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ADAPTATION REVIEWED: A PHYLOGENETIC METHODOLOGY FOR STUDYING CHARACTER MACROEVOLUTION

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Abstract.—We present a phylogenetic methodology to test hypotheses of adaptation and to discriminate adaptation from alternative causal explanations of character evolution. To constitute an adaptation, a character must be shown to provide current utility to the organism and to have been generated historically through the action of natural selection for its current biological role. The criterion of current utility is applied by comparing the performance of a derived trait to that of its phylogenetically antecedent state. If the performance of a trait exceeds that of its antecedent state, it constitutes an “aptation” for its observed biological role. Alternatively, if the performance of a trait equals or falls below that of its antecedent state, it constitutes a “nonaptation” or “disaptation,” respectively. The criterion of historical genesis is applied using the concept of “selective regime,” the aggregation of organismal and environmental factors that combine to determine the expected action of natural selection on actual and potential character variation. An aptation that arose on a lineage having the same selective regime as the focal taxon constitutes an “adaptation,” whereas one that arose on a lineage having a different selective regime constitutes an “exaptation.” For nonaptations and disaptations, the criterion of historical genesis serves to determine whether the nonaptive or disaptive status arose coincident with the trait itself or secondarily through a change of selective regime. We suggest that this phylogenetic approach will help to overcome general criticisms of adaptationist studies and will serve to bridge the gap between microevolutionary and macroevolutionary studies of adaptation. [Adaptation; exaptation; natural selection; phylogeny.]

There is considerable disagreement among evolutionary biologists regarding the meaning of adaptation and the methodology for studying it in nature. A focal point of this controversy is the revised terminology developed by Gould and Vrba (1982) to accommodate alternative causal explanations of the current utility and historical genesis of organismal traits. Following Williams (1966) and Gould and Lewontin (1979), Gould and Vrba (1982) recognized two categories of traits that are demonstrated to be of current utility to the organism. Traits that were built by natural selection for their current utility or “biological role” (all actions or uses of the trait by the organism during the course of its life history [Bock and von Wahlert, 1965; Bock, 1979]) are termed adaptations (*sensu stricto*). Traits whose evolutionary origin was not related to their current biological role are termed exaptations. Adaptations and exaptations form subsets of the category “aptations,” features that have current utility regardless of their specific evo-

lutionary history. A “nonaptation,” by contrast, is a trait that provides no current utility to the organism.

An important consequence of Gould and Vrba's (1982) approach is that adaptations must be viewed as historical rather than atemporal entities. To classify a given trait as an adaptation for a given function, it is necessary first to demonstrate that it enhances organismal performance (the “criterion of current utility”). Although this would be sufficient to confirm a hypothesis of adaptation as defined by Bock (1979), according to Gould and Vrba, the trait also must be shown to have evolved via natural selection for its current biological role (the “criterion of historical genesis”). This poses the problem of how these two criteria can be assessed in practice. The purpose of this article is to outline a phylogenetic methodology for testing adaptive hypotheses within the framework of Gould and Vrba (1982). It is necessary first to discuss some important responses to Gould and Vrba (1982) and to show that these differ-

ent viewpoints would all be served by a methodology that elucidates the evolutionary histories of characters.

RESPONSES TO GOULD AND VRBA

Gould and Vrba's (1982) definition of adaptation has been subjected to two contradictory criticisms. Sober (1984) questioned the relevance of current utility in assessing the adaptive status of a trait, stressing instead the criterion of historical genesis:

Adaptation and fitness (adaptedness) are complementary concepts. The former looks to the past, reflecting the kind of history that a trait has had. The latter looks to the future, indicating the chances that organisms have for survival and reproductive success. These retrospective and prospective concepts are mutually independent. An adaptation may cause problems for the organisms that have it; a changed environment may mean that an adaptation is no longer advantageous [Sober, 1984: 210].

This means that a trait failing the criterion of current utility could still be classified as an adaptation provided that it passes the criterion of historical genesis.

In complete contrast, Fisher (1985) stated that the criterion of current utility is paramount in identifying an adaptation, but that the criterion of historical genesis is irrelevant. Fisher (1985) argued that if adaptations are *by definition* built by natural selection, then natural selection cannot be used to *explain* the phenomenon of adaptation:

Darwin's (1859) intent, despite some heterogeneity in usage (Burian, 1983), was clearly to offer the process of natural selection as an explanation for features and relationships that can be observed in the world today (not to mention those represented in fossils). It is quite a different matter to assert by definition that adaptations are created by natural selection for current function [Fisher, 1985:123].

All things considered, it is preferable to define the state of adaptation in terms of its contribution to current fitness. Given the concept of fitness adopted here, any feature that we propose to recognize as an adaptation must have a causal relationship to reproductive potential [Fisher, 1985:124].

The differences among Gould and Vrba (1982), Sober (1984), and Fisher (1985) in the importance that they attach to the criteria of current utility and historical gen-

esis are definitional rather than substantive. If representatives of each viewpoint were given an authoritative description of the evolutionary history and current utility of a trait, they might disagree as to whether the trait should be classified as an adaptation, but would agree that both aspects of the trait's biology are interesting in their own right. Although Sober's definition of adaptation does not involve current utility, the current utility would be useful in developing causal hypotheses of trait origin. Likewise, Fisher's definition ignores historical genesis, yet this information would be useful for studying the "process" (as opposed to the "state") of adaptation (Fisher, 1985). Thus, regardless of the definition of adaptation preferred, overcoming the methodological barriers to studying the historical genesis and current utility of a trait constitutes a potentially rewarding challenge.

PHYLOGENETIC APPROACHES

Phylogenetic analysis forms the basis for two recently published methodologies that discriminate adaptations from the other causal explanations of character evolution (Greene, 1986a; Coddington, 1988). Although these two methodologies are based upon similar phylogenetic approaches (Eldredge and Cracraft, 1980; Wanntorp, 1983), they conflict with each other and depart conceptually from Gould and Vrba (1982) on several important points.

Greene (1986a) rejected Gould and Vrba's (1982) definition of adaptation because it requires demonstration of the past action of natural selection, which he judged to be impractical. Greene (1986a) removed natural selection from the definition of adaptation, but retained the criteria of current utility and historical genesis. Current utility is assessed by demonstrating the association between a trait and an organismal "performance advantage" conferred through its possession. "Performance advantage" refers to the increased capability of the organism to perform a narrowly defined task that can contribute to its potential for survival and reproduction (see Arnold [1983] for a detailed discussion of the

measurement of performance). For example, the performance advantage of wings in most birds is flight, whereas that in penguins is swimming. Greene's method invokes the criterion of historical genesis by testing for phylogenetic congruence between the origin of a trait and the measured performance advantage. For a trait to qualify as an adaptation, its origin must coincide with that of the performance advantage (i.e., both must be traced to the same internal branch of the phylogenetic tree). An exaptation is a trait shown to have evolved on an internal branch ancestral to the one on which the associated performance advantage arose. A phylogenetic analysis of birds showing that flight evolved on the same internal branch as wings would be consistent with the hypothesis that wings are an adaptation for flight. However, the performance advantage, swimming, evolved in penguins much later than did wings; wings in penguins therefore constitute an exaptation for swimming.

Coddington (1988) retained Gould and Vrba's (1982) definition of adaptation as a trait molded by natural selection for its current utility. However, his use of the criteria of historical genesis and current utility differed from that of Greene (1986a). The phylogenetic distribution of form/function complexes is assessed to ensure that the performances of derived states are compared to the appropriate antecedent conditions. Coddington's (1988) use of the term "function" is more general than Gould and Vrba's (1982) and refers simply to trait-specific utility. A separate "function" is associated with each hierarchically nested variant of form. Hence, changes in form and "function" are always phylogenetically coupled, unlike the relationship between form and performance advantage in Greene's method. To constitute an adaptation, a derived form must be found to be superior, relative to the antecedent form, for the derived "function." This does not preclude the antecedent form from being superior for its corresponding "function." Coddington's analysis differed from Greene's by using the phylogeny only to

establish the appropriate comparisons to be made among varying form/function complexes; it is not used directly to test historical congruence between phylogenetic changes of form and those of other fitness- or performance-related variables.

Coddington (1988) denied the importance that Gould and Vrba (1982) attached to the concept of exaptation. His approach emphasizes the nested hierarchy formed by homologous adaptations (form/function complexes) and views exaptation as adaptation described at an inappropriate hierarchical level. For example, a nested hierarchy of homologous structures is represented by the tetrapod forelimb, the bird wing, and the flipper-like wing of penguins, each of which has a distinct biological role. The derived characteristics of the less inclusive forms may constitute adaptations at their appropriate levels. The derived features that make a bird's forelimb a wing are perhaps adaptations for flight, although, when viewed at the more inclusive level, the forelimb of birds would be considered an exaptation for flight. We accept the importance of Coddington's observation that hypotheses of adaptation are meaningful only when formulated at the appropriate level of the phylogenetic hierarchy. Within this hierarchical framework, however, we find the concept of exaptation to maintain its usefulness for identifying features or components thereof that retain ancestral forms in the context of a derived biological role. The autopodial elements of the avian wing, for example, retain patterns of association inherited from their nonflying tetrapod ancestors despite their current biological role of flight. We choose to identify these structures as exaptations.

The methodology that we propose for testing hypotheses of adaptation follows Greene (1986a) and Coddington (1988) in combining the criteria of current utility and historical genesis. Following Greene (1986a), we find it useful to assess the phylogenetic congruence between changes in form and changes in fitness-related variables for assessing character utility. We differ from Greene, however, in retaining the

criterion of historical genesis by natural selection in our definition of adaptation. This is done by incorporating the concept of "selective regime" in our phylogenetic analysis.

THE SELECTIVE REGIME

A central axiom of the theory of natural selection is that evolutionary change is not random. Differential survival and reproduction of varying organisms (termed "sorting" by Vrba and Gould, 1986) is caused by the interaction between their heritable character variation and the environment. Different environments may favor the fixation of different traits. Furthermore, various aspects of the organism's biology may determine how selection will act upon novel variation. The "comprehensive selective regime" is defined as the aggregate of all such environmental and organismic factors that combine to determine how natural selection will act upon character variation. If natural selection drives evolutionary change, then the comprehensive selective regime can be viewed as the inherent directional component, the vector of microevolution.

The comprehensive selective regime should determine the expected fitness of all actual and potential character variation. It is difficult in practice to make an assessment of the comprehensive selective regime. Instead, critical aspects of the environment/organism interaction are identified and postulated to be major factors influencing the potential action of natural selection on the character variation under study. We use the abbreviated term "selective regime" to denote the subset of factors affecting fitness that is used operationally in studies of adaptation. This selective regime is specified anew for each analysis, contingent upon the traits under study and their hypothesized biological roles. For example, the hypothesis that a given floral trait is an adaptation enhancing the efficiency of bird-pollination would be tested by scoring subject taxa as having either the selective regime "bird-pollinated" or an alternative one (e.g., "insect-pollinated").

Although the comprehensive selective regime is unique to a particular taxon and a given interval of time, the subset of factors denoted "selective regime" may be shared among several taxa. This follows from the fact that although distinct lineages will never experience exactly the same selective forces, lineages having similar ecology and/or developmental constraints will tend to evolve similar features (as demonstrated by the phenomena of convergent and parallel evolution, respectively; see Lauder, 1981). The nature of organism/environment interaction in a lineage has conservative components, and hence selective regimes are expected to show some temporal stability (see discussion by Charlesworth et al., 1982). The fact that selective regimes may be shared by multiple lineages and may persist through time is critical for studying general hypotheses of adaptation, which we discuss below.

The selective regime of a lineage is used to predict how natural selection, as opposed to other evolutionary forces, would direct the evolution of the trait under study. If one could characterize the selective regime that was present when the trait evolved, it would be possible to test the hypothesis that natural selection was responsible for the trait's initial fixation. This hypothesis is falsified if the trait is shown to have evolved in a regime that did not favor the derived over the antecedent state. Alternative hypotheses for the fixation of a trait include (1) random genetic drift; (2) selection in a different context (a different selective regime); (3) developmental or genetic correlation with a different, selected trait; or (4) "effect sorting" (Vrba and Gould, 1986; Vrba, 1989) associated with processes analogous to natural selection operating at different levels of biological complexity (e.g., the effects of segregation distortion on the evolution of tail phenotypes in mice [Lewontin, 1968]).

The evolution of aposematism can be used to illustrate the use of the selective regime for testing predictions of the origin of a trait. In insects the selective regime "distasteful to an avian predator" would

favor the fixation of aposematic coloration. Thus, the hypothesis that aposematism is an adaptation in an insect taxon for protection from bird predation predicts that aposematism evolved initially in an ancestral population that was distasteful to birds. If warning coloration became fixed in a lineage of nondistasteful insects, then this specific adaptive hypothesis is falsified. Alternative hypotheses, such as Batesian mimicry, could then be considered.

The hypothesis that a given trait and its associated performance advantage (Greene, 1986a) arose through the action of natural selection for its currently observed biological role is tested by evaluating the selective regime in which the evolutionary change occurred. This places Greene's phylogenetic approach into a hypothetico-deductive framework designed to test the hypothesis of adaptation as originally stated by Gould and Vrba (1982): an adaptation is a feature that evolved by the action of natural selection for its current biological role.

SELECTIVE REGIME, NICHE, AND ADAPTIVE ZONE

It is important to note the distinction between selective regime and several different but related concepts. There is some superficial similarity between our selective regime concept and the modern ecological niche concept (Hutchinson, 1959), but these concepts are not equivalent. The ecological niche is a heuristic device for studying ecological competition. In contrast, the selective regime does not define the ecological circumstances in which an organism lives. Rather it assesses, given the ecological circumstance, how selection is expected to sort character variation. The niche describes the organism's ecology, whereas the selective regime describes the action of natural selection contingent upon the organism's ecology.

There are also some similarities between the selective regime and the adaptive zone concept as developed by Simpson (1953) and modified by Van Valen (1971). The adaptive zone, like the selective regime, refers to an organism/environment inter-

action (Wake and Larson, 1987). The adaptive zone is defined at the level of higher taxa, however, whereas the selective regime describes the microevolutionary forces presumed to be acting within populations. In either case, evolution can move lineages between zones/regimes when triggered to do so by organismal and environmental factors. Novel organismal features can produce a novel exploitation of the environment and hence move the lineage to a new adaptive zone. Similarly, a novel organismal feature can change the way selection acts upon other organismal character variation and hence modify the selective regime. Likewise, a purely environmental change such as the exposure of a plant population to a new pollinator can change both the adaptive zone and the selective regime.

The difference between the "comprehensive selective regime" and the "selective regime" in our terminology is somewhat analogous to the distinction between Simpson's and Van Valen's concepts of adaptive zone. Simpson's (1953) adaptive zone is occupied by a particular group of organisms and ceases to exist if that group becomes extinct. In contrast, Van Valen's (1971) adaptive zone, like the ecological niche, is independent of occupation. The comprehensive selective regime is, like Simpson's adaptive zone, unique to a given taxon at a given time and place. The selective regime concept that we employ in our methodology is closer to Van Valen's adaptive zone concept because it too may characterize multiple unrelated taxa.

THE RELATIVE NATURE OF CURRENT UTILITY

Although the biological role of a trait can be measured in a particular taxon without reference to other taxa, this will not suffice for evaluating the trait's adaptive status. In studies of adaptation, the assessment of current utility, like the selection coefficients in population genetics, is relative. For example, yellow petals may be said to increase the pollination efficiency in a bird-pollinated plant species if the alternative character state against which it is

TABLE 1. Phylogenetic definitions of adaptation and related terms.

Relative utility ^a	Selective regime ^b	
	Derived	Antecedent
Greater (aptation)	Adaptation	Exaptation
Less (disaptation)	Primary disaptation	Secondary disaptation
Equal (nonaptation)	Primary nonaptation	Secondary nonaptation

^a Relative utility of a derived character state relative to its antecedent state (measured in the selective regime of the focal taxon).

^b Selective regime of the internal branch on which the derived character state evolved (derived = selective regime observed in the focal taxon; antecedent = selective regime differing from that of the focal taxon and characteristic of a lineage ancestral to the focal taxon).

compared is white petals. If the alternative character state is red petals, then yellow petals might be found to be detrimental.

We follow Greene (1986a) and Coddington (1988) in advocating that the relative utility of a trait should be assessed always in comparison to the trait's phylogenetically antecedent state. This approach focuses attention on the evolutionary transition between the antecedent and derived traits and is critical for discriminating alternative causal explanations of character evolution. Furthermore, the assessment of relative utility must be made under the selective regime of the focal taxon (the taxon possessing the character under study). Because our protocol depends upon phylogeny reconstruction, assessment of character polarity and the nested hierarchy of homologous character states is automatically incorporated. For characters whose antecedent state is ambiguous, comparison must be made against all possible antecedent states. In the latter case, the trait's relative utility can be assessed in a meaningful way only when the alternative comparisons generate equivalent conclusions.

PHYLOGENETIC DEFINITIONS OF ADAPTATION AND ITS ALTERNATIVES

To constitute an adaptation, a trait must have enhanced utility relative to its antecedent state, and the evolutionary transition must be found to have occurred with-

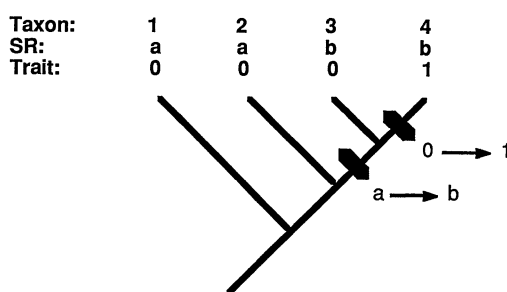


FIGURE 1. An illustration of the phylogenetic predictions of hypotheses of adaptation, primary disaptation, and primary nonaptation using the selective regime (SR). In all cases, the clade having the derived character (1) is nested within the clade having the derived selective regime (b). Using taxon 4 as the focal taxon, the hypothesis of adaptation predicts that the utility of the derived trait (1) will exceed that of the ancestral trait (0) under the derived selective regime (b). The hypothesis of primary disaptation predicts that the utility of the derived trait (1) will be less than that of the ancestral trait (0) under the derived selective regime (b). The hypothesis of primary nonaptation predicts that traits 0 and 1 have equivalent utility under the derived selective regime (b).

in the selective regime of the focal taxon (Table 1; Fig. 1). Two alternative outcomes are possible when a character change occurs while selective regime remains constant (Table 1; Fig. 1). If the antecedent and derived states have equal performance, the derived trait constitutes a nonaptation because it contributes no utility that was not already provided by the phylogenetically more inclusive antecedent condition. If the antecedent state is superior in performance to the derived condition, the derived trait may be termed a "disaptation" (*dis* + *aptus* = "not fit"). When a trait arises as a disaptation, which we denote "primary disaptation," we have the unexpected outcome that a trait of lower performance replaces a trait of higher performance. This result falsifies the hypothesis that the trait evolved directly through the action of natural selection. Darwinian theory predicts that primary disaptations will be rare or nonexistent in nature.

Exaptation constitutes the causal explanation of a trait that has utility for its current biological role but originally evolved for a different biological role (Table 1; Fig. 2). Exaptation occurs, therefore, only when

there has been a change of selective regime subsequent to the origin of the trait. A change of selective regime may have several alternative outcomes on the utility of a character. The change of selective regime may be found to be irrelevant to the character, in which case the character's prior status is unchanged. If the change of selective regime causes a trait to cease having utility, it becomes a nonadaptation. Such traits may be called "secondary nonadaptations" to distinguish them from "primary nonadaptations" (those described above) that lack utility when they arise.

It is conceivable that a change of selective regime can cause a trait to become detrimental when assessed against the potential utility of its phylogenetically antecedent state (Table 1; Fig. 2). For example, assume that carnivores ceased to have opposable thumbs through the action of natural selection (acting, e.g., on terrestrial quadrupedal locomotion). However, the panda lineage has switched its selective regime from carnivory to herbivory, and in the derived regime, the derived trait (unopposable thumb) may have lower utility than the ancestral trait (opposable thumb) for stripping bamboo leaves from stems. Thus, despite evolving via natural selection, the derived state would be detrimental in pandas. Such traits could be termed "secondary disaptations" to denote the fact that the derived state has lower utility than the ancestral state, but that this arose from a change of selective regime following the trait's evolutionary origin. Unlike primary disaptations, secondary disaptations are fully consistent with Darwinian explanations.

The phenomenon of preaptation is also evident within this phylogenetic perspective (Fig. 2). This term was proposed by Gould and Vrba (1982) to replace the older term preadaptation. Preaptations are recognized in practice as the phylogenetically antecedent conditions of exaptations. For example, the wings of the flighted sister groups of penguins constitute preaptations that were co-opted for swimming in penguins. Preaptations are tractable only in retrospect and then only when the exap-

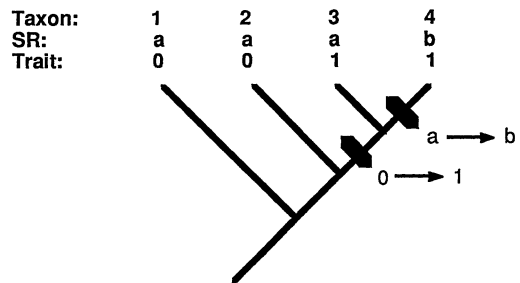


FIGURE 2. An illustration of the phylogenetic predictions of hypotheses of exaptation, secondary disaptation, secondary nonadaptation, and preaptation using the selective regime (SR). In all cases, the clade having the derived selective regime (b) is nested within the clade having the derived character (1). Using taxon 4 as the focal taxon, the hypothesis of exaptation predicts that the utility of the derived trait (1) will exceed that of the ancestral state (0) when assessed under the derived selective regime (b). The hypothesis of secondary disaptation predicts that the utility of the derived trait (1) will be less than that of the ancestral trait (0) when assessed under the derived selective regime (b). The hypothesis of secondary nonadaptation predicts that traits 0 and 1 have equivalent utility under the derived selective regime (b). Using taxon 3 as the focal taxon, the hypothesis of preaptation for the biological role manifested under the derived selective regime (b) predicts that the derived trait (1) has a different biological role (or lacks a biological role) under the ancestral selective regime (a). If the derived trait (1) constitutes an exaptation in taxon 4, then it will automatically constitute a preaptation in taxon 3.

tations to which they gave rise are represented in extant species or in the fossil record. Thus, the usefulness of the concept is open to criticism but, because it exists widely in the literature, we have retained it here.

The causal explanation of character evolution will be ambiguous if a trait is found to arise on the same lineage as a change of selective regime because it will be unclear which selective regime was occupied when the trait evolved. However, coordinate change of an organismal feature and the selective regime is the predicted outcome if the derived trait is instrumental in acquiring entry into a novel adaptive zone featuring novel selective regimes. Such traits have been termed "key innovations" (Miller, 1949; Lauder and Liem, 1989). The implications of our methodology for

studying key innovations are discussed below.

THE METHODOLOGY

Our phylogenetic methodology comprises eight steps described in order below. In practice, several steps may be considered simultaneously. Also, it may be necessary to modify early steps on the basis of considerations encountered later in the analysis. To illustrate the protocol we refer to data published by Larson et al. (1981) on the evolution of morphological novelties associated with arboreality in the salamander genus *Aneides*. This study preceded publication of the revised terminology of Gould and Vrba (1982) and its results therefore have not been discussed previously in this framework.

Choice of Subject Taxa

The phylogenetic methodology is applicable in theory to taxa of any rank, provided that evolution is primarily divergent rather than reticulate. Cracraft (1990) argued, however, that proper resolution of evolutionary novelty requires that species or subspecific units serve as the operational taxonomic units. The traits being studied normally will be fixed within each of the terminal units; however, the protocol may be useful in some cases of polymorphism where alternative morphs are discrete and where outgroup comparison provides an unambiguous evolutionary polarity for them. The alternative trophic morphs of the fish *Cichlasoma minckleyi* studied by Liem and Kaufman (1984) are an example of this phenomenon.

The illustrative example uses the five species of the plethodontid salamander genus *Aneides* as the main focus, with the genera *Plethodon* and *Ensatina* used as outgroups. The genus *Plethodon* is probably paraphyletic, so representatives of both the eastern and western lineages of *Plethodon* are included (Larson et al., 1981). The major adaptive question in this group concerns the evolution of climbing ability and arboreality in *Aneides*.

Phylogeny Reconstruction

Any methodology that produces a rooted tree for the taxa under study can be used to infer phylogeny (Eldredge and Cracraft, 1980). Ideally, phylogenetic characters should be sought in diverse organ systems and in molecular data (see Nei, 1987). It is important to ask whether the same characters whose adaptive status is being investigated should be used to reconstruct the phylogeny. Arguments that this practice necessarily leads to circular reasoning appear to be unfounded (see Appendix 4 of de Queiroz, 1989). However, it should be noted that where a suite of characters evolves in response to changes of selective regime, those characters will show selective covariance. Because maximum parsimony, maximum likelihood, and other algorithms for phylogenetic inference assume character independence, morphological characters used in studies of adaptation may be inappropriate for cladistic analysis. Thus, although circularity does not preclude basing the phylogeny on characters whose adaptive status is being investigated, the probability of nonindependence of these characters makes them problematic for phylogenetic reconstruction.

The phylogeny used in our worked example (Fig. 3) is based upon immunological and electrophoretic protein comparisons (after Larson et al., 1981). This tree is one step longer than the most parsimonious cladogram derived from 17 morphological characters (Larson et al., 1981).

Scoring Characters

An important prerequisite for the analysis of character evolution is an evaluation of character homology. This is a problematic area that is beyond the scope of this paper (see detailed discussions by Patterson, 1982, 1988; Kaplan, 1984; de Queiroz, 1985; Roth, 1988; Rieppel, 1989; Wagner, 1989). The important point to note here is that every effort should be made to ensure that the traits of different taxa are, in a meaningful sense, homologous and evolutionarily comparable. The nested hier-

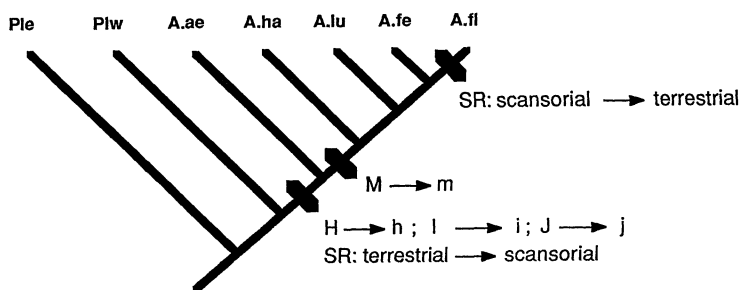


FIGURE 3. A phylogenetic tree topology based upon protein electrophoretic and albumin immunological data relating five species of *Aneides* (A.ae, *Aneides aeneus*; A.ha, *A. hardii*; A.lu, *A. lugubris*; A.fe, *A. ferreus*; A.fl, *A. flavipunctatus*) with eastern (Ple) and western (Plw) species of *Plethodon* used as outgroups (after Larson et al., 1981). The most parsimonious distribution of changes for characters H/h, I/i, J/j, and M/m, and selective regimes (SR) are shown.

archical relationships of homologous characters must be identified (Coddington, 1988).

Our worked example uses a subset of the characters described by Larson et al. (1981). These traits have been chosen because they are hypothesized to influence climbing ability in salamanders. The traits are all scored as instantaneous adult morphologies (de Queiroz, 1985). The basis for subdivision of the traits into categories follows past insights into trait structure and utility (Wake, 1960, 1963; Larson et al., 1981; Staub, 1989). The distribution of character variation is summarized in Table 2 using the letter designations assigned by Larson et al. (1981):

Tarsal organization.—(H) *Ensatina* and *Plethodon* have tarsal cartilages arranged as in all five-toed members of the generalized plethodontid outgroups (subfamily Desmognathinae and tribe Hemidactyliini): the fifth tarsal is small and is excluded from articulation with the centrale by the articulation of the relatively large fourth distal

tarsal with the fibulare. (h) In *Aneides* (all species), the fifth distal tarsal is relatively large and it articulates with the centrale; the relatively small fourth distal tarsal is thereby excluded from articulating with the fibulare. As a result of this reorganization, the entire tarsus is narrower than in more generalized salamanders, and there is a more channeled distribution of force from the arm to the digits (Wake, 1960, 1963: his Fig. 6, 1966).

Carpal organization.—(I) The carpus is relatively broad in *Ensatina* and *Plethodon*, and the centrale does not articulate with the ulnare because of a broad articulation of the intermedium and fourth distal carpal. This is the typical condition in generalized salamanders. (i) In *Aneides*, the carpus is narrowed and the four elements mentioned above meet, or nearly meet, in a four-way intersection (Wake, 1963: his Fig. 6).

Terminal phalanges.—(J) The terminal phalanges of *Ensatina* and *Plethodon* are like those of most salamanders in being round-

TABLE 2. The distribution of four morphological characters in *Aneides* and *Plethodon*. The primitive (0) and derived (1) character states were determined using outgroup comparison with *Ensatina*.

Character	Species					
	<i>Plethodon</i>	<i>A. aeneus</i>	<i>A. hardii</i>	<i>A. ferreus</i>	<i>A. flavipunctatus</i>	<i>A. lugubris</i>
H. Tarsal organization	0	1	1	1	1	1
I. Carpal organization	0	1	1	1	1	1
J. Terminal phalanges	0	1	1	1	1	1
M. Otic crests	0	0	1	1	1	1

ed at the tip. (j) Those of *Aneides* are distally flattened, expanded, and recurved, with a proximal, ventrally directed process for attachment of a large ligament (Lowe, 1950; Wake, 1963). The proximal portion of the phalanx has a pronounced ventral projection to which is attached a strong tendon (Wake, 1963).

Otic crests.—Dorsal crests in the otic region provide area for the origin of jaw and head raising muscles and are found in males of all *Aneides*. Low crests located in different positions and judged not to be homologous to these are found in *Ensatina* and *Plethodon*. (M) In *A. aeneus*, crests are present but poorly developed. (m) In the remaining species, the crests are well developed and conspicuous, except for female *A. hardii*, which lack otic crests.

Scoring Selective Regimes

The selective regime that one identifies is contingent on the particular hypothesis being tested, as discussed above. The selective regime of a taxon can incorporate abiotic environmental factors (e.g., wind-dispersed, marine), biotic environmental factors (e.g., bee-pollinated, herbivorous), organismal features (e.g., capable of flight, arborescent), or any combination of the above (e.g., aquatic carnivore, bat-pollinated understory shrub). Because the selective regime is a reflection of organism/environment interactions, a feature might in one analysis be the trait under study and in another may serve to define the selective regime. A detailed study of the natural history of the species being compared is required for precise characterization of the selective regimes (see Greene, 1986b).

In the example, we are testing hypotheses that the four traits in *Aneides* are adaptations related to enhanced climbing ability (traits h, i, and j in Fig. 3) and prey capture while maintaining a perch on a vertical surface (trait m) (Larson et al., 1981). All the traits are therefore hypothesized to contribute a performance advantage to climbing, and here the species are placed into two alternative selective regimes (terrestrial or scansorial/arboreal). *Ensatina* and

Plethodon utilize primarily terrestrial locomotion, whereas the species of *Aneides* occupy a variety of terrestrial to arboreal habitats (Wake, 1960, 1963). *Aneides hardii* has moderately developed climbing ability and is more scansorial than *Plethodon*, often being found climbing under the bark of fallen logs. *Aneides aeneus* is highly scansorial and is found mainly in vertical rock crevices. *Aneides ferreus* and *A. lugubris* have substantial climbing ability and arboreality, although they also utilize the terrestrial habitat. *Aneides flavipunctatus* is the only strictly terrestrial species of *Aneides* and is commonly found in rock talus habitats. A two-way classification of selective regime (terrestrial versus climbing) accommodates the variation in the comprehensive selective regimes of these species that is deemed relevant to this study. Species of *Ensatina*, *Plethodon* (except *P. petraeus*; see Wynn et al., 1988), and *A. flavipunctatus* are scored as occupying a terrestrial selective regime; the remaining species of *Aneides* are scored as occupying a scansorial/arboreal selective regime.

The dependence of this step upon precise knowledge of the ecology of the taxa under study (Greene, 1986b) is illustrated by the fact that different instances of arboreality in plethodontid salamanders represent very different selective regimes. For example, arboreality has evolved independently in the plethodontid genus *Bolitoglossa*, but in this case the surfaces climbed are smooth. Climbing on these surfaces favors a suite of morphological innovations different from those of salamanders climbing the rough surfaces exploited by some *Aneides* (specifically, webbed feet that provide suction and adhesion [Wake and Lynch, 1976; Alberch, 1981; Larson, 1983]). Despite the superficial similarity between the ecologies of these two plethodontid genera, their selective regimes are quite different. The genus *Chiropterotriton*, although closer phylogenetically to *Bolitoglossa* than to *Aneides*, demonstrates arboreality associated with rough surfaces and possesses derived carpal and tarsal arrangements resembling those of *Aneides* (Wake and Lynch, 1976; Larson et al., 1981).

Partitioning Character Changes on the Phylogeny

The principle of parsimony is used to locate character-state changes on a phylogeny (Fitch, 1971; Maddison et al., 1984). Provided that a given character switches state rarely relative to the frequency of lineage branching, the distribution of character changes requiring the minimum number of state transitions will be the distribution having maximum likelihood (Felsenstein, 1984). Maximum parsimony identifies only the most likely pattern of character evolution. The stochastic elements intrinsic to evolutionary change ensure that a proportion of characters will have patterns different from the most parsimonious arrangement. This problem is discussed at greater length below (Testing General Evolutionary Hypotheses). When the ancestral character-state assessment is equivocal, it is necessary to take the conservative approach and to consider all of the equally most parsimonious patterns together (Maddison et al., 1984; see also Donoghue, 1989).

In the worked example, traits *h*, *i*, and *j* are synapomorphies of the genus *Aneides* and hence it can be deduced that they evolved in the stem lineage of the genus (Fig. 3). Trait *m* is a synapomorphy of all *Aneides* except *Aneides aeneus* (Fig. 3), although it is sexually dimorphic in *A. hardii*. For the purposes of illustration, we will assume that the poorly developed otic ridges of *A. aeneus* represent an intermediate stage in the evolution of this character rather than a character-state reversal, although both patterns are equally parsimonious.

Inferring Selective Regimes of Ancestral Lineages

Two methods are available for inferring the selective regimes of ancestral lineages. The first involves the use of paleontological or biogeographic data. For example, the fossil record of *Banksia* (Proteaceae) in Australia extends back beyond the appearance of the honeyeaters, which pollinate a majority of the extant species. Ford et al.

(1979) used this to postulate that the genus was ancestrally pollinated by marsupials and lorikeets rather than honeyeaters.

When direct historical inference cannot be applied, as is often the case, selective regimes may be superimposed on cladograms using the principle of parsimony. In this case, the underlying assumption is that the rate at which lineages move between selective regimes is low relative to the rate of lineage branching. This means that if a clade manifests a derived selective regime, it is most probable that the regime arose on the stem branch giving rise to the clade, rather than through several independent events. This assumption is violated if a major extrinsic factor, such as climatic change, causes sister lineages to experience parallel regime switches, a possibility that sometimes can be tested using paleontological data (Greene, 1986a). With this exception, the principle of parsimony provides a means by which the selective regimes of ancestral populations can be inferred.

In our example, paleontology does not illuminate the ancestral selective regime of the chosen taxa. The parsimony approach places a transition from terrestriality to scansoriality on the stem lineage of *Aneides*. A subsequent reversal in *A. flavipunctatus* to a terrestrial habitat associated with rock talus is shown (Fig. 3).

Assessing Current Utility

As discussed earlier, the current utility of a trait is evaluated relative to its antecedent state. In a majority of cases the antecedent state is easily determined from the phylogeny. However, if the focal taxon has the clade's plesiomorphic character state, identification of its antecedent state will require a survey of outgroup taxa. One possible outcome is that superficially similar traits found in different taxa occupying the same selective regime can have different assessments of adaptive status. This arises when character similarity is convergent such that different terminal taxa have similar traits but different antecedent states. For example, in Figure 4 assume that under the selective regime bird-pollination, red

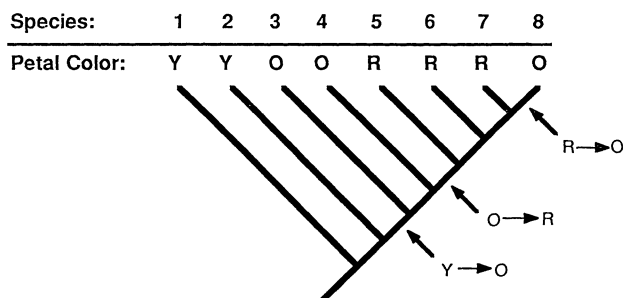


FIGURE 4. An illustration of the relative utility of character states. Eight bird-pollinated plant species, comprising a monophyletic group, have the phylogeny shown. Assuming that for bird-pollination, red petals (R) confer higher performance than orange petals (O), which in turn confer higher performance than yellow petals (Y), in the focal taxa 3 and 4, orange petals are aptations for bird-pollination, but the same trait is disaptive for bird-pollination in focal taxon 8.

petals have higher performance than orange petals, which in turn are better than yellow petals. Petal color in this example is homoplastic; orange petals have evolved twice, once from yellow and once as a reversal from red. Thus, the orange petals of taxa 3 and 4 are aptations for bird-pollination, whereas those in taxon 8 constitute a disaptation.

Strict fitness measurement, wherein the reproductive potential of the ancestral and derived character states is compared in a natural population that is polymorphic for the two states, is possible only when an antecedent state appears in a population through recurring mutation or developmental perturbation. In the absence of this situation, the assessment of performance (the advantage an organism gains by possession of a trait) is achieved using one of three methods. In all cases, the comparison between antecedent and derived states is performed in the selective regime of the focal taxon.

The first approach for measuring utility is to induce the ancestral character state in members of the focal taxon. It is then possible to evaluate the effect that such manipulation has on performance. For example, beetles hypothesized to show Batesian mimicry could be painted to resemble their cryptic ancestors, and predation rate could be assessed in the presence of the distasteful model. Another example of this approach is a recent study of the effects of toe fringes on the loco-

motor performance of sand-dwelling lizards (Carothers, 1986).

The second approach is to compare the focal taxon to a sister taxon that lacks the morphological feature being studied, but that shares the selective regime of the focal taxon. For example, the predation rate on the hypothesized Batesian mimic could be compared to that on its cryptically colored sister species. The comparison is made using the mimetic model and predator that constitute the selective regime of the mimetic species. Because of the nested hierarchical relationship of homologous characters, this test is not reversible. It evaluates the relative utility of a derived state (mimicry in the example), but is irrelevant in assessing the relative utility of the antecedent state, crypsis (which must be done in the context of its own antecedent state).

The third approach to assessing utility or performance is to use models based upon a detailed knowledge of organismal biology to predict the consequences of alternative character states. Using the example of the mimetic beetles, a mathematical model encompassing a knowledge of predator behavior and the abundance of the focal taxon relative to the other species of the mimetic complex could make reliable predictions concerning the performance of aposematism versus crypsis. This approach constitutes the paradigm method (Rudwick, 1964), which was evaluated in detail and extended by Fisher (1985). Performance is assessed by comparing a character

state with an abstract model, or "paradigm," designed to perform optimally within the limits of known developmental and structural constraints. The closer the observed character comes to the paradigm the higher is its inferred performance. Hence, the relative performance of the derived and antecedent character states is evaluated by asking which comes closer to the paradigm.

For the four characters in our example, it is impractical to evaluate current utility by experimental manipulation or by comparing sister taxa. Assessment of utility employs the paradigm method and mechanical models. The derived states of traits h, i, and j are mechanically superior for grasping and climbing relative to their antecedent states (H, I, and J), while trait m is superior for prey-capture while maintaining a perch on a vertical surface (Wake, 1960, 1963). Thus, for the arboreal/scansorial *Aneides* species these traits constitute aptations with the biological role of enhanced climbing ability. It is not known whether these traits influence performance in the secondarily terrestrial *A. flavipunctatus* and, if so, whether they enhance or diminish it relative to traits H, I, J, and M. Thus, the relative utilities of traits h, i, j, and m in *A. flavipunctatus* are unknown and, hence, they could constitute aptations, nonaptations, or disaptations. Well-developed otic crests (trait m) also enhance performance during aggressive intraspecific interactions, which occur in all species of *Aneides* and many related genera (see Staub, 1989). Thus, trait m appears to be an aptation for two very different biological roles, climbing and intraspecific aggression.

Classifying Traits into Categories of Utility/Historical Genesis

The final step is to place traits into their appropriate categories of utility and historical genesis. The criterion of historical genesis is applied by noting whether the trait evolved on an internal branch having the same selective regime as the focal taxon. If the trait evolved on a branch whose upper and lower nodes both share the se-

lective regime of the focal taxon (Fig. 1; Table 1), then an aptation is an adaptation, a nonaptation is a primary nonaptation, and a disaptation is a primary disaptation. If, on the other hand, the upper and lower nodes have a selective regime different from the focal taxon (Fig. 2; Table 1), then an aptation is an exaptation, a nonaptation is a secondary nonaptation, and a disaptation is a secondary disaptation.

The phylogenetic distribution of trait and regime switches can be used also to identify preaptations. If an exaptation of a focal taxon is shared by its sister taxon but fills a different biological role (or lacks a biological role) in the sister taxon, it may be termed a preaptation in the sister taxon.

Traits h, i, and j arose on the same branch as the switch in selective regime and, hence, they could be either adaptations or exaptations depending upon the order of events within this branch. Larson et al. (1981) considered traits h and i (tarsal rearrangement and carpal fusion) to be "key innovations," traits instrumental in permitting exploitation of the arboreal environment. This is testable as a hypothesis of general aptation (see below). These traits persist in the secondarily terrestrial *A. flavipunctatus*, and would constitute exaptations, secondary nonaptations, or secondary disaptations depending upon the assessment of their relative utility for terrestrial locomotion.

Trait m (otic crests) illustrates some of the complexities that are revealed by the phylogenetic methodology. This trait arises within the context of two different selective regimes (aggressive behavior, scansorial feeding), both of which are expected to favor the derived over the antecedent condition. Trait m is potentially an adaptation with two different biological roles. It is not unexpected that several different selective forces will impinge on a character simultaneously, sometimes acting synergistically and sometimes in opposition. This observation raises the question of whether the selective factor causing the evolution of trait m was climbing, intraspecific aggression, or both factors simultaneously. Further investigation of the evolution of this character is needed, involving perhaps

finer dissection of the character itself (e.g., making use of the sexual dimorphism manifested in *A. hardii*) and the selective regime components.

TESTING GENERAL EVOLUTIONARY HYPOTHESES

So far we have presented a protocol for evaluating the traits of individual taxa, each of which represents a unique historical event. In all branches of science, unique events of one sort or another are grouped into classes so that general theories can be tested using replication of the experimental or observational situation. For example, the disintegration of a particular nucleus represents a unique event, and hence it is impossible to predict with certainty when and how such an event will occur. In contrast, nuclear disintegration can be studied as a general phenomenon; predictive models can be developed and tested statistically by observing many instances of the phenomenon. Likewise, the evolution of fins in cetaceans may be a singularity, but the evolution of fins in aquatic animals is a class of events and, hence, accessible to replication and statistical analysis. Thus, a general hypothesis of character macroevolution comprises a set of specific hypotheses, one for each convergent event. Each of these specific hypotheses can be analyzed using our phylogenetic methodology and constitutes an independent test of the general hypothesis.

Recently, the use of phylogenies to test general evolutionary hypotheses has started to receive increased attention (Ridley, 1983; Felsenstein, 1985; Huey and Bennett, 1987; Sessions and Larson, 1987; Sillén-Tullberg, 1988; Donoghue, 1989; Losos, 1990; Maddison, 1990; Wanntorp et al., 1990). For example, Donoghue (1989) tested the general hypothesis that fleshy, animal-dispersed propagules promote the evolution of dioecy in seed plants. This can be rephrased according to our terminology as testing the general hypothesis that dioecy is an adaptation related (in some unspecified way) to the possession of fleshy propagules and animal dispersal. Using the phylogeny presented by Donoghue (1989),

and assuming that dioecy is an aptation for animal dispersal (i.e., that dioecy confers a performance advantage relative to other breeding systems in animal-dispersed taxa), it is an unambiguous adaptation in two cases (Myristicaceae and Amborellaceae) and equivocal in the other five cases of dioecious, animal-dispersed lineages. Statistical approaches that permit more precise testing of phylogenetic hypotheses have recently been developed (Maddison, 1990).

"Key innovation" is a special case of aptation that is testable in the context of replicated phylogenetic studies of character evolution. We define a key innovation as a trait that greatly modifies the selective regime of the lineage in which it evolves. Our use of key innovation differs from that of Lauder and Liem (1989), who described an alternative phylogenetic protocol for the investigation of this phenomenon. Their use of key innovation implies an increase in morphological diversity in the clade for which the character is a synapomorphy. Our use is neutral with respect to overall morphological diversity. The protocol of Lauder and Liem (1989) presents key innovation and developmental constraint as antagonistic concepts; the first is said to increase phylogenetic character variation, whereas the latter is said to decrease it. We suggest alternatively that a key innovation will produce both of these phylogenetic consequences simultaneously. The key innovation will burden some phenotypic traits with additional evolutionary constraints (Riedl, 1978). Likewise, the opening of a novel adaptive zone is expected to enhance the opportunity for divergent evolution in other character complexes. Our concept of key innovation implies primarily a change in evolutionary constraints and in the direction of morphological evolution.

In the worked example, an analysis of the evolution of climbing ability in *Aneides* showed that tarsal rearrangement (trait h) and carpal fusion (i) arose simultaneously with the switch to arboreality. Larson et al. (1981) suggested that these two traits are key innovations for climbing ability in

plethodontid salamanders. In the terminological framework we advocate, the concept of key innovation would apply to a trait that is instrumental for entering a novel adaptive zone, thereby producing a change of selective regime. Thus, the general hypothesis that traits *h* and *i* are key innovations for climbing can be refuted if arboreality is found to arise in related lineages that lack these traits.

Two separate phylogenetic origins of arboreal climbing of rough surfaces are known among plethodontids. Both *Chiropterotriton* section *alpha* (Wake and Lynch, 1976) and *Plethodon petraeus* (Wynn et al., 1988) have separately occupied this adaptive zone. The carpal and tarsal rearrangements (*h*, *i*) observed in *Aneides* are seen elsewhere only in *Chiropterotriton*, where they occur simultaneously with the switch to the arboreal regime. This is consistent with the prediction that they constitute a key innovation also in *Chiropterotriton*. In *Plethodon petraeus*, the carpal and tarsal rearrangements are not observed; however, the phalangeal tip expansion observed in *Aneides* (character *j*) is evidenced. These observations refute the general hypothesis that traits *h*, *i*, or *j* are individually required by plethodontids for evolution of the ability to exploit rough vertical surfaces.

DISCUSSION

The primary aim of this paper is to show that hypotheses regarding the causal explanation of character evolution can be tested in a hypothetico-deductive, phylogenetic framework. By using Coddington's (1988) phylogenetic criteria to recognize characters, Greene's (1986a) phylogenetic criteria for evaluating their performance advantage, and the selective regime to evaluate the selective basis of their historical genesis, we provide a framework in which alternative hypotheses of character evolution (Gould and Vrba, 1982) can be discriminated. The identification of convergent and parallel origins of derived character states permits general hypotheses of adaptive evolution to be tested by sampling a number of comparable unique historical events.

Our phylogenetic methodology and the revised criteria for discriminating adaptation from exaptation, nonadaptation, and disadaptation will be successful only if it can answer previous criticisms of adaptationist studies. One of the strongest general criticisms of adaptationist studies is that of Lewontin (1984), who identified several serious flaws in earlier, nonphylogenetic approaches. Lewontin (1984) criticized adaptationist studies for their artificial separation of organism from environment. He proposed alternatively that the organism and environment are to be viewed as an interacting system with each being simultaneously the subject and object of evolutionary forces (Levins and Lewontin, 1985). Our discussion of the selective regime emphasizes that the factors affecting the sorting of character variation in natural populations arise through the interaction of internal and external factors. This synthesis of organism and environment has a precedent in Simpson's introduction to the concept of adaptive zone:

Adaptation itself evolves. We do not simply have on one side a discrete something called "environment" with a neatly fixed set of prospective functions packaged into niches and on the other side discrete things called "organisms" or "populations" the evolution of which consists of progressive occupation of the niches. . . . it is equally or more useful to focus neither on environment nor on organisms but on the complex interrelationship in which they are not really separable [Simpson, 1953:199].

Lewontin (1984) criticized adaptationist studies further for artificially atomizing the organism into "traits" that are designed to solve specific environmental "problems." Mayr (1983) and Fisher (1985) have already argued that this criticism is oversimplified and that the problem is not characteristic of the best adaptationist research. Isolation of individual characters is perhaps a necessary starting point, but it must be followed by synthesis and reassessment of the hypothesized characters in the light of the phylogenetic analysis. Furthermore, even in the initial analysis, the phylogenetic methodology can minimize the risk of atomizing organisms into traits that lack

any evolutionary individuation. This is achieved by application of stringent conditions for character homology and the explicit identification of their nested hierarchical relationships. Similarly, the methodology avoids the unwarranted and untestable atomization of the environment into discrete "problems" that the organisms must solve (Lewontin, 1984). This can be seen in our preliminary analysis of the otic crest of *Aneides*, wherein the evolution of a morphological feature is found to be causally complex, involving more than one environmental factor.

Recent insights into biological homology (Wagner, 1989) suggest that characters become associated into individualized evolutionary units as a result of historically acquired constraints on their interactions. The traits analyzed in a phylogenetic, adaptationist study constitute testable hypotheses of historically acquired constraint. This can be seen most clearly in our methodology when a trait is found to be a primary disadaptation, thereby suggesting higher-level explanations including developmental constraint or genetic coupling. These higher-level explanations indicate that the trait as originally formulated may not show evolutionary individuation and suggest that it should be reevaluated as part of an interacting character complex. Thus, the phylogenetic methodology identifies the historical origins not only of isolated characters, but also of character complexes and of novel interactions among characters.

Alternative explanations of primary disadaptation such as random processes, or the effects of selective processes occurring at different levels of complexity (Vrba and Gould, 1986; Vrba, 1989), overcome Lewontin's (1984) third major criticism that adaptationist studies assume universal adaptation. It is common, he noted, for character variation to be presented as generally adaptive with deviations from the predictions of adaptive hypotheses being rescued by secondary ad hoc adaptive explanations. Our phylogenetic methodology should identify cases where adaptationist hypotheses are mistaken.

Another major criticism of adaptationist studies comes from the dichotomy between microevolutionary and macroevolutionary perspectives. From a microevolutionary standpoint, Epling and Catlin (1950) and Williams (1966) have discouraged the systematic approach to the study of adaptation, favoring quantitative population-level approaches. This perspective has produced research programs for studying adaptation as an exclusively intrapopulation phenomenon observed at a single point in time (see Lande and Arnold, 1983). It is evident from the more recent phylogenetic studies reviewed here that the confinement of adaptationist studies to a microevolutionary perspective is too restrictive. We hope that our methodology, with its emphasis on selective regimes, will help to bridge the gap between the ecological/population genetic and systematic levels. It provides a way for contemporary observations to contribute to historical studies (e.g., by defining selective regime and assessing current utility) and allows systematic analyses to yield ecological and genetic predictions (e.g., the expected sorting of variation in extant populations, identification of historically constrained character complexes). Indeed, we view the study of character macroevolution as a pluralistic science, with microevolutionary and macroevolutionary approaches being equal partners, each having much to contribute and even more to gain.

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