CLADISTIC TESTS OF ADAPTATIONAL HYPOTHESES

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Abstract—A cladistic viewpoint provides an historical definition of adaptation and an operational ecological test for evolutionary adaptations. Adaptation is apomorphic function promoted by natural selection, as compared with plesiomorphic function. Adaptation is thus a conditional, hierarchical, comparative term, like homology. Hypotheses of adaptation that do not specify levels of apomorphy are weak; they should refer to and explain the function at the level at which it is apomorphic with respect to the plesiomorphic (outgroup) condition. The adaptational hypothesis serves as a prior prediction in the comparison of the apomorphic function of the derived trait with the plesiomorphic function of the plesiomorphic trait serving as the null hypothesis. It is useful to distinguish whether hypotheses about characters identify selection as facilitating: 1) the origin of a character; 2) its maintenance; 3) neither; or 4) both. The latter two are uniformitarian and testable in a strong sense. The former two possibilities use ancillary arguments to protect the hypothesis of the role of natural selection in one way or another, but might still be tested by the weak criterion of plausibility. Given an hypothesis of both origin and maintenance due to selection, the test of adaptation may still be thwarted because only certain kinds of cladistic structure allow feasible tests. Few of the really classic and common examples of supraspecific adaptation survive this kind of cladistic test.

Introduction

Adaptation is without doubt the central prediction of Darwin's explanation of descent with modification. To mention only·two opinions, Lewontin (1980) remarked, "In Darwinism the element that is both central to the evolutionary world view and yet so powerful that it can destroy Darwinism as a testable theory is that of adaptation," and Leigh (1971) identified the explanation of the origin and nature of adaptation as the first requirement in any evolutionary biology. Krimbas (1984) quotes such architects or defenders of the New Synthesis as Bock, Dobzhansky, Mayr, Simpson, and Waddington to document that neodarwinism relies predominantly on adaptation to explain evolutionary change, and many if not most biologists continue to regard that view as the most plausible (e.g. Stebbins and Ayala, 1981; Charlesworth et al., 1982; Turner, 1981).

This article does not address the role of adaptation at the population level and below. That has been scrutinized elsewhere (e.g. Williams, 1966; McDonald 1983; Wallace, 1984; Endler, 1986) and the importance of selection in controlling gene frequencies in many cases seems established (Kettlewell, 1961; Dobzhansky, 1970; Ford, 1975). Fairly sophisticated techniques to document the action of natural selection have also been developed (e.g. Maynard-Smith, 1978; Clutton-Brock and Harvey; 1979; Oster and Wilson, 1978; Arnold and Wade, 1984a, b). However, the importance of adaptation as an explanation at higher taxonomic levels remains speculative and anecdotal.

This article addresses the concept of adaptation as an explanation of supraspecific evolutionary pattern from a cladistic point of view to provide a methodology allowing test and possible falsification. The cladistic technique is beginning to be used in various ecological contexts (e.g. Ridley, 1983; Brooks et al.,1984; Felsenstein, 1985), but the issue of adaption has not been clearly addressed. Darwin's theory of natural selection engendering and conserving adaptations provides a logical explanation of lineage origin and diversification and his historical, causal theories predict what cladists term synapomorphies. Adaptation is one possible general explanation of empirically observed synapomorphies among many. This situation of alternative causal explanations can be

exploited to deduce ecological comparisons that should reveal the extent and importance of adaptation as an explanation of evolutionary diversity, as compared with other possible explanations.

Before the tests can be explained, the particular meaning of adaptation and aspect of evolutionary theory involved should be clarified. The test is not applicable to all contexts in which "adaptation", broadly construed, might apply, and I don't intend to circumscribe these varied usages. It is a diverse concept, and will doubtless remain so. The claim is made, however, that the aspect of the theory and the meaning of the term adaptation as outlined here, do represent a major current of evolutionary thought.

The Darwinian Logic

Lewontin (e.g. 1978) has repeatedly emphasized that Darwin's theory of natural selection involves three propositions: (1) variation exists in phenotypic traits; (2) that variation is at least partly heritable; (3) variants reproduce differentially. This logic outlines the process of natural selection, but not adaptation, because it does not describe the interaction of heritable variation with the environment. Krimbas (1984), modified proposition 3 and added a fourth to explicate the role of adaptation in Darwin's theory: (3) some variants are better adapted (function better) than others in their environments; (4) the better adapted variants leave more offspring and thus contribute more to the genetic make-up of future generations. It seems doubtful that Darwin, who so emphasized the "struggle for existence", would have truncated his theory to point out only the fact of differential reproduction. The posited cause, adaptation, is an integral part of the selectionist viewpoint and honestly must be included in any formalization of that viewpoint (Brandon, 1978; Williams, 1966). Thus, Krimbas' (1984) restatement seems more in tune with both the original and "neo" content of the theory. It is the hypothesis of adaptation, the predicted effect of observed differential reproduction on evolutionary pattern, which makes Darwin's theory compelling.

A selectionist view of phyletic radiation sees the process primarily as an epiphenomenon of intra-populational events (Stebbins and Ayala, 1981; Mayr, 1982). Novel traits arise spontaneously by mutation or recombination and increase the relative Darwinian fitness of their bearers. The gene or genes coding for the trait ultimately are fixed in the deme by natural selection. That group may increase in numbers relative to other such groups via such processes as inter- or intraspecific competition or niche diversification, and reproductive isolating mechanisms may ensue. This lineage may speciate numerous times, supposedly as an effect of abundance caused by the advantage conferred by the originally novel trait. The origin of the trait was due to mutation followed by directional or disruptive selection and its maintenance is due to stabilizing selection (Simpson, 1953; Petry, 1982; Stebbins and Ayala, 1981; Charlesworth et al., 1982). Hence, the persistent similarity of the now defining trait is due to stabilizing selection predominating over factors that would otherwise alter it in any of the reproductively isolated lineages. Simpson (1953), in particular, argued that most features distinguishing higher taxa were adaptations. The adaptationist point of view causally explains the origin and persistence of most traits in most lineages by directional and stabilizing selection. Mayr (1982: 171–172) reiterated this basic model of evolutionary change:

"When a new species is competitively inferior either to the parental species or to one of its new sister species, it will become extinct without ever leaving a trace in the fossil record. Occasionally, however, the

genetic revolution in the founder population may lead to such a loosening up of constraints that the neospecies can enter a new adaptive zone or make some other kind of evolutionary innovation. This can have two (more or less overlapping) effects: either the new adaptation removes the neospecies from too serious a competition with already existing species, thus leading to an enrichment of the biota (and an increase in diversity) or the neospecies becomes a particularly successful competitor and causes the extinction of one or several existing species."

A persistent claim of the New Synthesis is that population-level adaptive change is a microcosm of lineage diversification and elementary texts still emphasize this viewpoint (e.g. Wallace and Srb, 1964; Futuyma, 1979). Clearly, not all New Synthesizers believe this exclusively; some role is accorded to non-selectionist explanation of evolutionary pattern. However, to test adaptation, its core prediction must be isolated. I argue that this central claim, the Darwinian vision or adaptive radiation due to evolutionary novelty, can be tested in a more rigorous way than it has to date. The first question is: if indeed natural selection and adaptation drive evolutionary change in most cases, then what should the resulting pattern and data look like?

Definition of Adaptation

In line with the form of the Darwinian logic outlined above, the meaning of adaptation can be clearly stated in cladistic terms: adaptation is apomorphic function due to natural selection. Of course, the term adaptation has many meanings (Krimbas, 1984; Mayr, 1982; Gould and Vrba, 1982), but because this paper focuses on its meaning at the species level and above, these alternative meanings can be set aside. For example, it is not the process by which a population becomes adapted, in the sense of Fisher (1985). Nor is it the overall state of adaptedness of a population, or optimality, as in the sense of Brandon (1978) or Oster and Wilson (1978). Likewise, it is not mere phenotypic accommodation to some physiological or environmental stress. Most particularly, it is *not* merely an ahistorical interpretation of the function of a feature or trait that has an effect on current fitness (Leigh, 1971; Clutton-Brock and Harvey, 1979; Wilson, 1980; Fisher, 1985). While function is an important element in the cladistic meaning of adaptation, the term should include and presuppose more than function, otherwise it becomes a pedantic synonym of that simpler word. I agree with Gould and Vrba (1982) that an evolutionary definition of adaptation must have an historical component specifying selection as the evolutionary agent responsible for the appearance of the feature. The ahistorical and historical meanings of adaptation are related as part to whole; historical analysis of adaptation includes identification of current utility as a necessary component, but current utility by itself cannot establish the historical dimension of an adaptation.

Adaptational hypotheses usually take the form: trait M_x is an adaptation in taxon C for function F_x. From a cladistic point of view, such a statement is incomplete. With respect to the phylogeny depicted in Fig. 1, the complete statement would be: the derived trait M_1 arose at time (t) in the stem lineage of taxa C, D, and E via selection for the derived function F_1, with respect to the primitive trait M_0 with primitive function F_0 in taxa A and B. Such a statement represents a more rigorous exegesis of a major claim of neodarwinian theory; the methodology presented here tests only this kind of claim.

Figure 1 separates form from function only for analytical reasons. Usually the two are tightly correlated and the test outlined here presumes that they are (although cladistically incongruent derivation of form and function merely complicates, rather than invalidates, the test). Derived features will have derived functions if the proximate cause of the derivation is natural selection and thus by definition, the apomorphy (form + function) is

TAXON	A	B	C	D	E
MORPHOLOGY	M_0	M_0	M_1	M_1	M_1
FUNCTION	F_0	F_0	F_1	F_1	F_1

■ TIME, t

HYPOTHESIS

M_0 NAT. SEL. at M_1

F_0 TIME, t F_1

PRIMITIVE   DERIVED
                            (NOVELTY)

Fig. 1. Conceptual model for the origin via natural selection of novel morphology (M_1) and function (F_1) as a supraspecific adaptation.

an adaptation. In so far as a single cause is hypothesized for both apomorphic feature and function, then the two are predicted to be congruent. Whenever one finds that particular apomorphy, the simplest prediction expects that particular apomorphic function.

However, not all apomorphic features, nor all apomorphic functions, are adaptations. Only those consistent with the implied or deduced results of natural selection should be considered adaptations and alternative explanations of apomorphy abound (see discussion). Only apomorphies arising through natural selection are adaptations. Moreover, not all functions that accomplish the same biological result are the same adaptation. Because adaptation depends on the concept of apomorphy, and apomorphy depends on the concept of homology, the term adaptation is constrained to apply to only homologous, apomorphic functions that survive the standard ecological tests for selective value, in which plesiomorphic functions are used as the null hypothesis or experimental control. Obviously this formulation mixes metaphors usually peculiar to ecology or systematics, but what other role has adaptation always served? Homologous function and apomorphic function are necessary and reasonable concepts.

Testing Adaptation

Given the phylogenetic history in Fig. 1, what should the ecological data look like? The adaptational hypothesis in the short form is: trait M is an adaptation in taxon C for function F. Workers who use adaptation to mean simply the function of a trait (Oster and Wilson, 1978; Clutton-Brock and Harvey, 1979; Fisher, 1985), presumably would test the

hypothesis by showing that trait M_1 had function F_1 and might conclude that M_1 is an adaptation in C for F_1, if experimental modification of the function lessened some measure of fitness (e.g. Wilson, 1980). This conclusion, however, seems only to restate the observation: M_1 functions in C to do F_1. Nevertheless, the above authors have explained in great detail the methodology appropriate to, and pitfalls in, the analysis of current utility of a feature.

For historical tests, one needs a data set similar to that illustrated in Fig. 2. This data set is designed to illustrate four potential tests of adaptation, and problems which exist in analyses if those tests are not acknowledged.

First, one has to know the cladistic structure of the group including taxon C and to avoid circularity, that structure should not be inferred from characters involved in the hypothesis of adaptation. Thus characters 1–2 and 4–9 establish the ingroup, test group, and higher taxon synapomorphies required as the context for the adaptational hypothesis involving the 3rd trait M, in taxon C. At present, the literature rarely considers in sufficient detail the phylogeny of the group to which the study organism belongs.

Second, unless M_1 is an autapomorphy of C, it is a trait apomorphic for more than a single taxon, as exemplified by its occurrence in D. Thus, hypotheses about M_1 in C are also predictions about M_1 in D; adaptational hypotheses must always consider traits at the hierarchical level at which they are apomorphic and this will usually imply generalizations about two or more species. The existence of M_1 in D affords one category of test of the adaptive value of M_1; one predicts that the function of M_1 in D will be testably homologous to the function of M_1 in C. Homology of function can be discerned in many cases if the understanding of the function and form is detailed; homologous functions operate by homologous means, whereas analogous functions may achieve the same end, but do so by non-homologous means.
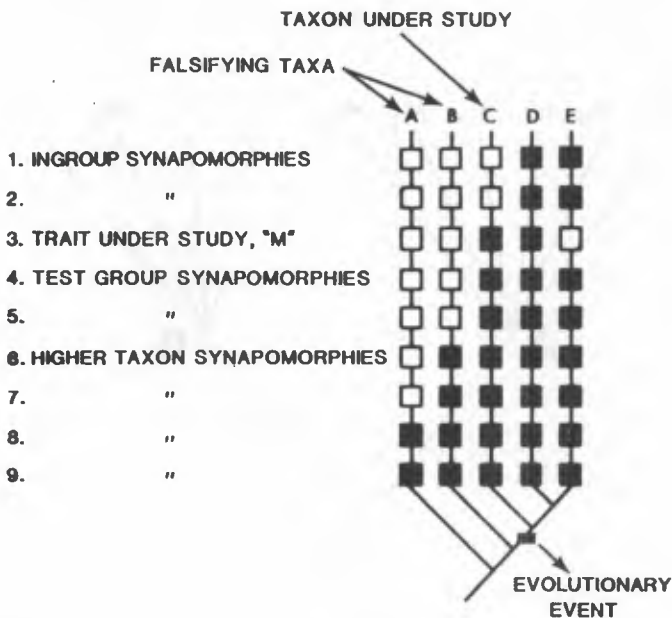

Fig. 2. Example data set required to test adaptation cladistically. The hypothesized adaptation is trait 3, "M", in taxon C. It has two phenotypic states, M_0 (open box, primitive) and M_1 (closed box, derived), involving two hypothesized evolutionary changes (gain of M_1, and secondary loss of M_1 in taxon E).

Third, the presence of the primitive homologue M_0 in A and B defines the appropriate control groups or null hypothesis for the critical test of the derived state M_1 as an adaptation in C. If the scenario outlined in Fig. 1 is applied to the data in Fig. 2, one must posit an evolutionary transition in M from state 0 to state 1 in the ancestor of C, D, and E, driven by natural selection. Hence taxa A and B with function F_0 of M_0 should be, in some definable and measurable sense, ecologically or functionally less well adapted than C or D, with function F_1 of M_1. For example, one expects M_0 to be an inferior solution to the design problem posed by F_1, but not necessarily that M_1 is a superior solution to the design problem posed by F_0. Any of the myriad components or correlates of fitness, such as engineering design, competition, ergonomics, fecundity, foraging, nutrient uptake rates, viability, disease resistance, predator or herbivore avoidance, dispersal ability, speed, or physiological efficiency, might be reasonably applied in particular cases.

Fourth, because the origin of trait M_1 in Fig. 2 is inferred to be an event coincident with the evolution of the ancestor of C, D, and E, the absence of trait M_1 in E is due to secondary loss, not primitive absence. In effect, M_0 in E is not homologous to M_0 in A or B and thus does not bear on the issue of the origin of M_1 because it happened after M_1 evolved. To attempt to understand the conditions leading to the origin of M_1 by studying the biology of E is incorrect, or at best is needlessly indirect. Therefore not all experimental controls are equally useful in elucidating the origin of M_1 and, in particular, not all absences are equal.

Figure 3 is a hypothetical data set which better represents reality. In Fig. 3, group B is monomorphic for trait M_3 and function F_3; we infer that the ancestor had the trait and the function. However, its sister taxon A exhibits three distinct traits each with different functions. The trait and function at node C is therefore ambiguous. Even if the state at node A were resolved to be $M_1 F_1$, for example, one would still not know whether $M_1 F_1$ was primitive to $M_3 F_3$ or vice versa. In other words, the polarity would be ambiguous and the direction of evolution unknown, thus ultimately frustrating ecological comparisons
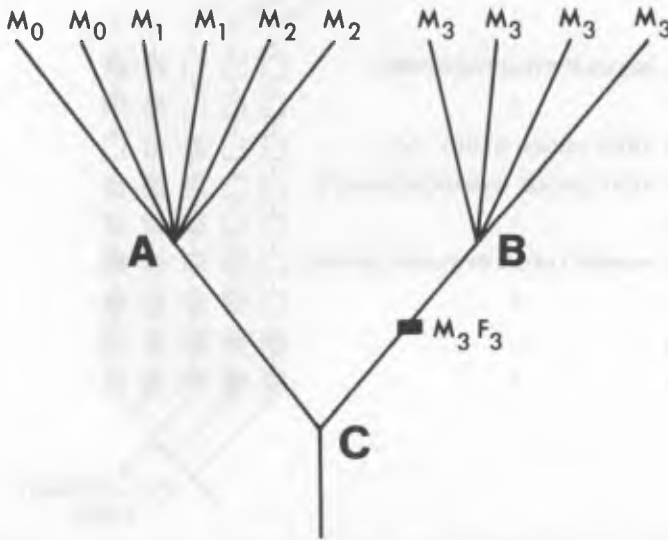

Fig. 3. Cladogram illustrating effect of unresolved cladistic structure on reconstruction of ancestral states required for an adaptational test. State at node B is $M_3 F_3$, but states at A and C are unknown.

Fig. 4. Cladogram illustrating testable (derivation of M_5F_5) and untestable distributions of taxa and characters. See text for further explanation.

between M_1F_1 and M_3F_3 because we can make no prediction about the outcome of the comparison. Cladistic structure like that in Fig. 3, prevents the test of adaptational hypotheses. This problem often affects hypotheses about synapomorphies at high categorical levels in which the cladistic structure of either in- or outgroups is controversial or unknown.

Figure 4 is more complex and includes one testable case and several that are not. The testable case is the evolution of M_5F_5 from M_4F_4. Applicable tests are all 6 pairwise comparisons between M_5F_5 and M_4F_4 species. The hypothesis states that trait M_5 will perform function F_5 "better" than trait M_4, with "better" pre-defined by the hypothesis in a way applicable to the trait. The doublet of species exhibiting M_4F_4 protects the test from uncertainty in the rest of the cladogram (Maddison et al., 1984): it will always be more parsimonious to suppose that M_4F_4 is primitive to M_5F_5. The rest of the tree reiterates the problems outlined in Fig. 3 concerning assignment of states to ancestors ("?" indicates uncertainty) and unresolved nodes (if node A were M_2F_2, adaptive hypotheses about M_0F_0 and M_1F_1 could be tested).

Examples

The following section illustrates this test of adaptation using real examples. The discussion certainly does not represent all the subtleties and nuances of each example, partly because they are drawn from fields outside my expertise and partly to conserve space. The examples have been chosen to explain the method, not to solve the problems raised by each case.

Common mistakes involve the generality and polarity of hypothesized adaptive traits. A century-old tradition in arachnology asserts that the orb web evolved from something

like the cob web because it is a superior strategy to catch flying prey (review in Coddington, 1986a). Evidence for its adaptive value included the assertion that it had evolved convergently in two distantly related taxa. A cladistic re-analysis of the problem (Coddington, 1986a, b) indicates that the orb web is an ancient behavioral feature of a large group of spider taxa, that it only evolved once and defines a monophyletic taxon, and that cob web weavers are derived from orb weavers, rather than vice versa. Thus, the original hypothesis makes no sense because the presumed polarity of the traits was backwards. Note that the orb web might still be an adaptation in some sense, but only with respect to the outgroup taxon (currently unknown), not the ingroup taxon (cob weavers and relatives), which "lost" the feature or transformed it beyond any recognizable similarity to the orb web (NB. trait 3 in taxon E, Fig. 2).

A similar example was pointed out by Wanntorp (1983). Otto and Nilsson (1981) hypothesized that retention of dried leaves throughout the winter in young specimens of *Quercus robur* and *Fagus sylvatica* was an adaptation to conserve their investment in nutrients, as compared with other temperate forest trees that shed their leaves in the fall. Wanntorp points out that: (1) leaf retention in Fagaceae is probably primitive, so that the trait is not apomorphic in these species; (2) if anything, leaf shedding is derived, so that the appropriate question is why leaf shedding, not why leaf retention. While Otto and Nilsson may be correct that leaf retention in these species *functions* to conserve nutrients, it is not an adaptation to do so in the historical sense of the term.

Ridley (1983) used cladistics to test whether precopulatory mate guarding was adaptive, but the analysis was largely invalidated by the sorts of problems illustrated in Fig. 3. He generalized about all arthropods, or all spiders, in an effort to establish the ancestral state at basal nodes. However, the cladistic structure of these huge groups of organisms is so poorly known that Ridley's efforts remain speculative at best (Coddington, 1985). Although one may often try to generalize about huge groups that display some heterogeneity for a trait, ignorance about the detailed evolutionary history of those groups will undermine the generalization.

To turn to a species level problem, in an influential and much cited paper, Lewontin (1978) contrasted African two-horned rhinos versus Indian one-horned rhinos to illustrate non-adaptation. He suggested that one or two horns represented equally good "adaptive peaks" and suggested that they functioned as a defense against predators. Although Lewontin's general point is doubtlessly valid—that alternative, equally functional solutions to biological problems exist—rhinos are a poor example for interesting reasons. This re-analysis draws on information not available to Lewontin in 1978.

The family Rhinoceratidae includes 4 living genera and 5 species: the Indian one-horned *Rhinoceros* (2 spp.); the Asiatic two-horned *Dicerorhinus*; the African two-horned *Diceros*; and the African two-horned *Ceratotherium*. Lewontin's argument (1978, p. 225–226) implies 1) the ancestor of modern rhinos was hornless; 2) the one-horned and two-horned conditions each evolved once and independently; and 3) each condition evolved via natural selection as an adaptation for predator defense. One-horned rhinos should be one lineage and two-horned rhinos another.

Even without recourse to recent cladistic information, that argument seems flawed. All extant rhinos have nasal horns, but two-horned rhinos possess frontal horns in addition. Nasal horns in all living rhinos are probably homologous as nasal horns. Lewontin's argument implies that the nasal horns evolved independently in the two groups. The lack of frontal horns in Indian rhinos shows that the two traits can vary independently. One-

horned rhinos are one-horned either because they never evolved the second horn (thus primitive), or secondarily so because they lost the frontal horn (thus derived).

Groves (1983) re-analysed the phylogeny of rhinoceratids using characters of dentition and osteology, not horn number. *Diceros*, *Ceratotherium*, and *Dicerorhinus* (as well as extinct genera such as *Punjabitherium*) are all outgroups to *Rhinoceros* and are two-horned (Fig. 5). Secondary loss of the frontal horn is clearly the simplest explanation of the one-horned condition in *Rhinoceros*. Therefore, two adaptive questions are involved: why did this lineage rhino evolve two horns and why did *Rhinoceros* lose one but not both horns? The first question probably applies to more taxa than the recent two-horned genera, because the extent of the monophyletic group defined by two horns is still undetermined. Predator defense is a viable hypothesis, but could be assessed best relative to those rhinoceratids that primitively lacked horns, all of which are extinct. Perhaps extant hornless perissodactyls could serve as the control, but which ones and by what evidence? One would still have to demonstrate that the perissodactyl biology was a retained primitive context, reflecting the condition present in their common ancestor with hornless rhinoceratids.

It is even more difficult to see how the hypothesis of predator defense can explain the secondary loss of the frontal horn in *Rhinoceros*. If two horns are an adaptation against predators, one horn is not likely to be better. Completely different hypotheses of horn function, such as sexual competition or courtship display seem more fruitful. In any case, the entire question of one or two horns evolving independently from a hornless ancestor is awry and misleading. Without the phylogenetic context, we cannot be assured of forming an adaptational hypothesis that is even reasonably relevant. With a phylogenetic hypothesis, we can at least infer that the existence of one- and two-horned rhinos are probably separate and distinct questions.
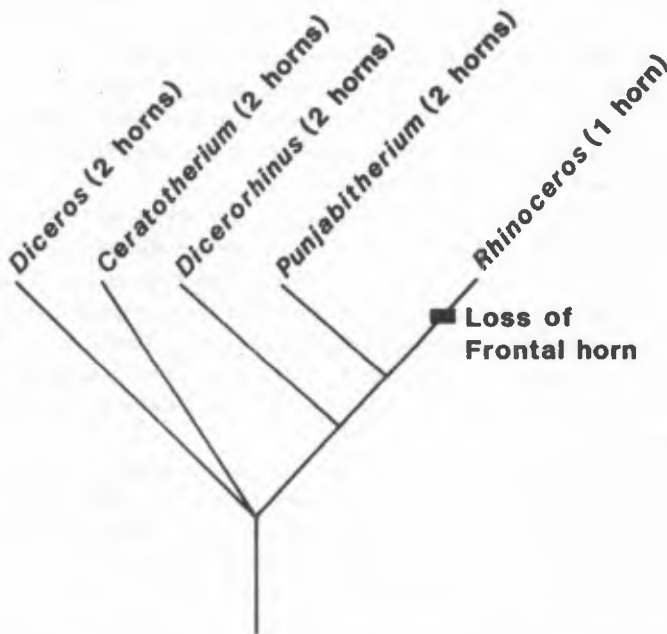
Fig. 5. Cladogram of living and some extinct genera of rhinos with data on horn number overlaid, based on Groves (1983).

Perhaps the most famous example of adaptation at the species level is that of bill morphology and diet in Darwin's finches. The Geospizinae have been the subject of numerous phylogenetic (Lack, 1947; Schluter, 1984; Yang and Patton, 1981) and ecological studies (Abbott et al., 1977; Bowman, 1961; Grant, 1981; Schluter and Grant, 1984). As Grant (1981) summarized, two major hypotheses have been advanced to explain diversity in bill morphology and diet: selection to decrease interspecific competition due to dietary overlap and selection to adapt to different floras on the different islands. Because I only intend to explain how such hypotheses might be tested, only the first will be considered here.

The competition hypothesis apparently implies that close relatives should display greater dietary overlap than more distant relatives because selection supposedly acts during the evolution of the finches to reduce dietary overlap. The cladistic test, therefore, involves pairwise or ingroup–outgroup comparisons between close and distant finch relatives to show that the predicted trend in dietary overlap did occur. Falsifying evidence might consist of trends opposite to the prediction (more recent sister taxa have less overlap) or that no consistent trend exists.

The first requirement is a reasonable phylogenetic hypothesis for the finches based on evidence independent of diet and bill morphology. However, none of the three trees mentioned above was produced by a method well-designed to infer phylogeny and unfortunately those of Schluter and·Lack were based primarily on bill morphology and/or diet, so that the test is partially circular. Although the lack of reliable phylogenetic information cripples the test (and invalidates the finch example as a corroborated case of adaptation), I have taken the available information at face value and combined the three trees into a consensus tree in Fig. 6. Considering only *Geospiza*, all authors agreed that the trio *Geospiza magnirostris*, *G. fortis*, and *G. fuliginosa* was monophyletic, though they did not concur on relationships within the trio. (Actually, if Yang and Patton's allozyme data are analysed as presence/absence characters, rather than as distance data, even this result is contested.) Lack, and Yang and Patton, considered *Geospiza* and the lineage including *Camarynchus*, *Cactospiza*, and *Platyspiza* as sister taxa; Schluter's data do not contest this. None of the authors was able to identify the sister taxon to Geospizinae, but because detailed ecological information is only available for *Geospiza*, outgroups beyond the Geospizinae may not be necessary for this test.

The cladogram in Fig. 6 is hardly well enough resolved to test a detailed adaptive hypothesis. Given the terminal trichotomy of *Geospiza* species and the more basal four-way polychotomy relating that trio to the other *Geospiza* species, any of 45 dichotomous cladograms might be true for the genus, with each of them implying slightly different scenarios under the general hypothesis of adaptive evolution. Worse, at least 44 partially resolved trees are also consistent with Fig. 6. Partially resolved cladograms result from simultaneous evolutionary events, hybridization, or missing data, and any of these factors may be important in this case.

Lack (1947) explained the existence of the three *Geospiza* ground finches by differences in bill depth as adaptations to reduce competition for food (in order of small to large bills: *fuliginosa*, *fortis*, *magnirostris*). But which way did it go? Was the primitive state a small billed species that budded off sister taxa with ever larger bills, or vice versa? Unfortunately all the candidate outgroups have beak depths roughly similar to various ingroup taxa (*conirostris* to *fortis*; *difficilis* and *scandens* to *fuliginosa*). *Geospiza difficilis* has a beak depth almost identical to that of *fuliginosa*, which might imply a transformation series of increasing bill depth in accord with Lack's hypothesis. On the other hand, Schluter's
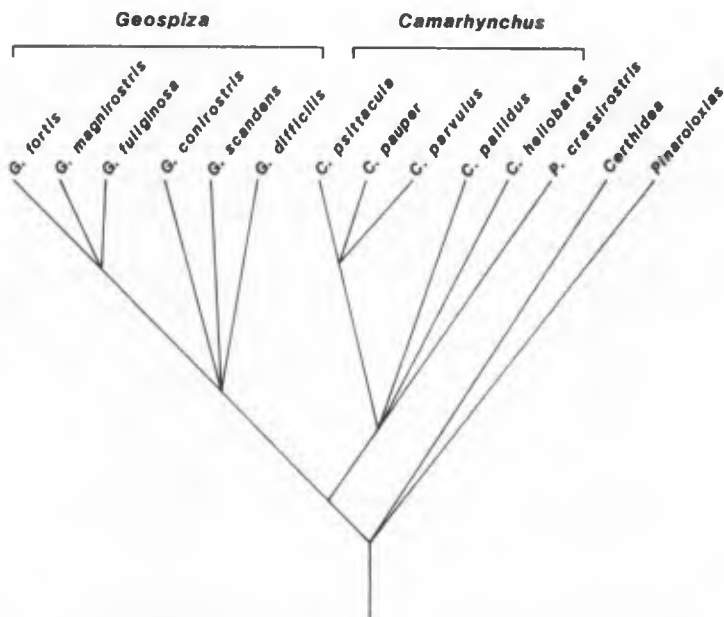
Fig. 6. Consensus cladogram of Darwin's finches; data from Lack (1947), Yang and Patton (1981), and Schluter (1984).

cladogram suggests that *conirostris* is the sister group to the ground finches, and its beak depth is more similar to the intermediate *fortis*, implying divergent evolution leading to the smaller *fuliginosa* and the larger *magnirostris*. Without better phylogenetic estimates, these hypotheses will be difficult to distinguish, although conceivably one could evaluate the ecological data under all 89 trees to see if it supported the adaptive hypothesis under test.

Unfortunately, the ecological studies of the finches were designed mainly to assess current levels of competition, not to elucidate historical genesis of bill sizes (Abbott et al., 1977). The necessary raw data apparently were collected, but current sympatry specified which pairwise comparisons were reported rather than cladistic relationships. To test the reason for the origin of larger bills in *fortis* and *magnirostris*, one should measure diet overlap in these taxa as compared to possible outgroups, such as *fulginosa*. Abbott et al. (1977) did not provide diet overlap figures for *fortis* and *magnirostris*, although both Lack (1947) and Schluter (1984) suggested that they were sister taxa. Lack's hypothesis suggests that it should be greater between the two than between either species and *fuliginosa, conirostris, scandens,* or *difficilis*.

One weak test of Lack's hypothesis is perhaps plausible. If the figures for dietary overlap in *Geospiza* species are partitioned into the ingroup (*fortis, fuliginosa,* and *magnirostris*), versus the outgroup (*conirostris, scandens,* and *difficilis*), the average overlap between ingroup pairs should be less than the average overlap of ingroup outgroup pairs. The average pairwise ingroup overlap is 0.45 ± 0.3 and the average pairwise overlap between in- and outgroup taxa is 0.54 ± 0.3. The difference is in the right direction, but is insignificant.

The finch example is interesting for several reasons. The results of the test, such as it is, seems to indicate that the origin and persistence of divergent bill morphologies in *Geospiza* cannot be ascribed to adaptive differentiation on the basis of the available data, at least

under the specific interpretation of the adaptational hypothesis advanced here. Indeed, the proponents of the dietary overlap theory should explain more clearly what empirical results their theory predicts. Given such predictions, the example does show how to structure and test them. Before a strong test could be made, one would clearly need a much better estimate of finch phylogeny independent of bill and diet characters. The example also illustrates that although Abbott et al., (1977) designed their study to detect current interspecific competition in *Geospiza*, a different analytical structure is required to test the evolutionary adaptive hypothesis.

The final example best exemplifies the test of adaptation that I propose, although it too is incomplete. Williams and Peterson (1982) showed remarkable convergence in digit pads in members of three groups of lizards: anoline iguanids, highly derived gekkonids, and the scinid *Prasinohaema virens*. Their suggested functions for this (polyphyletic and non-homologous) trait is "setae enable the animals to climb by adhering to surfaces that will not accept the claw, such as smooth walls, leaf surfaces, and glass." The only easily testable adaptational hypothesis concerns *Prasinohaema virens*, because the cladistic structure of "anolines" and "derived gekkonids" is too poorly known to specify relevant outgroup taxa in each case. Luckily the genus *Prasinohaema* contains just 3 species, and the authors obliquely indicate that *virens* is probably sister to the other two. The sister genus to *Prasinohaema* apparently is *Lipinia*, and the digit pad morphology of 3 *Lipinia* species is similar to the 2 derived *Prasinohaema* species, therefore plesiomorphic to that of *virens*. The primitive condition is a "fold-ruffle" morphology that also permits climbing on and leaping between smooth surfaces (Fig. 7). For example, the authors mention that *L.*
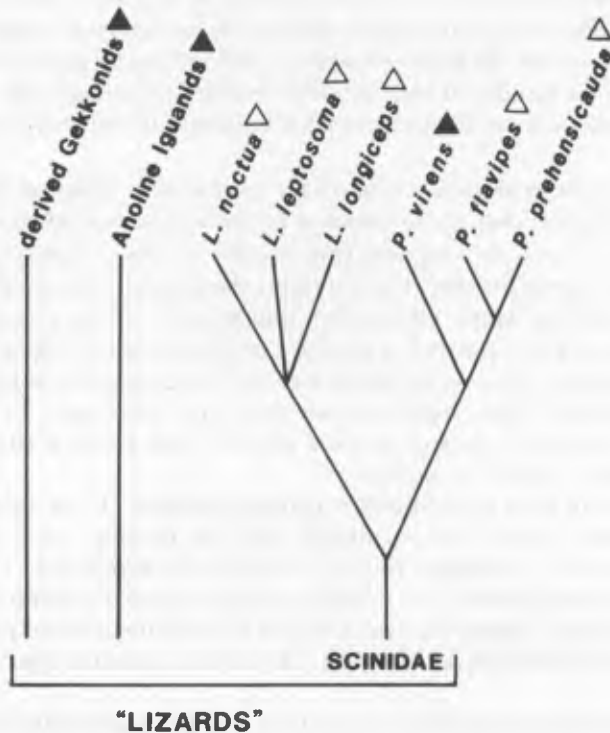

Fig. 7. Cladogram of lizard taxa mentioned by Williams and Peterson (1982). ▲ Setiform digit pads; △ fold ruffle digit pads.

leptosoma leaps 1·5 to 2 feet between leaves. This then, might represent the clearest possible case for testing adaptation: an autapomorphy whose plesiomorphic form and function are known. Unfortunately, no direct observations of the function of the setal pads in *P. virens* exist. The similarity to the morphologies in anoles and gekkonids did not convince the authors that the condition in *P. virens* was adaptively superior to that in other *Prasinohaema* or *lLipinia* species. Nevertheless, the ecological test seems well-structured: the adaptive hypothesis predicts that the setal pads in *P. virens* will provide a more efficient adhesive grip, as compared to its primitive homologue in outgroup taxa. This test seems particularly uncomplicated because the derived and primitive functions are comparable and probably quantifiable. If the derived condition does not provide a better grip, the hypothesis specified here is false.

In summary, the examples treated here span a wide variety of taxa and taxonomic levels, yet none fulfill the conditions necessary for a valid test of adaptation as a driving force behind evolutionary diversification. The tests fail for various reasons: unknown cladistic structure, taxonomic level too high, ambiguity of state at ancestral nodes, failure to identify appropriate outgroups, flawed experimental design, or less than rigorous analysis of current utility. In each case, except those of pre-copulatory mate guarding or the orb web, which involve thousands of species, the test is feasible, but merely incomplete or badly designed. Thus, the neodarwinian viewpoint may be right, but before that can be determined we will need carefully chosen and more thoroughly investigated test cases.

Discussion

The foregoing analysis outlines how the analysis of adaptation might proceed under a cladistic rubric. This type of analysis focuses on historical genesis of adaptation, not merely current utility, and it seeks to test the strongest assertion of neodarwinism—origin and maintenance of adaptation via natural selection. The intent has been to show how to test such assertions, and one may fully appreciate that if cherished examples (e.g. Darwin's finches) fail the test, the general claim of adaptation can be saved by various means. In and of itself, I see nothing wrong in this, because most theories or methodologies (including cladistics) escape falsification. The important result is that the theory required an *ad hoc* explanation to survive—such is the essence of test. Three topics require further consideration: the meaning of the term "stabilizing selection"; the classical view that instances of convergent evolution are evidence of adaptation *ipso facto*; and the consequences of relaxing the assertion that natural selection causes both the origin and maintenance of adaptation.

STABILIZING SELECTION

Although many neodarwinists claim that the persistence of adaptive features is due to stabilizing selection, they may do so from a willingness to call any selection that enforces a central tendency in character variation "stabilizing", rather than distinguishing homologous from non-homologous selection. To illustrate the potential confusion, suppose that a population acquires an adaptive apomorphy that is maintained by stabilizing selection and then subsequently fixed in the population. Further suppose that the trait is then integrated into the developmental program so that other strongly selected traits depend on it epigenetically. It is then valid to explain the persistence of the trait not by its original function, but because it is part of a "co-adapted" complex. In this case, the selection maintaining the trait is a different kind of stabilizing selection than the one

which maintained it in the population initially. To call both stabilizing selection may be correct in a functional sense but also misleading, for then "stabilizing selection" as a concept becomes merely "that which explains stasis". If that kind of shifting usage is actually what enables neodarwinism to claim that "stabilizing selection" explains stasis, then the claim is empirically empty and a logical error. Only if stabilizing selection means homologous selection that stabilizes is it a useful term in this context.

Frequently, of course, workers do distinguish between homologous and analogous selection. Arnold and Wade (1984a, b) explain how the total selection on a trait may be parsed into its logically distinct parts. Likewise, Eberhard (1985) differentiated two explanatory hypotheses because they invoked different selective forces, even though they might produce similar morphological results. The identification of directional selection by its mode of action rather than its effect is not new and presumably the same criteria are applied to stabilizing selection. If so, my reading of the selectionist explanation of stasis or synapomorphy fairly represents the claim.

CONVERGENCE AND ADAPTATION

This paper argues that it is important to distinguish between two meanings of adaptation: as the current utility of a feature ahistorically and ahierarchically viewed, and as a selectionist explanation of synapomorphy. The second is more meaningful in a supraspecific context. Convergence is often considered evidence of adaptation, but it only seems to be evidence for adaptation in the former, not the latter sense.

By definition, convergence involves a polyphyletic set of species displaying an analogous feature. The delimitation of both the feature and the set of species is often at the discretion of the observer. If the resemblance is marked (and sometimes even if it is not), the coincidence is attributed to identical selection acting independently. That automatic attribution should be questioned for three reasons.

First, selection is not the only agent causing change in genomes. Others include viral transmission of genetic information, developmental canalization, or genetic drift. Thus the cause of convergence may not be natural selection acting on the function of the trait. The convergent loss of features, as in cave faunas, provides a concrete instance. Primitive eyelessness (cave oligochaetes) and derived eyelessness (cave fish) are both lack of eyes, but the first never "arose" at all, and the second possibility may have arisen because of a lack of selection altogether. Phenotypic similarity for reasons other than selection clearly is irrelevant to adaptation as construed here.

Second, convergence is often disturbingly subjective. It is in the eye of the observer and thus extends only so far as the observer chooses. It makes little sense to speak of "wings" as an adaptation to "flight", simply because birds, bats, squirrels, spiders, insects, fish, snakes, lizards, and dandelion, ash, and maple seeds, to name only a few, all evolved a range of morphologies which sometimes function to allow flight. This difficult situation of subjectively defined and arbitrarily delimited phenomena contrasts *strongly* with an approach using homology, in which the taxa and the phenomena to be investigated are more objective. We get nothing more from noting that various creatures are at times airborne than the observations we originally used to construct the theory.

Third, if the phenotypes considered did arise by selection, the different instances should have been due to the same selective pressure or force on phenotypes that lacked the derived morphologies if the phenotypes are to be considered as adaptations. Only then would evidence exist for truly parallel events. Adaptation is a causal, hierarchically

organized hypothesis about polarized, directional evolution. The observation of a functional trait in a single taxon clearly can tell us nothing about how and why it arose and, indeed, adaptation as current utility makes no claims about origin. It makes only the weak claim that if the trait functions one way in one case, then maybe similar traits function the same way. On the other hand, if for each instance of convergence one has elucidated the function of the derived trait as well as the primitive homologue and the derivation is consistent with selection for the derived function, then one has essentially performed the kind of analysis advocated here. Mere observation of the function of a "trait" in a taxon is but the initial speculation in a long process—it is not *ipso facto* evidence of adaptation. Given successful cladistic tests of several phenotypically and functionally similar adaptations (=convergence), the repeated instances may lead to interesting generalizations about the likelihood of particular solutions in particular lineages, or to particular kinds of problems, but repetition by itself is neither necessary nor sufficient evidence to infer adaptation.

For evidence that the different perspectives make a difference, consider a classic instance of convergence—coral snake mimicry. The phenomenon was reviewed by Greene and McDiarmid (1981). Their intent was only to show that mimicry occurred, so I use their review in a way they did not intend. They stated, "The mimicry hypothesis postulates increased survival of coral snake phenotypes among a spectrum of available patterns, from the exposure of predator populations to a dangerous coral snake model." Their analysis attempted to show that the similarity between mimic and model was not due to chance and was of current utility. However, the more cogent test would show that a mimic suffers less predation due to its visibility than do species retaining the primitive color pattern of its ancestor. Such tests, apparently, have never been carried out. If in some cases the plesiomorphic color pattern is cryptic (e.g. *Atractus*), being a palatable mimic may entail a higher rate of predation than simple cryptic concealment. *Lampropeltis triangulum* and *Erythrolamprus guentheri* also mimic several species of coral snakes, but their sister taxa are unknown, and several cryptically colored candidates exist. If the sister taxa to these mimics are cryptic and if the cryptic species suffer less predation than the palatable mimics, then the hypothesis that the coral snake phenotype is an adaptation to reduce predation is seriously jeopardized. Furthermore, until the answer to that question is known to be negative, the assertion that the phenotype is adaptive is still speculative. Evidence that it functions to reduce predation in normal mimics relative to experimentally manipulated mimics is only half the argument. The hypothesis of adaptation in the historical sense depends on sister taxa, not on a polyphyletic set of non-homologous "convergent" coincidences.

ORIGIN AND MAINTENANCE OF ADAPTATION

One objection to my analysis of adaptation may be its presumption that the neodarwinist model sees natural selection both originating and maintaining adaptations in a uniformitarian way. Consider the extreme cases of either involvement or non-involvement of natural selection in either the origin or maintenance of adaptive traits. Four possibilities result which parse the diversity of opinion into manageable categories (Fig. 8), to be discussed in turn.

Origin and maintenance—This, I think, is the predominant neodarwinian viewpoint, and it is quite testable. Its testability derives from the willingness to suppose continuity of cause, a kind of uniformitarianism, from the origin of the trait to present times. The trait

	ORIGIN	NOT ORIGIN
MAINTENANCE	ADAPTATION	EXAPTATION
NOT MAINTENANCE	DEVELOPMENTAL CONSTRAINTS	DRIFT, NEUTRALISM
	PHYLOGENETIC INERTIA	EARTH HISTORY

Fig. 8. Schematic diagram of modes of evolutionary change contrasted by involvement of natural selection in origin or not, and/or maintenance or not. See text for further explanation.

arose and was fixed by natural selection because it improved some component of fitness relative to the primitive sister group. It further supposes that the empirically observed stasis in traits (which forms the basis for taxonomy and phylogenetic reconstruction) is due to stabilizing selection. Under the origin + maintenance hypothesis, homologous and identical function of the trait in a number of taxa is evidence that the original function of the trait has been conserved. If so, conditions similar to its origin persist, and may be investigated in present ecological time. By this means, theories about the origin of the trait may be promulgated and tested.

Origin, not maintenance—As Fig. 8 declares, this possibility includes such hypotheses as phylogenetic inertia and developmental constraints. It also includes a host of what might be called "correlative *ad hocs*" such as large population size (drift and selection ineffectual), genetic homeostasis, epistatic interactions, linkage, pleiotropy, or, most baldly, assertions of correlation with some unidentified trait that is strongly selected. These explanations are often invoked when the primary hypothesis of selective value fails. Such theories predict no consistent trend in data from ingroup–outgroup ecological comparisons. Consistent trends might bear on the "not maintenance" assertion, but would be silent about origin. They also predict no particular commonality or homology in function between ingroup taxa, but the observation of improbably similar functions of a trait in many taxa would not falsify the assertion, because the hypothesis of inertia or constraint on morphology also explains similar functions. Such theories make no claim about current utility at all. They also insulate any hypothesis about origin from direct test because they deny continuity between conditions prevailing at the origin and conditions now. Such theories are hard to disprove.

The view that features may have been adaptive at some point, but are now maintained by something other than selection, is probably the most widely accepted explanation of synapomorphy among biologists today. It is a weak theory which nevertheless may be correct for the majority of features. A now classic example is the suggestion that tropical trees have large fruits because they were once dispersed by vertebrates now extinct, such as New World camels, glyptodonts, and gomphotheres (Janzen and Martin, 1982). It is an hypothesis about adaptive origin, but not about adaptive maintenance. Many workers concur with Howe (1985) that it is at best weakly testable. A more mundane example could be any remarkably consistent taxonomic feature that has no [known] strongly selected function. To draw from a group of animals I know well, although several exactly specifiable convolutions of the ejaculatory duct within the male secondary genitalia of

theridiosomatid spiders defines the family (Coddington, 1986b), it is unlikely that anyone would assert that this extraordinary conservatism is caused by relentless stabilizing selection, on the route of the duct in all theridiosomatid lineages.

Because arguments about stabilizing selection are so weak at high taxonomic levels, the darwinian paradigm is best tested at low taxonomic levels. At such levels, true novelties may still be maintained by stabilizing selection in all lineages. Their conversion into developmental "constraint" or phylogenetic "inertia" may not have yet happened. Another reason why the search for verified adaptations should focus on lower taxonomic categories is that the natural history tends to be more recoverable and more comparable; homology of function and selection is easier to establish. The effect of origin not maintenance theories, then, is to stifle research on adaptation because it is a weak, relatively untestable theory which nevertheless probably applies at those higher taxonomic levels at which arguments about adaptation traditionally occur.

Not origin, but maintenance—The neologism "exaptation" of Gould and Vrba (1982) fits this category. Features arise by allometry, linkage, heterochrony, past bouts of selection, or whatever, and are suddenly frozen in form and function by selection. To the extent that the origin of a feature might be attributable to a simpler cause than adaptation, exaptations may be real. However, such a feature would have to exhibit from the beginning the kind of efficient design adaptations usually do, so that subsequent change does not take place. Otherwise, the "exaptive" portion of the feature is simply plesiomorphic, and the adaptive portion becomes the adaptation. The idea that exaptations are "available for cooptation" and subsequently are modified by selection, ignores the hierarchical nature of adaptation. Clearly, all hierarchically more general adaptations are "exaptations" with respect to less general homologues and thus all we gain by labelling them "exaptations" is a term useful in disguising our ignorance about the level at which the "exaptation" is an adaptation. Apomorphy and plesiomorphy cause similar confusion; all plesiomorphies, if homologues, are synapomorphies at some more general level (Patterson, 1982). Of course, "exaptation" could be redefined to be merely primitive to "adaptation", in strict analogy to plesiomorphy and apomorphy, but Gould and Vrba seemed to see a larger role for this term than as a junior synonym of plesiomorphy. In any case, a "not origin but maintenance" theory, like its inverse, separates origin and maintenance in such a way that hypotheses about origin become untestable, although of course hypotheses about maintenance are still testable.

Neither origin, no maintenance—Some may think that the final category is nihilistic, but such agents as earth history (Raup, 1986), drift, linkage disequilibrium, neutralism, or even non-equilibrium thermodynamics (Wiley and Brooks, 1982) may explain much of what adaptation has not. By decoupling the trait from its environment in both origin and maintenance, these theories at least re-enter the uniformitarian universe and become more testable. Their chief prediction would be that evolutionary novelties are not usually attributable to selection. Their chief obstacle is the rather overwhelming circumstantial evidence of the current utility, dare we say adaptation, of traits.

Conclusions

Cladistics offers clarification and testability to ecological hypotheses that otherwise can be judged only by their plausibility. The cladistic approach to evolutionary ecology has the following strengths and weaknesses.

First, discussions of homology of function or selection could become meaningful and commonplace. One can analyse the taxonomic distribution of any trait—color, behavior, physiology—and still speak meaningfully of homology of function. Past studies of this type have tended to limit discussions of homology to the morphologies that produce similar functions, but conceivably homologous functions may compete with more conventional kinds of homology in phylogenetic inference.

Second, blending cladistics and ecology will allow the specification of more exact evolutionary histories of ecological traits. Heretofore, evolutionary ecology has often used the same theory it sought to test—natural selection—in elaborating evolutionary scenarios about the course evolution supposedly took. Using the theory to analyse the data, and then using the results of the analysis to corroborate the theory is circular, and will not produce discordance between results and theory. The use of cladistic theory to analyse ecological or behavioral data will probably imply scenarios that differ substantially from selectionist predictions. Cladistics can also add the essential historical element to comparative fields like biomechanics or evolutionary ecology. These fields have already developed the analysis of biological function and design efficiency into remarkably precise sciences; one must next ask whether evolution in fact behaved the way the theory predicted it should have.

Third, cladistics can suggest experimental designs, whether observational or manipulative, that are meaningful in an historical context as well as predictive. The primitive sister group is the most appropriate null hypothesis. Without this insight, the mistakes of inverting primitive and derived states or confusing secondary loss and primitive absence, become more likely.

Fourth, cladistics may offer a bridge between two increasingly distant parts of evolutionary theory—micro- and macroevolution. Population biology can show that a trait has an effect on fitness, or that a trait functions near an engineering optimum, but population biology has failed to explain the consistent occurrence of traits across phylogenetic lineages in a satisfactory way.

These are the strong points of the blend suggested above. The weak points are, first, that the cladistic analysis is only as good as the data it uses (as mentioned above, I make no claim for any of the cladograms included here), and even so the method must be applied correctly.

Second, and something not stressed in any of the above examples, strict parsimony methods are agnostic about gains versus losses. However, one gain and one loss versus two independent gains are cladistically, but not biologically equivalent. A single strategically placed homoplasious event in a cladogram can result in so many ecological scenarios that checking each one becomes prohibitively difficult.

Third, the test outlined here is most applicable to hypotheses claiming both origin and maintenance of the trait by natural selection. As suggested above, at least three other logical possibilities exist. Nonetheless, the use of independent data to infer phylogenies for evolutionary ecological scenarios, and the use of those phylogenies to guide ecological comparisons should clarify and sharpen retrospective explanations of important events in evolutionary history.

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REFERENCES

ABBOTT, I., L. K. ABBOTT AND P. R. GRANT. 1977. Comparative ecology of Galapagos ground finches (*Geospiza* Gould): evaluation of the importance of floristic diversity and interspecific competition. Ecol. Monogr. 47: 151–184.

ARNOLD, S. J. AND M. J. WADE. 1984a. On the measurement of natural and sexual selection: theory. Evolution, 38(4): 709–719.

ARNOLD, S. J. AND M. J. WADE. 1984b. On the measurement of natural and sexual selection: applications. Evolution, 38(4): 720–734.

BOWMAN, R. I. 1961. Morphological differentiation and adaptation in the Galapagos finches. Univ. Calif. Publ. Zool. 58: 1–302.

BRANDON, R. N. 1978. Adaptation and evolutionary theory. Stud. Hist. Phil. Sci. 9: 181–206.

BROOKS, D. R., R. T. O'GRADY, AND D. R. GLEN. 1984. Phylogenetic analysis of the Digenea (Platyhelminthes: Cercomeria) with comments on their adaptive radiation. Can. J. Zool. 63: 411–433.

CHARLESWORTH. B., R. LANDE, AND M. SLATKIN. 1982. A neo-Darwinian commentary on macroevolution. Evolution 36: 474–498.

CLUTTON-BROCK, T. H. AND P. H. HARVEY. 1979. Comparison and adaptation. Proc. R. Soc. Lond. B 205: 547–565.

CODDINGTON, J. A. 1985. Review of The Explanation of Organic Diversity: The Comparative Method and Adaptations for Mating. J. Cladistics, 1: 102–107.

CODDINGTON, J. A. 1986a. The monophyletic origin of the orb web. *In*: W. A. Shear (ed.). Spider Webs and Spider Behavior. Stanford Univ. Press, Palo Alto, California.

CODDINGTON, J. A. 1986b. The genera of the spider family Theridiosomatidae. Smith. Contr. Zool. 422: 1–96.

DOBZHANKSY, T. 1970. Genetics of the Evolutionary Process. Columbia Univ. Press, New York, New York.

ENDLER, F. A. 1986. Natural Selection in the Wild. Princeton University Press, Princeton, New Jersey.

EBERHARD, W. G. 1985. Sexual Selection and Animal Genitalia. Harvard University Press, Cambridge, Massachusetts.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. Amer. Nat. 125: 1–15.

FISHER, D. C. 1985. Evolutionary morphology: beyond the analogous, the anecdotal, and the ad hoc. Paleobiology 11: 120–138.

FORD, E. B. 1975. Ecological Genetics, 4th edn Wiley, New York, New York.

FUTUYMA, D. J. 1979. Evolutionary Biology. Sinnauer, New York, New York.

GOULD, S. J. AND E. S. VRBA. 1982. Exaptation—a missing term in the science of form. Paleobiology 8: 4–15.

GRANT, P. R. 1981. Speciation and the adaptive radiation of Darwin's Finches. Amer. Sci. 69: 653–663.

GREENE, H. W. AND R. W. MCDIARMID. 1981. Coral snake mimicry: does it occur? Science 213: 1207–1212.

GROVES, C. P. 1983. Phylogeny of the living species of rhinos. Z. zool. Syst. Evolut.-forsch. 21: 293–313.

HOWE, H. F. 1985. Gomphothere fruits: a critique. Amer. Nat. 125: 853–865.

JANZEN, D. H. AND P. MARTIN. 1982. Neotropical anachronisms: what the gomphotheres ate. Science 215: 19–27.

KETTLEWELL, D. H. B. 1961. The phenomenon of industrial melanism in Lepidoptera. Ann. Rev. Ent. 6: 245–262.

KRIMBAS, C. B. 1984. On adaptation, neo-Darwinian tautology, and population fitness. Evol. Biol. 17: 1–57.

LACK, D. L. 1947. Darwin's Finches. Cambridge University Press.

LEIGH, E. G. 1971. Adaptation and Diversity: Natural History and the Mathematics of Evolution. Freeman, Cooper, and Co.

LEWONTIN, R. C. 1978. Adaptation. Sci. Amer. 239: 212–230.

LEWONTIN, R. C. 1980. Adaptation. Encyclopedia Einaudi, Milan.

MADDISON, W. P., M. J. DONOGHUE AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. Syst. Zool. 33: 83–103.

MAYNARD-SMITH, J. 1978. Optimization theory in evolution. Ann. Rev. Ecol. Syst. 9: 31–56.

MAYR E. 1982. Adaptation and Selection. Biol. Zbl. 101: 161–174.

McDONALD, J. F. 1983. The molecular basis of adaptation: a critical review of relevant ideas and observations. Ann. Rev. Ecol. Syst. 14: 77–102.

OSTER, G. F. AND E. O. WILSON. 1978. Caste and Ecology in the Social Insects. Monographs in Population Biology. No. 12. Princeton University Press, Princeton, New Jersey.

OTTO, C. AND L. M. NILSSON. 1981. Why do beech and oak trees retain leaves until spring? Oikos 37: 387–390.

PATTERSON, C. 1982. Morphological characters and homology. Systematics Association Special Volume 21: 21–74.

PETRY, D. 1982. The pattern of phyletic speciation. Paleobiology 8: 56–66.

RAUP, D. M. 1986. Biological extinction in earth history. Science 231: 1528–1533.

RIDLEY, M. 1983. The Explanation of Organic Diversity: The Comparative Method and Adaptations for Mating. Oxford Univ. Press, Oxford.

SCHLUTER, D. 1984. Morphological and phylogenetic relations among the Darwin's finches. Evolution 38: 921–930.

SCHLUTER, D. AND P. R. GRANT. 1984. Determinants of morphological patterns in communities of Darwin's finches. Amer. Nat. 123: 175–196.

SIMPSON, G. G. 1953. The Major Features of Evolution. Columbia Univ. Press, New York, New York.

STEBBINS, G. L. AND F. J. AYALA. 1981. Is a new evolutionary synthesis necessary? Science 213: 967–971.

TURNER, J. R. G. 1981. Adaptation and evolution in *Heliconius*: a defense of neodarwinism. Ann. Rev. Ecol. Syst. 12: 99–121.

WALLACE, B. 1984. Adaptation, neo-Darwinian tautology, and population fitness: a reply. Evol. Biol. 17: 59–71.

WALLACE, B. AND A. M. SRB. 1964. Adaptation. 2nd edn Prentice-Hall, Englewood Cliffs, New Jersey.

WANNTORP, H. 1983. Historical constraints in adaptation theory: traits and non-traits. Oikos 41: 157–160.

WILEY, E. O. AND D. R. BROOKS. 1982. Victims of history—a nonequilibrium approach to evolution. Syst. Zool. 30: 1–11.

WILLIAMS, G. C. 1966. Adaptation and Natural Selection. Princeton Univ. Press, Princeton, New Jersey.

WILLIAMS, E. E. AND J. A. PETERSON. 1982. Convergent and alternative designs in the digital adhesive pads of scinid lizards. Science 215: 1509–1511.

WILSON, E. O. 1980. Caste and division of labor in leaf cutter ants (Hymenoptera: Formicidae: *Atta*). II. The ergonomic optimization of leaf cutting. Behav. Ecol. Sociobiol. 7:157–165.

YANG, S. Y. AND J. L. PATTON. 1981. Genic variability and differentiation in the Galapagos finches. Auk 98: 230–242.