally agenda-laden and quasi-engineering concepts of function that eschew adaptations and adaptedness, such as the kind of functional conceptualization advocated by Cummins (1975), Amundson and Lauder (1994), and others.

Ontological Perspectives on Functional Biology and the Omission of "What Something Is For"

I am not critical of the epistemologically significant distinction found in practical research programs that pursue sundry important functional aims in the laboratory without immediate concern for field-related bioroles. But we are repeatedly reminded of the fact that the concept of function is understood very differently by many who consider themselves to be structuralists, functionalists, phylogenists, or adaptationists; a somewhat unfortunate, although often understandable, compartmentalization of what should be a theoretically cohesive whole.

In addition to the varied meanings of function, for example in the community of students who study musculoskeletal morphology, there are a variety of technical approaches that require novel conceptualizations. New approaches addressing questions on sundry levels and that apply equally to skeletons, bones, trabecular structure, and bone tissue types have been, and are being, developed. Such epistemological avenues rest on different assumptions from level to level, as researchers consider bone tissues, bones, and skeletons from different perspectives. Nevertheless, beyond the basic epistemological issue (namely that there are clear conceptual differences between mechanical functions and biological roles), there has been an increasing conceptual redefinition and narrowing, as well as confusion, concerning the theoretical meaning of functional studies. Theoretical positions have been taken by authors proposing various exclusive meanings for the concept of function. Whereas some of these positions are largely epistemological in nature, some have taken on the cloak of ontological propositions in claiming some special theoretical virtue for them.

For example, in a long series of papers going back two decades, Lauder (see Lauder 1981; Amundson and Lauder 1994; Lauder 1996; and references therein) advocated a rather narrow view of functional morphology that sought connections between the parsimony-based taxograms of "pure" systematists and a quasi-engineering type of functional analyses. These efforts either implicitly or explicitly eschewed connections to adaptation, and they were devoid of any input from a selectional (= Darwinian) perspective. In fact, in Amundson and Lauder (1994) the claim was made that adaptations are all but impossible to identify and therefore the search for the "why" of attributes (namely what selectional causes molded a feature) is doomed to failure. The justification for this narrow view of func-

tionalism (actually a form of structuralism, see later) is that they believed that the mechanical transformation of structures is what functional biology is about, without regard for the specific time-contextual roles of natural and sexual selection. Yet this theoretically restricted perspective did not prevent Amundson and Lauder (1994) from calling their conceptualization, inexplicably, “causal role function.”¹¹

This “causal role function” perspective (with its thinly disguised disdain and its rejection of the “less rigorous” research under “old adaptationism” aimed at uncovering adaptive functions; see Rose and Lauder 1996) is a direct outgrowth of the “cladogram first” research program (e.g., Eldredge and Cracraft 1980; Lauder 1981). This strictly conformist and fundamentally Kuhnian research program subjugates biological character analysis to taxic schemes of bifurcations and foregoes the necessary prerequisite of testing character transformations with the aid of methods derived from tested evolutionary theory (i.e., the phyletics of features). But any evolutionary scheme or theory is wanting and distorted without adaptation as part of the evolutionary process.¹² Ironically, such a pattern of cladogeny is just as unknowable in terms of certainty (particularly without phyletics, and not only because the concept of scientific corroboration of an ancestral stage is excluded from cladistic theory) as is the adaptive function jettisoned by Lauder and colleagues. In fact, there are gradational or incremental probabilities in the testing procedure (corroboration, verification, or rejection), often with a considerable overlap between both phylogenetic and adaptational hypotheses. It is such overlaps in the analysis that allow for the distinction between homologous and homoplasious similarities.

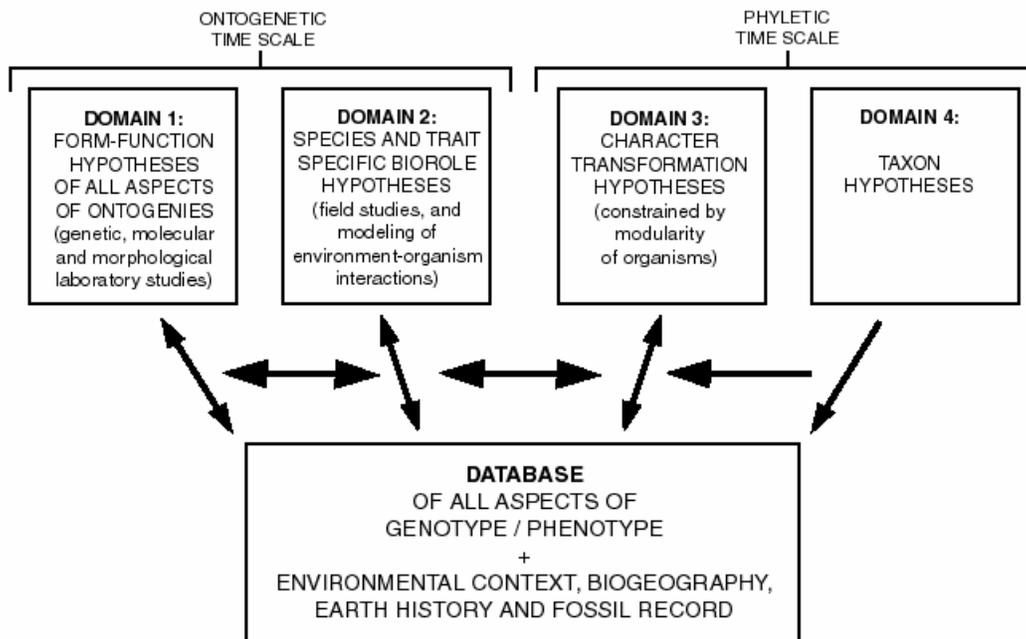
On theoretical grounds that seriously considers the role of developmental biology (particularly modularity) in the evolutionary process and the irrelevance of parsimony-based decision making for character transformation, I do not believe that an engineering analysis of taxa based on their position on taxograms is a meaningful approach to phylogeny estimation. This approach, which depends on a misplaced fealty to someone else’s cladogram (and to the parsimony paradigm) to explain evolutionary transformations, is flawed at its foundations by its circularity. Yet obviously functional, phyletic, and cladistic evaluations of distributional data must be an integral part of reliable phylogeny estimation. Both the establishment and the explanation of meaningful patterns (not just the structural and mechanical manifestations of shape) require some adaptationally-framed assessment to

contextualize polarity determination, as well as the stratigraphical and biogeographical contexts, all at a level that information and the applications of valid methods permit. This is an attempt to understand the phyletics of features. These strictures apply proportionately to the degree that any of these activities can be brought to bear on a research project. This, in turn, obviously depends on the nature of available evidence (including both deductive and inferential information). But the various levels of inference permitted by data and context do not alter the validity of a conceptual methodology derived both from descent and from natural and sexual selection in a specific space and time. To claim theoretical primacy for a phylogeny based on statistical sorting of structural patterns, combined with only a *sensu stricto* functional analysis which would transfer functional evolution into a non-Darwinian vacuum is not based on sound theory. It is a flawed conceptual method for attaining an understanding of “functional evolution” as its professed goal. The concluding remarks of Leroi et al. (1994, p. 398) regarding phylogenetics are significant in this context. “Such analyses will be all the more robust for lacking unsupported assumptions, unwarranted inferences, and untestable hypotheses about the history of evolutionary mechanisms.” It can be added that these linear analyses of nonlinear relationships are also not only sterile, but theoretically vacuous.

The theoretical stance of Amundson and Lauder (1994), in which they attempted to exile Darwinism from functional biology, is in essence a narrow functionalist (structuralist) exegesis of the early wave of zealotry of Anglophone cladistics that declared its total independence from evolutionary biology and claimed primacy for nested cladograms of taxa, taxograms, before all else. The additional claim for primacy for a pure mechanics-based view of function in biology also reflects a view that regards deduction from physical laws as superior to the inductive procedures necessary for historical explanations. Because a strong inductive component is required in all adaptational and historical assessments of patterns (see Bock, 1981; Szalay and Bock 1991), the connections of functional-adaptive analysis (including transformational analysis) to phylogenetics (see Figure 1) is usually unacceptable for doctrinaire cladists and “new adaptationists.” Although parsimony-based cladistics strives to recover history, it also aims for a completely deductive, Popperian methodology (openly admitted only by pattern cladism; see especially Schuh 2000).

The combined perspectives of parsimony-based cladistics and “causal role function” proto-

OUTLINE OF CONCEPTUAL RELATIONSHIPS BETWEEN CONNECTED DOMAINS OF RESEARCH DERIVED FROM AN EXPANDING DARWINIAN SYNTHESIS TO YIELD TESTED TRANSPECIFIC HISTORICAL EXPLANATIONS (I.e. PHYLOGENY)



Hypotheses of Domains 1-3 are tested against data they generate and against well-tested hypotheses of the other two domains. Hypotheses of Domain 4 are tested against all data and the tested hypotheses generated by the other domains. Because lineages (and taxa) are recognized based on research in Domains 1-3, data and tested hypotheses of these domains or transformation hypotheses are not tested against supraspecific taxon hypotheses of Domain 4. Species taxa are recognized based on field data (reproduction, ecology, behavior) and their genetic and phenotypic expressions. Supraspecific taxa are delineated monophyletically (recognizing both paraphyla and holophyla).

(Szalay, F.S. 1999; prepared by Warshaw, J.S.)

Figure 1. An interim schema for Darwinian phylogenetics. The directional arrows indicate the causal interdependency of the first three domains for both generating data and testing hypotheses. Note that, although the interrelationships for the first three domains are really "temporally looped," they are not circularly dependent on Domain 4, which is to be derived from them. The direction of arrows indicate the domains, databases, and tested hypotheses within these domains against which other hypotheses are tested.

cols that consider adaptational understanding unattainable are being made obsolete by many multidisciplinary efforts created from the fusion of genetic, morphological, developmental, ecological, and paleontological perspectives and practices, to mention only a few.¹³ The deduced engineering patterns in a "causal role function" approach, of course, can be superimposed onto, if not meaningfully interdigitated with, parsimony-based cladograms. Such practice of circularity is essentially similar to attempts at a "transformational analysis" that hope to procure evolutionary transformations from taxograms.¹⁴

So, in contradistinction to the paradigm of "causal role function" advocated by Amundson and Lauder (1994), such restrictive functional approaches lack a valid framework for evaluation without the ecological (adaptational) component, as vague as adaptive meaning may be in some instances. The pivotal role of contingency-based

evolutionary analysis means a contextually variable dependence on adaptation-related considerations. These are manifested (e.g., in vertebrate paleontology) mostly as structural patterns of aspects of skeletal remains.

I include here a relevant, albeit rhetorical, query. What does the comparative assessment of engineering parameters mean without any conceptual room left for the reasons for these differences? Whenever civil or aeronautical engineers plan the construction or analysis of structures, there is always a particular goal in mind. That goal is, properly, the Aristotelian final cause, namely "what something is for." This implicit factor is absolutely and fundamentally connected to any mechanically oriented enterprise, and if such an effort is separated from its context it loses not only its directives and limits but also its meaning. Unlike the "causal role function" protocols, Bock (1999), who also maintains a sharp divide between function and

adaptation epistemologically, makes the obvious connection between these efforts. In Bock's view, functional and adaptational or utilitarian analysis come under the same conceptual and theoretical heading; both are functional explanations.

It is hard to contemplate how a particular well-substantiated biorole (or one inferred with a lesser degree of probability than samples of direct observations provide), correlated with form-function, would not have played a major causal evolutionary role in the becoming of that complex, except in a strongly structuralist conceptualization of biodiversity. An increasingly narrow emphasis on engineering function can result in a peculiar evolutionary conceptualization, not to mention the problem of discordant semantics. Is such conceptualization really good theory? The fundamental insight of Lamarck, reworked within Darwinian theory, that the combined function and role of attributes is part of the causal interaction responsible for their evolution has been pursued by many biologists and philosophers; its theoretical consequences are not discussed here.¹⁵ In a definitional sense, at any moment in lineage history a form-function complex that exists is a set of initial conditions and the sundry causes that act on the organisms are, strictly speaking, the causes that mediate subsequent evolution (survival and resulting fitness differences). But it cannot be overlooked that the very phenotype-based activities of organisms generate a great deal of the specific causal forces acting on them, as has been repeatedly pointed out. The feedback loop is mutually dependent, and the understanding of the process fully justifies an expansion of the conceptual methodologies based on it. Epistemological advances follow such a theoretical stance.

But what about the specific research protocols that should rest on conceptual foundations different from those of engineers if the goal is an evolutionary understanding? Strictly functional explanations, although they may justify deductive issues dealing with features, are incomplete for species-specific phenotypic attributes. To recast and paraphrase Dobzhansky, they lack explanations for their species-specific, hence idiosyncratic, workings. The perspective criticized here, repeated for decades both by doctrinaire cladists, as well as by the pure "functionalists" such as Lauder and colleagues, is quite different from Bock's frequently taken stance (e.g., Bock 1988) that functional (*sensu stricto*) and ecological components of, for example, morphology, are independent and complimentary. Nevertheless, Bock does profess a belief that a sharp theoretical dichotomy regarding function and adaptations is the proper view and that the investiga-

tions of the latter should depend on the former.¹⁶ Bock's theoretical perspective appears to be tied to Mayr's (1961) claim regarding distinct proximal (which Bock called functional) and ultimate (which Bock called evolutionary) causes (which Bock more meaningfully called explanations). Bock (1999) maintained that functional morphology answers "how" questions, namely how things work. I, and others, obviously do not disagree. But the questions and problems of functional biology (*sensu lato*, the sense endorsed here for the theoretically most inclusive concept) arise from a much broader context than just structural statics and mechanics, or chemistry. Bock's own view on evolutionary explanations that these are responses to questions of "... why attributes of organisms came into being originally and have modified (= evolved) over historical time" (1999, p. 49), indicates, however, that a certain critical theoretical perspective is missing.

This quasi-artificial "functional" versus "evolutionary" theoretical dichotomy highlights a lack of formal recognition that in any evolutionary change the usual "why" question alone is not an adequate formulation of the nature of evolutionary explanations. Evolutionary functional explanations (*sensu lato*) have an ineluctable transformational component that render mechanical or role-related notions of function incomplete and therefore theoretically inadequate. In fact, any full evolutionary explanation that deals with specific lineages of organisms has, as its integral component, the issue that how something works, in light of what it is for. And therefore it is critically dependent on how a particular trait prevalent in a lineage came to be historically transformed and ontogenetically constructed that way. At first this may appear to be insignificant. But on second thought, it should be realized that contingent lineage-specific changes are not "merely what happened" (*contra* Bock 1999, p. 56). Such changes, the selectional guidance notwithstanding, were profoundly influenced or guided by preexisting stages (as they will have influenced subsequent changes). There is virtually universal agreement that these contexts (the heritage) guide both the nature of transformations as well as their adaptive "goodness," "latitude," and even built-in seeds of doom (in retrospect) or new opportunities of given lineages in given environmental or competitive contexts they will encounter.¹⁷ Realtime constraints (rooted in history) do not only constrain, but they direct and facilitate subsequent modifications.

Such conceptualization should have profound implications for methodologies that aim to decipher evolutionary history. For example, the literature on

the history of understanding the origin, transformation, and function of tribosphenic teeth of therian mammals and the resultant evolutionary patterns constrained by the genetic and occlusal dynamics of the original molar system supply some of the most numerous and persuasive examples of the meaning of constraint. Both the historical and the functional (occlusal and ecological) constraints profoundly affected morphology, function, and biological roles throughout phylogeny. Examples abound in virtually all systems of vertebrates, the skeleton being no exception.

Bock's (1988, p. 207) view that adaptational explanations are not evolutionary but functional, therefore, is also problematic, particularly because Bock (1999) continues to maintain the legitimacy of the theoretical independence of functional (proximate) and evolutionary (ultimate) explanations. Explanations of adaptations are in fact inseparably both; they are "temporally looped" rather than hierarchically and dependently related to form-function. While natural and sexual selection are law-like explanations, their consequences in lineages are also fundamentally historical and time-dependent processes that are never disembodied from the particular lineage histories (e.g., Szalay and Costello 1991). As Bock (1993) so aptly emphasized, natural selection is cause, mechanism, and process, depending on our use of and the context of the concept. The acquisition of new adaptations or a new form of adaptedness (both are processes) is a large component of evolutionary history, and much of phenotypic evolution, as most evolutionists suspect (and long championed by Bock), is fully Darwinian; it is causally propelled at the organism level (see also the organism-centered biosystemist approach of Mahner and Bunge 1997).

Ecomorphology (or any aspect of the phenotype related to bioroles) is conceptually very much a part of this endeavor to understand attributes because this field forms the context with its inseparable feedbacks into the strictly functional efforts in laboratories. The deductive base of these efforts does not make them superior or axiomatically antecedent to ecomorphology. Although Bock (1999) argued for the distinction of ecological morphology from functional morphology and the notion that the former is built on the latter, he nevertheless fully endorses the importance of adaptational analysis. This is in contrast to Lauder and colleagues (see Lauder 1990, 1996; Leroi et al., 1994), whose expressed futility regarding adaptations is more in service of "causal role function" than any theoretically and empirically tenable position in Darwinian theory. In spite of his stance, however, Bock (e.g.,

1977, 1981) applied what I believe to be a somewhat restrictive, more logic- than probability-based perspective when it comes to extinct organisms. Given good and complete specimens, specific adaptive strategies can be understood in fossil taxa with high confidence, because the judicious and phyletically contextual use of combined mechanical, adaptational, and ecological models of living organisms can render great certainty to this type of paleobiological analysis. This type of modeling through the use of carefully delineated aspects of living species can yield an important understanding for both adaptational and phylogenetic analysis (Szalay and Sargis, in press).

It bears repeating here that very often we can corroborate far better the adaptive strategies of well-known fossil species than their phylogenetic affinities. I suggest, therefore, that perhaps the construction of completely deductive, syllogism-like, ontological statements that are deduced from the logical consequences of otherwise clear empirical research-based definitional differences (such as the distinction between function and biorole) is not the most useful approach to theorizing in this area of evolutionary analysis. Such assertions carry well-corroborated definitional concepts to their logical extreme, but not necessarily to new, theoretical heights. Both the deductive and the purely epistemological limitations, as in the case of strict functionalist theory, are unjustified.

Let me also reiterate the obvious. First, the level at which adaptations and adaptedness may be ascertained in organisms is unequivocally the highest for living species observed in nature. But lest we forget, it is equally obvious that existing features in an organism may reflect causal correlations between these form-function complexes and the use they had in the past. In fact, the very logic of descent with adaptive modification demands that, given the temporal nature of the evolutionary process, it be understood clearly that the current attributes of organisms are the products of selectional forces acting on past generations. Activities at a given time (in the particular context of the existing environment) generate the selectional forces that either maintain or transform the frequencies of fit individuals with the appropriate phenotypic attributes. But this frequency-changing (or -maintaining) response regarding the adaptations is in the succeeding populations. This temporal relationship is critically important.

The only (probability-based) factor that is likely to assure successful programs in adaptational studies (those with high truth content) is based on the realistic assumption that the rate of environmental change is usually slow in relation to

generation time (certainly gradual or static, short of extraterrestrial impacts or violent local disturbances), or often approaches zero (in generational terms), resulting in stabilizing selection, often with a fully Darwinian progressive change for the same biological functions. What organisms do, therefore, in their currently observed environment is probably causally connected to their features.

In addition to the foregoing general theoretical point regarding the absolutist perspective on the study of adaptations in our own time, there are several other issues that have surfaced in regards to an exegesis of the logic of "current utility." The statement by Bock (1999, p. 55; and personal discussions regarding adaptational analysis in fossils) that the "[s]tudy of biological roles must be done by observations of the organism living naturally in its environment—they cannot be determined by observations made in the laboratory or other artificial conditions" is a case in point. No one would argue that for highly specific activities contained in the form-function features of living organisms information from the natural setting is critical. But we can counter that a host of highly relevant explanations about fossil taxa, using rigorously constructed models already alluded to, are equally justified, often approaching a high degree of probability at given levels comparable to those made about living organisms. In fossil mammals, based on this type of rigorous and relevant modeling, there are role-related attributes at these levels such as cursorial modifications, aquatic adaptations, digging adaptations, habitual hanging, obligate arboreality or terrestriality, and hosts of obligate dietary adaptations such as grazing, myrmecophagy, piscivory, and hypercarnivory, all on a level of generality that can be securely ascertained (Court 1994; Szalay 1994; Szalay and Lucas 1996; Szalay and Schrenk 1998; Szalay and Sargis, in press; and references therein). A particularly excellent example is Court's (1994) analysis of limb posture and gait in the primitive Eocene fossil proboscidean *Numidotherium*. Such modeling employs ecologically and functionally well-understood living species that cross size and higher taxon limits, thus providing a degree of adaptational assessment through the convergence method, which is not only highly reliable but which forms a critical link to other activities such as phylogenetic estimations (e.g., Szalay 1981; Szalay and Sargis, in press). As in any other methodology axiomatically derived from underlying tested theory, none of this is logically full proof but rather is probability-based.

Therefore, to consider the assessment of causal factors for the features that derive from the obligate activities of organisms to be a method in

ecological morphology that is applicable to living species only is unfortunate. It appears to be a monotonic logic-bound consequence that unnecessarily truncates adaptational analysis, which is always probability-based. It also unjustifiably narrows the valid epistemological limits of the testing of a tremendous range of issues in macroevolution. I emphasize again that adaptational assessment of well-known fossils is not any less dependent on probability judgements than is phylogeny estimation in general.

FUNCTION, ADAPTATION, AND PHYLOGENETIC ANALYSIS

In examining the problem of conflicting views about mechanical and adaptive functions and phylogenetics, I will not argue that some degree of functional knowledge in the broad sense is important for any causally meaningful understanding of character ordering and polarity to estimate evolutionary history. To me this is obvious. Taxograms based on parsimony analysis, as Mahner and Bunge (1997) called them, are only "pretheoretical classifications", with their studied emphasis on pretheoretical, not phylogenies. But in reading the literature related to functional analysis and its connection to phylogeny, it is also obvious, as alluded to previously, that even students who are deeply convinced that functional explanations must be somehow part of phylogenetic explanations have conflicting views on the very concepts of function: what is and what is not "scientific" in functional biology, and how functional studies bear on phylogenetic explanations.

There are usually obvious levels of resolution, both for adaptational and phylogenetic assessments, and these will vary according to the nature of available evidence. As I see it, there are, minimally, two important and related questions regarding the significance of adaptational analysis and its relationship to phylogenetics: How reliable and independent are functional, adaptational, and phylogenetic estimations, and can they be truly independent?; and how is phylogenetic analysis connected theoretically, and therefore methodologically, to functional biology (*sensu lato*)?

It is my position that the feedbacks in a rigorously comparative framework between form, function, adaptive appraisal, and phyletics of features (the temporally looped relationship noted previously) and the full consideration of the fossil record make for robust hypothesis testing. Employing holistic Darwinian explanations for character complexes is far more scientific, in a biological sense, than any Popperian, deep-time-deprived, and

structuralist pursuit of morphology by itself can be.¹⁸ With this combinatorial analysis of extant and fossil data and with a full immersion in the most current understanding of developmental biology (including developmental genetics), if the level of analysis demands or permits, homologies can be distinguished from homoplasies with confidence.

We may ask now, in what specific way is functional analysis conducive to phylogenetic estimation? I would first like to reject the theoretical position inherent in often-cited cover statements to the effect that an investigator “will consider function whenever it is useful beyond ‘character’ analysis” or “functional information is merely more grist for the mill” in the construction of ephemeral databases for parsimony analyses heading for “consensus,” as both of these positions are sometimes stated and implied (e.g., Simmons 1993; I will not expand the discussion here on the obvious that a science of evolutionary history that aims to distance itself from a causally meaningful testing of phylogenetic hypotheses is a greatly diminished one).

Quite simply, as originally outlined by Bock (1981), functional-adaptive analysis is character analysis aiming to establish the reliable homologies, be they synapomorphies or transformational homologies with highly corroborated directions and sequences, as distinct from homoplasies.¹⁹ This is fundamentally a Darwinian approach to phylogenetics, because it is a selection-related evaluation of features in an evolutionary context. In fact, the foundations of this view were clearly enunciated by Darwin.²⁰ Given the geological and geographical contexts and an understanding of developmental homologies, functional-adaptive analysis of fossils and living forms (the latter the designated models that are researched in detail; Szalay and Sargis, in press) can inform with often great confidence about homologous versus homoplasious features in the comparison of details of functioning complexes that perform an adaptive function.

As one example, in a recent study Szalay and Schrenk (1998) compared the living “edentate” and digging mammals (the xenarthran Cingulata and Myrmecophagidae, and the Pholidota), with fossil “edentates” such as palaeonodons and the Messel Eocene **Eurotamandua**. The numerous function-driven polarity determinations of this study of the enigmatic phylogenetic relationships involved a high-probability adaptive framework, specifically that the fossils were also myrmecophagous and had obvious digging adaptations, either to get at food or shelter. Going beyond the well-established similarities relating to the myrmecophagous and digging habitus, it was concluded, based on the

disparate form-function strategies in achieving that way of life, that the various clustered “synapomorphies” derived from parsimony analysis (most of these being previously poorly assessed adaptive or merely verbal “similarities”) of the living species of the American and Old World groups were not homologous by either structural or functional-adaptive criteria. Consequently, they are not indicative of ties between the palaeonodons and **Eurotamandua**, on one hand, and pangolins, on the other. The inferred adaptational background for the fossils and their structural-functional assessment in that light were fundamental in reaching these taxic conclusions. Homoplasies could be rejected prior to taxic analysis. Subsequently, corroborated phylogenetic trees fall out of such a character analysis.²¹ The Darwinian method is certainly not the straw man characterized by claims of cladists regarding functional-adaptive analysis (e.g., Schuh, 2000) that “only adaptive characters are used in phylogenetics” by Darwinians. In fact, it is the incidental and phyletically informed attributes in addition to the adaptive solutions that are sought to add to a data base as either shared and derived or transformationally revealing attributes.

The alternatives to a Darwinian analysis of morphological attributes particularly the cranioskeletal characters that vertebrate paleontologists rely on and that I am most familiar with, usually offer a method through which a mixed suite of similarities are subjected to parsimony procedures to sort out homoplasious and homologous similarities. The evolutionary vacuum (i.e., a lack of theoretical justification) within which, I believe, this method is practiced has been discussed elsewhere (Bock 1981; Szalay 1994). But beyond the general weakness is the complete elimination of the explicit research-based phyletics of the characters used. Phyletics, which includes both the ordering and polarization of characters, is conflated with taxic analysis, as often there is nothing beyond taxic sister-group arrangements that might give justifiable indications of a direction of transformations of non-identical (hence, not truly synapomorphous) traits. Stratocladistics also endorses a parsimony-driven cladistic approach but adds a stratigraphical dimension that improves the reliability of its taxograms (see Fisher 1994). It invariably appears that parsimony-based cladistics happens without attempts to independently test postulated synapomorphies.

The whole enterprise of phylogenetic estimation or analysis is a highly probabilistic one. If this is accepted—and I believe that it should be—there can be no theoretical objections to a procedure that is based on the guidelines provided by the mechanical and adaptational analysis of living and

fossil species and their specific aspects. Most important, adaptational assessment sets a framework for a character analysis that is also necessarily transformational, as we need to decide rationally (based on sound theory) the ancestral and derived conditions. Such character analysis permits the rejection of homoplasies and allows for ancestor-descendant or branching level-specific corroboration of homologies for taxic analysis, based on some biologically and paleontologically meaningful probability assessment. Taxon phylogenies fall out of such Darwinian analysis and render the former far more probable than an axiomatized and abiological parsimony search for the congruence of often atomized traits of various taxa.

ON THE ROLE OF TRANSFORMATIONAL ANALYSIS OF PROPERTIES, AND THE MEANING OF MOSAIC EVOLUTION IN PHYLOGENETIC ANALYSIS

Literal transformation is in the realtime of an individual organism only, its entire ontogeny; it is not what is meant by evolutionary transformation. "Universals" having to do with development, even the immensely deep homologies (orthologies) of hox-genes are contingency bound. They are therefore subject to historical understanding, not just to rules that consider some developmental attributes universal or to the methodology of parsimony algorithms. Darwinian phylogenetic analysis is a historical narrative method to attain contingency-based explanations, and it represents the combination of several research programs, not just morphological approaches. Darwinian phylogenetics addresses the issues of contingency and adaptation that cannot be isolated from one another when we seek to understand phylogenetic transformations of attributes and lineage reconstructions.

Spatio-temporal and functional factors surrounding morphology provide the grist for the mill of phyletics in character analysis. Both the phyletics and cladistics of taxa depend on these. Rapid advances in developmental genetics, the understanding of modularity in the developing organism, and a concerted use of functional and ecological biology, together with a fossil record, can play a critical part in this approach that has to be tailored both to the groups analyzed and the levels at which it is employed. However, "ultrafunctionalist" perspectives on adaptations (e.g., some gene-selectionist, sociobiological, explanations), in which cost-benefit evaluations and a lack of historical perspective dominate, are not concordant with Darwin's own history-guided understanding of adaptive evolution.²²

Transformational analysis, whether based solely or partly on the sequences offered by the fossil record, and morphological analysis based on functional-adaptive foundations are the cornerstones of phylogenetic analysis. Any and all theoretically meaningful contextual determinations of which trait is primitive and which is advanced involves some type of transformational assessment and should use a geographical and stratigraphical perspective when these are feasible. Sometimes very convincing stratigraphical distributions of abundant data dramatically demonstrate how attempts to shoehorn such evidence into the prescriptions of cladistic analysis distort a phylogeny when segments of lineages are forced into "terminal" species taxa to conform to cladistic practice. This was dramatically and painstakingly demonstrated by Redline (1997) in his rigorous stratigraphically controlled study of the largely Wasatchian (North American early Eocene) small mammal, the condylarth *Hyopsodus*. Such information (and astute analysis) is often rare at the population or taxonomic species levels, but the context of biostratigraphical information is critical, even if problems and analysis are at a higher level, removed from species taxa.

Beyond the best estimate of phylogenetic topology for the groups of organisms studied, an important goal of taxonomy (in keeping with Darwinian aims) is to strive for properly demarcated, monophyletic taxa diagnosed by apomorphies of their stems with the clear understanding that the base delineation must depend on both the availability of information and some heuristically meaningful sense. The unsuitability of the Linnean system for evolutionary depictions, created at a time when non-evolutionary and atemporal sorting was the aim of taxonomy, has been often discussed in spite of its suitability for punctuationism and taxogram views of evolution. The continuity of evolutionary lineages and the inability of the Linnean system to deal with time make taxic analysis of phylogeny flawed from its very inception (but for some recurrent suggestions for fossils see Redline 1997). In taxic analysis, taxa are considered the starting point for both the phylogeny of the taxa themselves and, subsequently, for the understanding the polarity of traits. This is a fundamental tenet of most parsimony-based cladistics. Nearly invariably, these views are tied to an ontological conception of species (which are in reality species taxa) through time. Ontologically a species in a moment of time is a segment of its lineage, and only extant representatives are unequivocally terminal, although undoubtedly millions of lineages became extinct. Nevertheless, those practicing taxic analy-

sis base their ideas of a species taxon on the conception that species and other taxa are "individuals".²³ These same systematists also often oppose the transformational analysis of taxonomic properties in systematics and argue for the decoupling of phylogenetic analysis from evolutionary theory (e.g., Rieppel 1993). The result is an advocacy of methods based on a structuralist theory of evolutionary transformation that is wedded to and derived from the practical procedures of delineating species and other taxa. Such efforts invariably yield theories that selectively mix the conceptual foundations of tested evolutionary dynamics with epistemic criteria and notions derived from the latter. Consequently, such theories are simply epistemic, without ontological foundations and provide inadequate conceptual methods for character analysis.

Systematists who reject transformational analysis also usually adhere to the notion that there is something causally and processually distinct in the origin of a new lineage (speciation) and its perseverance from anagenetic (= phyletic) evolutionary change itself.²⁴ They realize that transformational analysis poses a core disagreement with the tenets of hierarchic punctationism, a fundamentally taxic (and speciational) view of evolution. Yet such a disagreement is minor. The conceptual step needed to acknowledge is that the real history of lineage continuity and splitting appears jagged due to extinction and the missing fossils of the variably evolving lineages. Only unwarranted assumptions about species (lineages) and the artificial gaps in the fossil record permit a fully taxic view of the evolutionary process. Punctationists and cladism-based taxonomic theorists have had a long history of sidestepping the issue of transformation, but their real problem is with the concept of anagenetic change in lineages.²⁵ Anagenetic transformation is an obvious impediment for those who want to have a causal macroevolutionary evolutionary theory in which taxa, the "individuals," do the evolving. Populations and species evolve, lineages are their record, and there are no theoretically meaningful boundaries in time-successive real-time populations/species to satisfy taxonomic conventions. Delineations of time-successive species taxa are necessary, but they do not, by themselves, inform about the nature of the evolutionary process itself in undivided lineages. As a result of this theoretical conflict, an expanding Synthesis stands in the way of taxic and hierarchic punctationists who want to weave another evolutionary theory from taxic operationalism (Szalay 1999a).

Linked attacks on the phenomenon of mosaic evolution, a genuine pattern description, as a

"hoary old concept" in order to drive arguments against the straw man of transformationism in systematics are unfortunate. Such views are particularly surprising in light of the increasing evidence from developmental biology that modularity (and the often striking independence of the modules within the same organism) is very probable.²⁶ It is a mistake to believe that natural selection cannot favor individuals that retain some attributes that continue to interact with selection in an unchanged manner while these same individuals have new characters that fulfill other aspects of their adaptability. Any argument against the phenomenon of mosaic evolution not only betrays too much reliance on outdated concepts of epistasis, but it also misses fundamentally pattern-based observations about taxa.

Adherents of parsimony-based cladistics or punctationism, whether they are against transformational analysis or against the observationally based concept of mosaic evolution, often inadvertently reject some of the great advances of both Darwinian evolutionism and the Modern Synthesis, yet they also strive at the same time to accommodate the centrality of adaptation. The facts that functionally and adaptively highly-correlated attributes of one character complex may have remained stagnant (e.g., due to stabilizing selection), whereas others have evolved in various directions (even in populations of the same species), attest to the differential adaptability of different lineages. Students of speciose groups of vertebrates know well that, although some attributes are species-specific, other complexes can remain virtually identical at higher taxonomic levels. It has been repeatedly corroborated that aspects of taxa evolve at different rates (Simpson 1953). It has also been noted that often chronologically older adaptations contain the structural and functional limits needed for new behaviors, and therefore these older complexes do not evolve significantly for long periods of time. Equally prevalent are some well-established structural adaptations that simply channel the relevant functions associated with newer roles.

As examples of mosaic patterns, the attainment of functionally well-honed stages in the metapodials (as well as the carpals and tarsals) of different genera of perissodactyls, artiodactyls, or the universal modification of the first phalanx of the first ray of the foot of all bats to be approximately 1.5 times longer than the equivalent units lateral to it (probably for an ancestral tail-hook landing technique connected with the attainment of flight; see Szalay and Lucas 1993) did not prevent a riot of cranial and dental, and a plethora of other evolu-

tionary differentiation within these groups. How could we contemplate the recovery of phylogeny if it were not for the persistence of homologous similarities of varying antiquity?²⁷ Highly and causally corroborated correlations of homologies and synapomorphies in different lineages attest to the fact that the phenomenon of mosaic evolution is a cornerstone of an independent transformational analysis of traits, in contradistinction to taxon-driven, and most often parsimony-driven, "transformational" analysis. Whatever the rate of evolution of such events, hundreds of examples may be cited from the patterns of vertebrate taxic diversity.²⁸ Even episodic changes are gradual because gradualism in the Darwinian sense is rate-independent (see Simpson 1953).

Taxonomy reflects the painstaking and only partially recovered evidence of evolving lineages and their diversity at any time. It is a result of efforts to construct meaningful taxonomic species and somehow express their relationships in higher monophyletic taxa in order to gauge organic diversity and to provide the necessary heuristics for the study of the history of life. Fossil-species taxa are not reliable equivalents of modern species, which can be delineated by their reproductive discontinuity in contrast to other species. They are certainly not all "terminal taxa." Rather, fossil species are estimates devised by trained taxonomists and based on selected models of extant species that have been well studied regarding their geographical distributions, attributes, and sometimes genetics, as well as the various forms of intergradations of their populations (Jolly 1993; Szalay 1993; various papers in Kimbel and Martin 1993). These fossil species taxa are certainly not all new lineages but many undoubtedly represent lineage segments, as all taxonomic species do. This notion of taxonomic species also applies to living-species taxa that often incorporate samples of precedent populations of varying antiquity.

CONCLUSIONS AND SUMMARY

As recently stated by Gingerich and Uhen (1998, p. 3), "Evolution is first and foremost a history of ancestors and their sometimes-divergent descendants." This is a Darwinian generality that has profound consequences for estimating the evolutionary history of all organisms, but one that is often ignored by systematists who practice a taxogram approach.

The obvious question is, what are the guidelines or parameters that circumscribe and inform transformational or polarity determinations of characters and the relationship of taxa beyond a some-

times compelling fossil record of successive fossils samples of the same kinds of organisms? As briefly outline in this paper, the Darwinian context of lineage transformation sets the boundaries within which the contingent attributes of different lineages at all time levels, or stages of the same lineages, may be recognized and weighted as being either more probably homologous or homoplasious. Practitioners of mathematical linearity as a substitute for biological and paleontological analysis - and who, as a rule, do not order and polarize the characters they use without algorithms - eschew the need for a conceptually interdisciplinary and Darwinian context for character analysis. Parsimony-based cladists customarily rely on diverse databases without any causal input into the selection of these traits and employ algorithm-driven congruence to order and polarize characters. They claim to follow such linear practices in order to fulfill the need for notions of "consistency" and 'scientific' (= Popperian) respectability for the testing of what is in fact a highly idiosyncratic and mosaic manifestation of lineage choreographies of evolving species and speciation events, phenomena that do not correspond with paleontological species taxa. They hold, for all intents and purposes, that a tested disembodied "genealogy" of taxa can be attained without an understanding of the factors responsible for the properties of organisms.

The following major points are a brief summary of some aspects of these issues, which are discussed in the body of the paper in some detail.

1. What phylogeny (but not classification) is has bearing on how we should try to recover it. Descent with ancestrally constrained (but also facilitated) adaptive (and other) modifications, largely through natural and sexual selection, contains a host of post-Darwinian advances in evolutionary biology that relate to this fundamentally Darwinian view of the evolutionary process. This complex array of precepts is both the theoretical foundation of a Darwinian phylogenetic analysis and the basis for any comprehensive theory of function (in a broad sense) and structure. Meaningful functional (in a full Darwinian sense) and phylogenetically oriented biology is the study of the results of selection and other attributes, and of the process of their acquisition.
2. Fundamentally structuralist approaches consider the goals of adaptational and other evolutionary analysis to be unattainable for fossils and extant organisms. Yet adaptations or sexual-selection-related paraphernalia in extinct

species are often better understood than their phylogeny. Such attributes may form the framework of an analysis. A functional and adaptational (ecologically utilitarian) assessment of traits in both extant and extinct organisms (whenever possible) is necessary in order to reliably establish polarities of homologous features. Such practice enables students of phylogeny to cull convergent attributes from a body of characteristic features. The Darwinian method, contrary to misconstrued characterizations that it permits only the use of adaptive characters in phylogenetics (e.g., Schuh 2000), informs of the incidental and phyletically relevant attributes in assessing the adaptive solutions. The homologously shared and derived, or transformationally homologous, features so obtained are the taxonomic properties against which lineage and taxon phylogeny hypotheses may be tested.

3. A Darwinian evolutionary explanation involves both the causal and historically mediated components of a particular transformation, an evolutionary becoming. Its macrotaxonomic expression is constrained by heuristics, which are not directly relevant to phylogenetics. A sharp divide between functional and evolutionary explanations, distinction are more practice-based than theory-based. These should be replaced by a less dichotomous, less hierarchic, and far more interrelated or "temporally looped" set of theories and concepts regarding the relationship between the evolution of function and biorole of features. Functional analysis (broad, Darwinian sense) and the biostratigraphical record are the valid bases of transformational analysis of organismal attributes in phylogenetics (Bock 1981). The results of the transformational analyses of features and the subsequent understanding of the relationships of lineages, independent of parsimony taxograms, are prerequisites for a meaningfully tested taxon phylogeny. Both adaptational and phylogenetic analyses are inferential about specific events in the past. Mapping the results of the "causal role function" approach of Lauder and colleagues onto taxograms, a structuralist perspective that is now labeled by its practitioners as the "new adaptationism," does not advance the cause of phylogenetic reconstruction.
4. In spite of the obvious data-based limits of the past that were previously noted, there is no reason to reject either specific historical narra-

tive explanations or their rigorous tests dealing with adaptations or phylogenetic estimates of character transformations. These activities are the core of comparative biology and macroevolutionary science, and the testing of phylogenetic hypotheses of lineages and taxa fundamentally relies on them (Figure 1). Organisms are adapted (= "fit," in a fully Darwinian sense) and an understanding of selection-produced attributes (e.g., mechanical adaptations or dimorphisms) can have a significant influence on choosing features against which phylogenetic estimates can be tested. Thus, functional understanding is essential in any estimation of phylogeny. Model-based analysis of attributes of selected extant species is a cornerstone of this activity.

5. Taxograms, bereft of specific taxic derivation (origins), do not reflect the lineage-based reality of phylogenetics. Axiomatized attempts to reflect the history of organisms as taxograms, node-based holophyla, without paraphyla is an illusory practice. It is contradicted by the continuity of all lineages in the evolutionary process, and the necessity to make arbitrary demarcations when delineating taxa.

In closing, I note that the attempt at the expurgation of the fully Darwinian (= adaptive) context of evolutionary change from both conceptual and operational methods has been largely driven by a belief that analysis of patterns independent of tested evolutionary theory will yield a theory of evolution of such generality, and that this theory will replace an expanding Modern Synthesis (see Eldredge and Cracraft, 1980; Grande and Rieppel, 1994; Rieppel and Grande 1994). Beyond claims that Darwin has been reinvented (Eldredge 1995; and in this process, not coincidentally, omitted from phylogenetics) and the rise of a hardened taxic paradigm of parsimony-based cladistics, nothing of the sort has materialized thus far.

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profile evolutionary systematists in the past have not followed rigorously a methodology that is inherent in Darwinian precepts of adaptive evolution.

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NOTES

1. See, for example, Schuh's (2000) textbook on cladistics.

2. In a theoretically rigorous sense Szalay and Sargis (in press) see bone tissues and skeletal structures as a complex expression of the genome that reflects the interaction of ancient phylogenetic history as well as its real-time environment. Both tissues and whole bones are primarily entities with attributes also strongly channeled by developmental (ontogenetic) history. Growth rates and other organizational parameters in the genome, coupled with the level of homeostasis, endocrinology, and loading due to activity patterns and size, become the final arbiters of both bone shape and microstructural tissue attributes. Ancient gene homologies reflect the expression along a range of these gene-environment factors. All genetically mediated aspects of this organization are guided by ecology (selection) through geological time. A holistic understanding of the specifics of such systems is one of the least trivial aspects of the science of form.

3. Much of the systematic literature of the last decade has focused on the categorization of abstract models of phylogenetic-cum-taxon patterns. The terminology to describe the various axiomatized taxonomic patterns of taxograms and an ongoing redefinition of these concepts (e.g., DeQueiroz 1992, 1994; DeQueiroz and Gauthier 1990, 1992; Rowe and Gauthier 1992; Sereno 1999) has reached a state of rococo confusion, as is evident from Sereno's (1999) instructive review and his tabulated list of definitions (although he continues to add to this list). In addition to definitions, the specter of a straw man of the essentialistic perspective was also raised and misunderstood by DeQueiroz (1994) in order to justify this curious debate of abstractions. It is ironic, therefore, that after the extensive and sometimes surreal literature it should become obvious again that taxonomic expression without heuristics is an activity that creates confusion and does not serve the larger community (Szalay 1999b). As Sereno (1999, p. 350) concludes, "Survivorship, diversity, morphology, and tradition are heuristic criteria for placement of node-stem triplets." The issue of "stems" as real evolutionary units (and therefore potentially real taxa if we knew of them and they were given taxonomic expression) is a complex one that has relevance for the monotonic notion of "unreality" of paraphyla. Novacek (1996, p. 340) is not alone when he notes that paraphyletic taxa "are not credible biological entities." What this means, of course, is that based on a chosen (and deeply flawed) taxonomic ontology regarding ancestral biological entities, the real stems of various groups should be axiomatically barred from taxonomic recognition. The best estimates of such stems are often genera in the fossil record.

4. The conceptual roots of modern phylogenetics, the combination of descent and adaptive modification, are fully Darwinian. They have not been derived from the theoretically reformulated and somewhat truncated, more recent versions advocated by Remane and Hen-

nig, contrary to suggestions by Haszprunar (1998). This does not mean that Hennig's contribution has been unimportant to modern phylogeny estimation. It should be obvious to anyone reading Hennig that he was interested only in using synapomorphies that were biologically convincing to him. The notion of having an algorithm decide the fate of similarities as being either homologies or homoplasies is a post-Hennigian invention based on the methods developed by the school of phenetics.

5. For all practical purposes the realtime (not to be confused with the meaning of real time) of individual organisms is the length of their life. In neontological practice, however, realtime also stands for a short stretch of population and species duration. So realtime is the frame of duration for a) either the living organisms that are subjected to the causes that shape an evolving entity such as a population or species to which the organisms belong, or b) for the species-populations, the "instantaneous" segments that are doing the evolving compared to antecedents stages. The concept of realtime for specific populations and species, of course, can rapidly become both a theoretical and empirical greased pig (Szalay 1999a).

6. I believe that this was a red herring, as no one I know thinks of preadaptations as teleological. A similar characterization of adaptationism is often employed in discussions of "causal role functions," namely that an adaptationist perspective is somehow "teleological."

7. The whole issue of a variety of straw-man perspectives on adaptationism cannot be commented on here in any meaningful way. This topic has been pursued using some of the most absurd argumentation, substituting monotonic (and, to some, convincing) argumentation. For example, Lewontin (1978), one of the most vocal critics of "adaptationism" (as defined by him) of the past several decades, has even been quoted as one of the champions of Darwinian sobriety! Novacek (1996, p. 314), walking the tightrope of "balance", notes that "[I]ndeed, Lewontin (1978) and Gould and Lewontin (1979) have argued that functional morphology *flirts with the untestable*; an adaptive explanation that fails is often substituted with another explanation rather than rejecting the basic premise that the system under observations demands explanation" (emphasis added). This is interesting because, when a phylogenetic hypothesis is proven untenable, Novacek or any of us certainly do not abandon the premise that phylogeny did occur, but rather we go on to find one that fits the available information better. But more to the point are Lewontin's (1978) statements that "if ecological niches can be specified only by the organisms that occupy them, evolution cannot be described as a process of adaptation because all organisms are already adapted" (p. 215) and that "[a]daptations are not necessary conditions of the existence of the species..." These notions are capped with the observations that although the fur of polar bears is an adaptation (because otherwise they would freeze to death), the adaptive meaning of its white color is questionable. I simply note that if ptarmigans, snowshoe

hares, arctic geese, and polar bears have white color as a property, then this coloration is far more plausibly an adaptively essential camouflage than a "just-so story," as it is asserted to be. This is an overwhelmingly probabilistic and corroborative testing of a proposition, deduced from the most basic ecological theory of competition enunciated by Darwin. Although without a doubt not all the specifics of evolutionary change are adaptive in the history of life, that does not mean that the process is not fundamentally selection-mediated. In fact monotonic logic (and agendas), as the literature and quotations here suggest, are part of an effort to underplay the core role of Darwinian selection in the evolutionary process. These are the major underpinnings of the celebrated attacks on the straw man of "adaptationism" by Gould and Lewontin (1979).

8. Mahner and Bunge (1997) have a problem considering events in ontogeny as causal. I prefer to consider all events in the realtime of an organism genuinely causal. Events in ontogeny have consequences well beyond the unfolding of the genetic blueprint or the heritage of the zygote.

9. The resultants of past causes simply manifest themselves as the constraints that will guide the unfolding of the zygote, with its cellular contents, context, and included genotype, in the epigenetics of development or even in an individual's "culture" (nongenetic transmitted predilections among organisms) in realtime. In some ways the genotype and its zygote-based context represent the distillation of the past evolutionary history of an organism, and therefore the causes in the history of lineages are inseparable from real constraints that are parts of the initial and boundary conditions for any organism in its realtime. So "ultimate" causes as such are part of the admittedly difficult conceptual area of constraints and are not real causes. There are, therefore, only proximal and more distal causes that affect the individual organism during its life history in its realtime existence, and these have evolutionary consequences for its population or species.

10. Ultrastructuralists who hope for a universal science of form miss, I believe, the full meaning of phylogeny. The descent of differentially successful ontogenies should indicate that because of the differences, and not because of their universality, ontogenies succeed differentially through time. The historical and adaptive processes that Goodwin (1994, for example) tries to marginalize are an obvious threat to any neo-Platonic universality that he attempts to deduce from the complexity of the structural transformation of embryos. The commonality of patterns and processes of organization are not transcendental truths but the footprints of a phylogeny. For another extreme structuralist perspective by someone who, in addition, considers Darwinism a reprehensible theory, see Salthe (1989, 1993).

11. In the significantly titled "Post-Spandrel Adaptationism" by Rose and Lauder (1996) and the introduction to their edited volume on adaptation, which strongly reflects their particular perspective on phylogeny (and

very little on adaptation), these authors speak of the "rise" and subsequent impetus of cladistics and the "new adaptationism." While they and others speak of "rigor" regarding interspecific comparisons (e.g., Harvey and Pagel 1991), they omit critical theoretical issues. They overlook the fundamental importance of an ancestral condition-centered phylogenetic tree for all valid non-independence methods (cf. McMahon 1999), such as those concerned with analyzing adaptations with statistics in multiple lineages. The output of parsimony cladistics devoid of causally meaningful ancestral reconstruction is not amenable to such efforts.

12. The structuralist bias of Lauder (1982, p. 57) is well reflected in one of his early contributions: "The synthesis of a structural/phylogenetic approach to historical morphology with the analysis of extrinsic limits to form may provide the level of resolution needed to generate testable mechanistic hypotheses regarding the distribution of extant organismal forms in the hyperspace of possible morphologies." The adaptational vacuum is evident, the functional prescription is non-Darwinian, and the theoretical position is totally concordant with the paradigm of taxogram-generated cladistics.

13. "Multidisciplinary" merely means that previously the components of a research program represented distinct disciplines.

14. Unfortunate and inappropriate uses of monotonic logic are Gaffney's (1979) and Wyss and Flynn's (1993) stances on character transformation. Their representative views reflect the taxic perspective on a caricature of "character transformation." This taxic practice attempts to render illegitimate the cornerstone of evolutionary understanding, namely comparative analyses of homologous character complexes in their own adaptive context. Parsimony-based cladists who do not order and polarize their characters, consider character transformations merely corollaries of taxon-phylogeny hypotheses. Such efforts, in light of the modularity of functional complexes in organisms, are particularly egregious even when functionally well-understood complexes are "mapped" onto a previously generated taxogram for a different region of the organism. For example, even if a cladogram of cranial and dental characters were true, superimposing postcranial traits on it does not necessarily render the transformational history of that mapped complex meaningful. The demands on and consequences of selection are different for different aspects of organisms (see later). In using monotonic logic instead of biological sleuthing, a taxic perspective also implies that the evolution of all character in lineages is bound up in the concerted, orchestrated, and magical origin of species taxa through speciation. Punctuationalism, even if many cladists profess disdain for any evolutionary theorizing, is obviously implicated here.

15. The philosophical literature on that one topic alone is enormous. Most of it is marred by a syllogistic presentation of issues about trait, function, and organism and the omission of the time-sequential nature of the workings of selection. As a consequence, there is the lack of

realization of the shifting base of what the features and roles are from generation to generation; or a customary lack of consideration of selectionally mediated, directional, form-function changes for the same biological roles that are the core of Darwinian progress.

16. Bock (e.g., 1999) eschews the assessment of adaptations without previous mechanical analysis and, therefore, implicitly rejects the proven value of correlating carefully selected variables in morphology with shared bioroles and ecological factors. That is unfortunate because the latter is the powerfully predictive convergence method. For example, detailed biometric comparisons of osteological parameters of diversely adapted and unrelated species will often result in highly instructive clusters of both divergent and convergent complexes that can be strong indications of similar adaptations, and/or multiple solutions for similar roles (e.g., Stafford 1999). Numerous carefully selected comparisons based on massive samples and carefully derived indices result in valuable correlations that are often proved to be causal regarding certain bioroles. Such correlational statistical studies often pave the way for more focused functional analyses. In general, attempted theoretical cubbyholing of dynamically inseparable evolutionary issues that grow out of search for increasingly complete explanations are doomed to be reconstituted.

17. Studies such as Benton (1987), Hulley et al. (1988), Masters and Rayner (1993), Rayner and Masters (1995), and Walter (1988), for example, suggest or assert that the Darwinian imperatives of ecological competition are somehow not reflected in "objective" analyses of the fossil record or community structure and that variance-shifted punctuated trends (Vrba 1980; Gould 1988) are substitutes for most explanations of evolutionary progress driven by directional selection. Like many such studies, these attempt to marginalize the critical importance of Darwinian selectional dynamics in evolutionary explanations. Not a few of such contributions are strongly driven either by political ideology or social dynamics, or by a combination of both (see a review of the role of paleontology in macroevolutionary dynamics in Szalay 1999a). The geneticist Hurst (1998, p. 50-51) noted regarding a number of books (by M. Behe, S. Kauffman, S. J. Gould, B. Goodwin, N. Eldredge, and S. Rose) that: "[a]lthough anti-selectionists often have little in common (except a preference for seeing selection downgraded in the public imagination), I have noticed one strange regularity. They all belong to what I shall call the 'c' club. Entry to this club requires a member to adopt a word beginning with 'c' with which to attack selectionists, if only by obfuscation. Evolution is constrained, chaotic, catastrophic, contingent, or complex (irreducible or otherwise). My main problem with these books is that the ratio of assertion to fact is too high ... Worse still, assertions are often sold as facts with the merest peppering of anecdote to support them ... Gould's use of the word 'constraint' and 'contingency' have, for example, left a mess of confusion that has generated a sterile mini-industry in semantics to clean up after him. Of course it would be wrong to suggest that evolution is all sorted out

and that selection is everything. I don't think anyone believes this, although the anti-selectionists usually see it as necessary to construct a false target to attack."

18. The recent book by Gee (1999), senior editor of **Nature**, is an example of a popular version of the taxogram approach to phylogenetic estimation that is devoid of the paleontological method and character analysis. In stating, for example, that: "[w]hat we need is an antidote to the historical approach to the history of life—and kind of 'anti-history' that recognizes the special properties of Deep Time" (p. 5), Gee reached the zenith of a movement that fully embraced Popper and subsequently denied that induction exists or that it is important. In his railing against the comprehensibility of deep time and paraphrasing the often-implied spirit of some of S. J. Gould's writings, specifically that trends and their Darwinian progressive explanation in the fossil record are really "... misleading tales ... part of popular iconography ..." (p. 5) Gee provided insight into the irrational physics-envy of a large part of the systematic community. This book, praised only by a few paleontologists, is really not about the scientific significance of the geological and paleontological record, in spite of its paleontological pretensions. The smugness of the half-truths and rhetoric of this book is permitted by the overwhelming disregard by the author for the connections of evolutionary theory to taxonomic practice, a Kuhnian team perspective that has been rigorously enforced by the cladistic movement of the past several decades. More specifically, the assumption that theories about evolution should be based on the taxic perceptions of taxonomists has supplied a hollow authoritative tone that is based on the pattern-process paradigm. Gee's claims that deep-time, historical narratives ("evolutionary narratives," as he called them, but in the pejorative tradition of spandrelism) are all either incomprehensible or human-biased (i.e., nonscientific). He asserts that all should adopt the parsimony-based cladist's perspective of merely seeing patterns rather than what he considers the unknowable evolutionary process responsible for these patterns. Gee's book is a telling exemplar in what can happen to theory and practice in paleontology in the hands of Popperian systematists.

19. I disagree with Galis (1996, p. 124) that transformational analysis is "a new approach in functional morphology." Furthermore, her example of bat relationships regarding micro- and macrobats is fundamentally flawed for the simple reason that the skeletal morphology is not considered with any kind of functional and phylogenetic understanding. Galis's treatment is similar to Pettigrew's original suggestion, in a series of papers (e.g., 1986), that the two groups are "independently" bats. Galis's theoretical approach mirrors the "causal role function" perspective of Lauder and others, omitting a historically constrained adaptational analysis from her theoretical prescriptions.

20. "We may err in this respect in regard to single points of structure, but when several characters, let them be ever so trifling, occur together throughout a large group of *beings having different habits*, we may feel

almost sure, on the theory of descent, that these characters have been inherited from a common ancestor. "(Darwin 1859, p. 426; emphasis added). Note the decisive reference, the ecological context, included in this statement by Darwin. It is not merely the sharing of characters, but the ruling out of convergence due to divergent habits, which makes such correlated and aggregated characters (to paraphrase Darwin) genuine traits of common unique heritage (i.e., synapomorphies) in different taxa. The opposite but ancillary rule of this tenet, the convergence method, is that shared characters (but not whole complexes or major attributes) of animals correlated with similar activities or habit (*habitus*) should be suspected as convergent. Functional-adaptive explanations of phenotypic strategies are the key to analyzing what the similarities and differences mean in terms of the phylogeny/adaptation continuum in a real ecological context (one that is model-based in paleontology). So the solution of this dilemma is the consideration of the adaptive context prior to choosing phylogenetically meaningful attributes. Whereas Darwin understood that the meaning of phylogenetically significant attributes is hidden in an adaptive package that has to be unwrapped with the aid of sound methods derived from evolutionary theory, too many other systematists who followed, most recently parsimony-based cladists, failed to consider this theoretical stricture.

21. Conceptual methods should fall out of tested theory. Workers advocating a taxic version of the evolutionary dynamic (perhaps the handle "taxism" is not entirely out of place for that perspective) conveniently ignore this general dictum, namely that the valid methods of phylogenetic analysis of taxa should fall out of the underlying tested mechanisms of the evolutionary dynamic (populational, developmental, and functional) and not out of its shifting taxonomic perceptions.

22. "Historical" explanations in sociobiology tend to be patently ahistorical, and therefore flawed (see the critique in Szalay and Costello 1991).

23. I do not accept the notion that taxic individuality is the proper and decoupled way of looking at evolutionary dynamics, as characterized in doctrinaire cladism and hierarchic punctuationism (Szalay 1999a, 1999b; see also Mahner and Bunge 1997, and their total rejection of bionominalism; and Bock's in press detailed rebuttal of Ghiselin 1997). The "essentialistic class" versus "individual" dichotomy applied to the phenomena of life is an outdated, originally ancient Greek, metaphysics that was simply not applicable after 1859, in spite of Ghiselin's (1997) brilliant but quixotic effort. The discovery of variational evolution by Darwin and Wallace has changed the nature of a valid metaphysical perception of the world, particularly of species and other aggregate biological phenomena. Evolutionary units are not individuals.

24. Speciation certainly results in a new and eventually genetically isolated lineage, a significant major event in diversity and overall phylogenetic pattern, but this mode of the evolutionary dynamics is a consequence of anagenetic change and (usually) isolation, and not a

causally different aspect of "new species" (Szalay 1999a).

25. A recent instructive example regarding this theoretical effort is Nixon and Wheeler's (1992) view of the ontology of "species." Without discussing their thesis (see Szalay 1999a), they stated that "Finally, from the standpoint of phylogenetic species concept, character transformations always produce new species, so *anagenesis cannot occur within species ...*" (p. 136; emphasis added). This interesting attempt to equate taxonomy with evolutionary theory is merely one example of the nature of contributions in which the wedding of punctuated chunks and invariant taxa supply the "objective" patterns of the history of life and a distorted view of evolutionary ontology.

26. Recent work on the nature of functional integration, because this involves both modularity as well as heterochrony, at least in the skeletal system (Raff 1996; Smith 1996, 1997; Nunn and Smith 1998; and references therein), strongly support older ideas that parts of bodies are modularly controlled by both the developmental system and the evolutionary process itself.

27. I am not aware of any evidence that humans were other than bipedal for at least the last two (and probably three or more) million years, yet our thorax and shoulder and elbow joints are not significantly different from a brachiating knuckle-walking ancestor that obviously predated the one we probably descended from. So, our upper body is a mosaic compared to the quite thoroughly and more recently reconstructed pelvic limb; it is an area rich in homologies connecting us with the great apes. Subsequent to bipedality in hominids, the pelvic limb did not change significantly for at least the past million and half years (or more). In spite of such modular stasis, many other changes did occur in sundry segments and various evolutionary units (populations) of our lineage. Taxic reconstructions of hominid phylogeny would have up to 12-15 taxonomic species implying speciation events and closed lineages. Yet the corroboration of more than two (or possibly three) bushy lineages through lithosympatry does not exist. Hominids are a perfect and high-profile example of the failure of cladistic, OTU-driven (i.e., operational taxonomic unit-driven) attempts at the reconstruction of evolutionary history. The species-level misapplication of the taxogram paradigm gives a distorted history, in contrast to a reasonable stratigraphical control, a fossil record, and meaningfully chosen extant models that set the limits of evolutionary understanding. Ongoing and repeated arm waving not only about how speciose the family was, but also by implications about how many independent lineages came to be during hominid evolution have repeatedly failed to demonstrate the synchronous co-occurrence of acceptable species-level lineages other than the robust and gracile hominids.

28. Carroll's (1997, p. 2) attribution of the notion of "constancy of evolutionary patterns" to Darwin, based on Darwin's single figure in the *Origins*, is both inaccurate and sells short Darwin's complex conceptualization of

the evolutionary process. It, unfortunately and probably inadvertently, reflects the revisionism that punctuationism has ushered in. That simple iconography does not begin to reflect Darwin's views on rates of evolution; Darwin was not a "rate-dependent gradualist," in spite of that straw-man wrapping created for him by hierarchic punc-

tuationism. Darwin's understanding of the rate-independence of evolutionary change, in spite of his clear adherence to gradualism (i.e., contra the saltationist views of his contemporaries), has been amply corroborated numerous times (Szalay 1999a, and references therein).