5 Adaptation

The search for a functional (adaptive) fit between an organism and its environment is one of the dominant themes in evolutionary biology (see, e.g., Lewontin 1978; Dunbar 1982; Coddington 1988). There are three components to adaptation: origin, diversification, and maintenance of characters. Microevolutionary studies concentrate on the maintenance of traits in current environments where the processes shaping the interactions between the organism and its environment can be observed and measured directly. Having untangled this complicated web, these researchers then extrapolate backwards to the processes involved in the character's initial appearance in, and subsequent spread through, the ancestral species.

Historical ecology complements these studies by providing direct estimates of phylogeny, which can be used as a template for reconstructing the historical patterns of character origin and diversification. Such a template can help ecologists to focus their search for the processes underlying adaptation. For example, consider an interesting (but improbable) group of species with the following characteristics (table 5.1) and phylogenetic relationships (fig. 5.1).

In this group the relationship between a character and the environment in which it originated can be investigated for only one taxon and one character state, namely, the evolutionary increase in size (big) in species D (fig. 5.1). Researchers interested in the processes involved in character origin and adaptive success, if any, should concentrate their efforts on this species. The presence of small, blue, and square in species A, small, red, and square in species B, small, red, and round in species C, and red and round in species D are all ancestral legacies. Studies of these species will uncover the processes involved in character maintenance. Combining the results from all these studies will provide us with a more direct estimate of the relationship among the processes underlying the origin, spread, and maintenance of potentially adaptive traits. The incorporation of both the patterns of the past and the processes of the present into our framework of evolutionary explanations will thus strengthen our hypotheses of adaptation.

In this chapter we are going to examine the types of questions about adaptation that can be investigated from a historical ecological perspective. In

Table 5.1   Distribution of three characters among four members of a monophyletic group (species A + B + C + D) and the outgroup (taxon X).

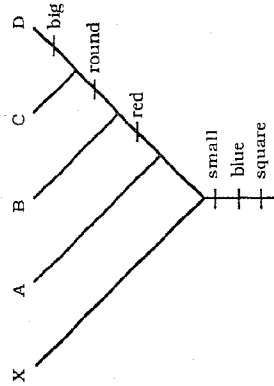| Trait	Species				
	X	A	B	C	D
Color	blue	blue	red	red	red
Shape	square	square	square	round	round
Size	small	small	small	small	big

Fig. 5.1. Examining adaptationist hypotheses. Phylogenetic tree for the improbable species with the distribution of the three characters in table 5.1.

so doing, we hope to expand upon the long-standing tradition of examining adaptation within a comparative framework, advocated and illustrated by numerous researchers "ever since Darwin." Before we begin, however, it is necessary to reemphasize and expand upon some general methodological points from chapter 2.

Character Optimization: How to Interpret Characters on a Phylogenetic Tree

One cardinal rule in historical ecology is *never bias your analysis by using the ecological information you want to study to build your phylogenetic tree.* Historical ecologists must begin their explorations with two pieces of information, a phylogenetic hypothesis and the relevant ecological data. The best-supported (most-parsimonious) sequences of evolutionary transformations for the ecological characters, be they binary or multistate, can then be determined by reference to the phylogenetic tree. This is called character optimization. We will discuss optimization procedures beginning with the method originally developed by Farris (1970), which has become known as Farris optimization.

Unambiguous binary character

1. Figure 5.2 depicts a phylogenetic tree for a hypothetical group of taxa. The distribution of a binary ecological character (states a and b) is mapped at the ends of the branches.

2. "Generalizing down" the tree (fig. 5.3): Label the two nodes that are farthest from the ingroup node in the following manner: (1) label the node "a" if the two closest nodes or branches are either both a or a and a, b; (2) label the node "b" if the two closest nodes or branches are either both b or b and a, b; (3) if the closest branches/nodes have different labels (one a and the other b), then label the node "a, b." Continue working towards the ingroup node in this manner. (Does this sound familiar?) Let's start on the left side of the tree. Node 1 connects two species exhibiting character a, so we generalize
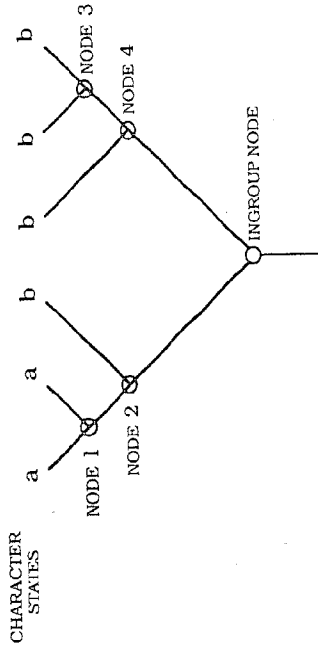

Fig. 5.2. Phylogenetic tree with the distribution of ecological character states a and b.
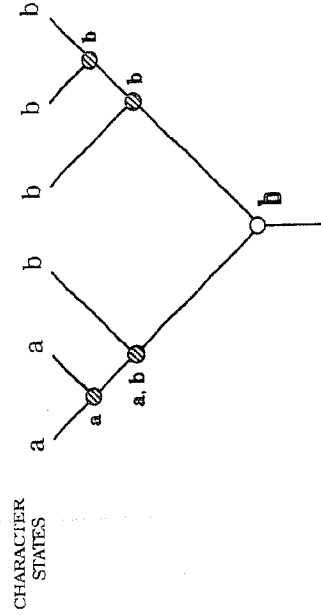

Fig. 5.3. Step 1 in Farris optimization of a binary character: generalize down the tree.
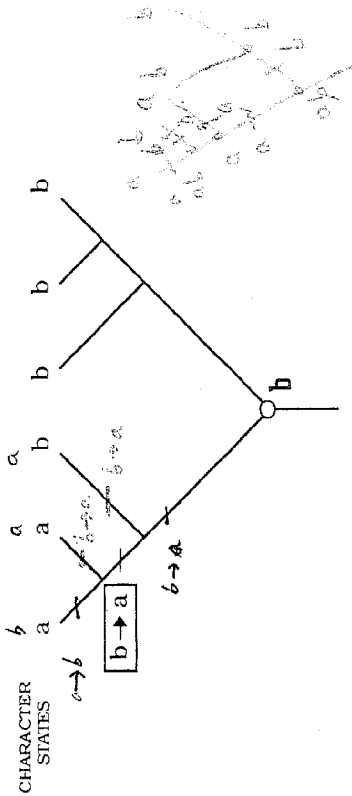
Fig. 5.4. Step 2 in Farris optimization of a binary character: predict up the tree.

that the nodal (ancestral) state is a. This node, in turn, has a sister-group relationship with a taxon exhibiting state b; therefore, the state at node 2 is ambiguous for a or b. On the right side of the tree, nodes 3 and 4 are both labeled "b" because all three taxa exhibit that character state. Finally, we assign a value of b to the ingroup node because the two nodes directly above it have states a, b and b, so b "wins out" over a by majority vote (the principle of parsimony). Any ambiguity at the ingroup node may be resolved by reference to outgroups. (Starting to sound familiar yet? If not, refer back to the discussion of resolving the outgroup node, presented in chapter 2.)

3. "Predicting up" the tree (fig. 5.4). Move from the ingroup node up the tree, resolving any ambiguity by comparing the value of the ambiguous node with the value of the node directly below it. In this example only node 2, designated "a, b" in figure 5.3, is ambiguous. Since the value of the node below it is b, node 2 is reassigned state b. All nodal states have now been unambiguously resolved on the tree. Farris optimization thus provides us with the following evolutionary hypothesis for this binary character: (1) state b is a persistent ancestral condition in four of the six terminal taxa (plesiomorphy); (2) there was a change from b to a in the ancestor of the two species that now exhibit state a (apomorphy).

Unambiguous multistate character

1. Figure 5.5 depicts a phylogenetic tree for a hypothetical group of taxa. The distribution of a multistate ecological character (states x, y, and z) is mapped at the ends of the branches.

2. Generalizing down the tree (fig. 5.6): Using the same logic as that described for binary characters, node 1 is labeled with state z because both taxa connected by the node exhibit state z; node 2 is y, z because it connects a z
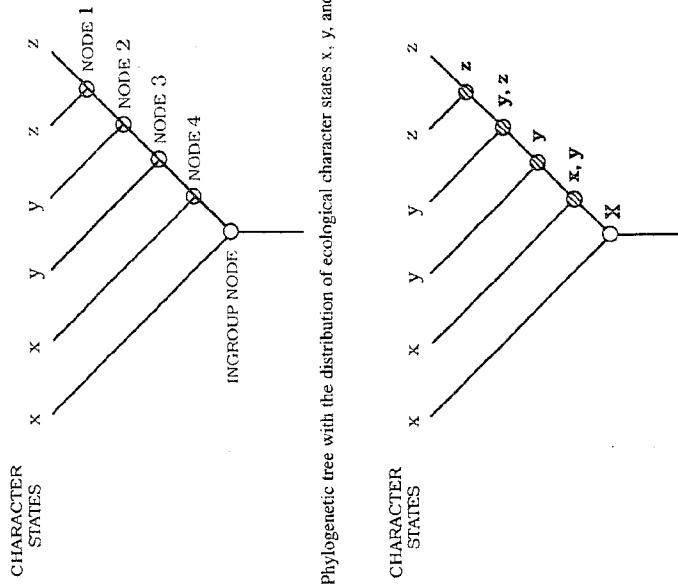
Fig. 5.5. Phylogenetic tree with the distribution of ecological character states x, y, and z.

Fig. 5.6. Step 1 in Farris optimization of a multistate character: generalize down the tree.

node with a y branch (taxon); node 3 is y because it connects a y, z node with a y branch; node 4 is x, y because it connects a y node with an x branch; and finally, the ingroup node has a value of x because it connects an x, y node with an x branch.

3. Predicting up the tree (fig. 5.7): Nodes 2 and 4 are ambiguous in this example. As discussed for the binary character, resolution of these ambiguous nodes is dependent upon the character state of the node immediately below them. Accordingly, node 4 is reassigned a value of x and node 2 is labeled "y." All nodal states have now been unambiguously resolved on the tree. Farris optimization thus provides us with the following evolutionary hypothesis for this multistate character: (1) state x, occurring in the oldest two taxa, is plesiomorphic for the clade; (2) there was a change from x to y in the common ancestor of the remaining four taxa (apomorphy); (3) there was a change from y to z in the common ancestor of the terminal two taxa (apomorphy). All the ecological traits are persistent ancestral conditions in the

2. The first stage of Farris optimization proceeds as previously described (fig. 5.9).

3. The fun begins when we proceed to the second stage of the optimization procedure. Predicting up the tree produces the solution presented in figure 5.10. According to this solution, (1) s is plesiomorphic, (2) t evolved from s twice (convergence), and (3) s evolved from t once (reversal). This implies

Fig. 5.9. Step 1 in Farris optimization of an ambiguous, binary character: generalize down the tree.

Fig. 5.10. Step 2 in Farris optimization of an ambiguous, binary character: predict up the tree.
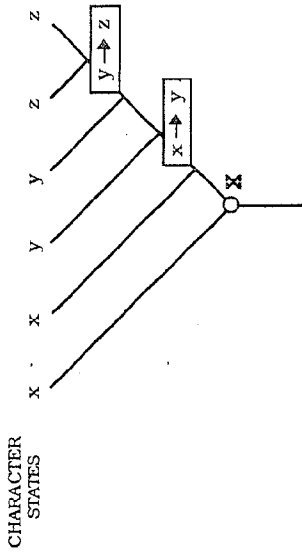
Fig. 5.7. Step 2 in Farris optimization of a multistate character: predict up the tree.

species that are extant today (and there is no reason to believe that any of them evolved more than once).

Like many aspects of the natural world, optimization does not always produce such unambiguous results. In the remainder of this book we hope to show you that the real world is a mixture of cases, some readily interpretable and others not. But first, let us consider an example that cannot be fully resolved.

Ambiguous binary character

1. Figure 5.8 depicts a phylogenetic tree for yet another hypothetical group of taxa. The distribution of a binary ecological character (states t and s) is mapped at the ends of the branches.
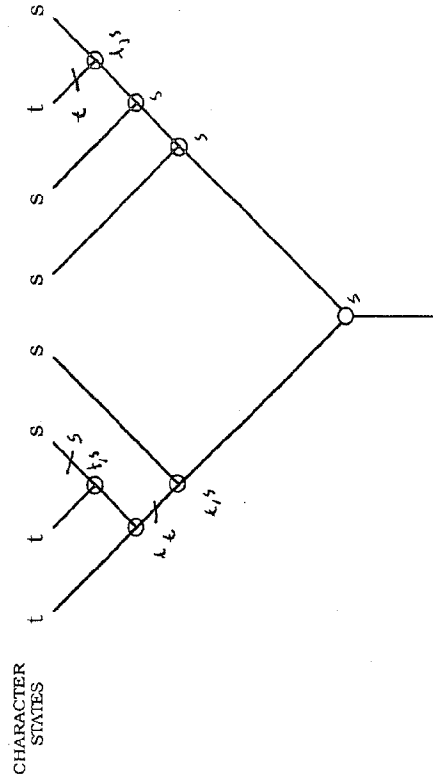

Fig. 5.8. Phylogenetic tree with the distribution of ecological character states t and s.

when multistate characters are considered (Swofford and Maddison 1987). Donoghue (1989) noted additional theoretical and empirical examples in which optimization failed to resolve the sequences completely. Although we would like nature to provide us with a perfect record of evolution, this does not always happen. In such cases, we expect that phylogenetic optimization will tell us exactly where the ambiguity lies, even if it cannot provide an unambiguous interpretation.

Methodological Caveats for the Historical Ecologist

First, remember that phylogenetic trees can be rotated at their nodes without changing relationships. For example, figures 5.12a and 5.12b are the same phylogenetic tree.

Second, remember that a robust phylogenetic tree is based on analysis of numerous characters, each of which was polarized using outgroup comparisons. Any of the characters used may exhibit some degree of homoplasy, in which case the distribution of the characters on the phylogenetic tree does not correspond exactly to the sequence postulated originally when the characters were polarized (the transformation series; fig. 5.13). *Thus, it is not methodologically sound to polarize one character using an outgroup and then to assume that the postulated character transformation series represents the true phylogenetic sequence of events.* This type of error results from a subtle misunderstanding of the purpose of outgroup comparisons. While it is true that polarizing character states through outgroup comparison produces a hypothesis of the sequence of evolutionary changes in that character, it is also true that this hypothesis can only be tested by comparing it to the hypothesized evolutionary sequences of other characters. In other words, a character

Fig. 5.12. Rotating phylogenetic trees around their nodes does not change the phylogenetic relationships among the taxa.
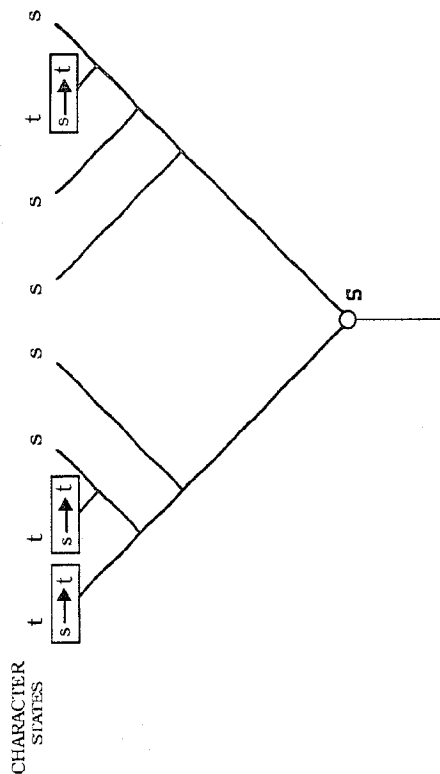
(a)   (b)

ROTATE

CHARACTER STATES

Fig. 5.11. An equally parsimonious interpretation of the evolution of the binary character in figure 5.10.

that not all the species exhibiting either t or s inherited that trait from the same ancestral source.

4. If we examine this particular example more closely, however, we realize that the result of Farris optimization is not the only hypothesis that explains the distribution of t and s among these species. An equally parsimonious interpretation of these data is that (1) s is plesiomorphic, and (2) there have been three transitions from s to t (convergence) in extant species (fig. 5.11). This implies that all species displaying s inherited that trait from the same ancestral source.

Despite the fact that phylogenetic optimization does not provide an unambiguous answer in this case, all is not lost. In some systems, additional biological information (e.g., developmental or biochemical data) can be brought to bear on the problem. In other systems, we can attempt to evaluate the conflicting hypotheses by direct experimental studies in both the field and the laboratory. For example, figure 5.11 suggests that t has arisen independently from s three times in recent species. In cases of convergent evolution, common selective pressures from the environment are immediately suspected. If the species exhibiting t share an environmental regime that is not associated with the other members of the clade, all of which exhibit s, we would have reason to support this hypothesis. If we found that the species exhibiting t did not occur in common environments, we might turn our attention to the evolutionary sequence depicted in figure 5.10.

As you can imagine, the potential for alternative explanations increases

Fig. 5.13. Dangers inherent in assuming that the transformation series for one character represents the true evolutionary sequence of character change. In this example, the outgroup state for the character is x. Since both the outgroup and some members of the ingroup possess the character state x, the character transformation series is hypothesized to be x to y. However, when the character is optimized on a phylogenetic tree constructed from a number of different characters, the actual phylogenetic transformation is discovered to have been x to y to x.

transformation series does not stand on its own, independent from the underlying phylogenetic relationships of the organisms.

A final point to remember is that an adaptive explanation can be weakened if some members of the study clade are removed from the analysis. The world of phylogenetic reconstruction is fraught with enough difficulties in terms of sampling procedures and the incorporation of fossil evidence (Doyle and Donoghue 1986; Donoghue et al. 1989), without augmenting the problem by eliminating available information from the analysis. For example, consider a monophyletic group of fishes bearing the nest-building characters w, x, y, and z (fig. 5.14).

Failure to incorporate some of the taxa bearing trait w into the analysis will produce the incorrect postulate of a linear sequence of character change from w to x, x to y, and y to z (fig. 5.14a). When all the members of the group are considered, the evolutionary sequence is demonstrated to be the nonlinear w to x, w to y, and w to z. The situation depicted in figure 5.14b is slightly different. Here, although the hypothesized sequence from w to x to y to z is correct, this analysis will grossly underestimate the degree of phylogenetic constraint on the proposed evolutionary change. In this clade, 75% of the taxa bear the ancestral character state w (i.e., 25% of 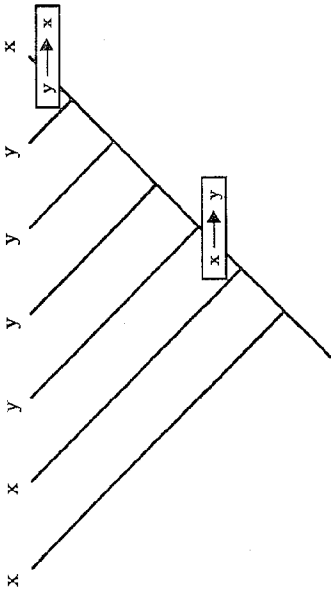the distribution supports a proposal of historical lability in the trait). Eliminating taxa bearing the plesiomorphic condition from the analysis artificially inflates to 50% the proportion of taxa displaying a derived character state, thus making it appear that the character has been evolutionarily labile.

Now, on to the exciting world of adaptive changes in phylogeny. We will

present this material in the following sequence: (1) formulating hypotheses of adaptation within a phylogenetic framework; (2) examining the temporal sequence of adaptive changes; (3) examining the evolutionary association of traits ("coadapted traits" within a clade); (4) examples of convergent adaptation; (5) examples of divergent adaptation; and (6) examining phylogenetic constraints on ecological diversification, including a discussion of phylogenetic approaches to documenting adaptive radiations.
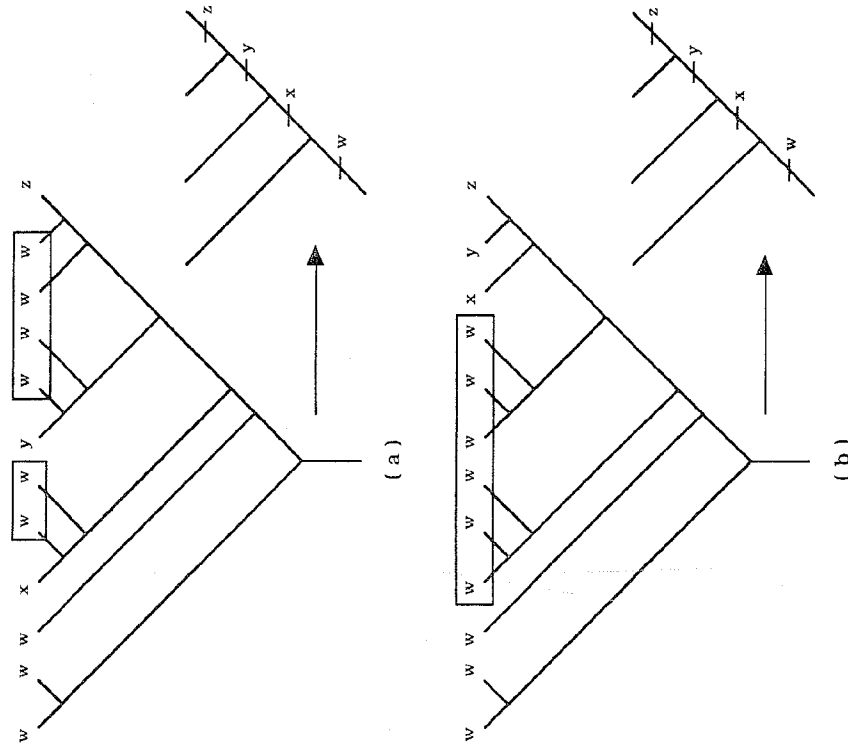

Fig. 5.14. Example demonstrating the problems that can arise when adaptive hypotheses are formulated within an incomplete phylogenetic framework. (a) A nonlinear evolutionary transformation of traits appears linear when taxa are removed. (b) The amount of phylogenetic conservatism is greatly underestimated by removing taxa from consideration.
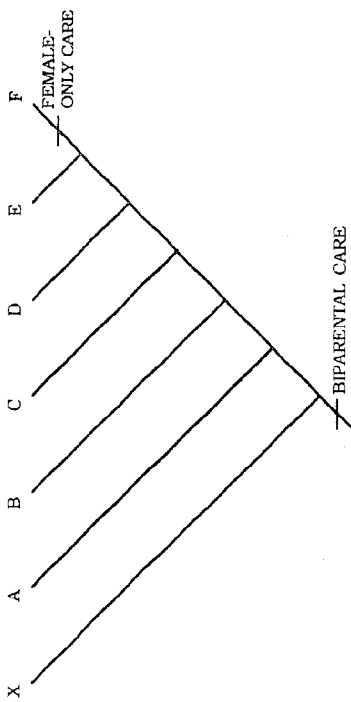
Fig. 5.15. Hypothetical example outlining the applicability of phylogenetic systematics to questions concerning the evolution of behavioral/ecological traits. The distribution of parental-care behaviors in the hypothetical fishes has been mapped onto a phylogenetic tree constructed from characters other than the parental-care trait (e.g., morphological data). The occurrence of biparental care is correlated with the phylogenetic relationships of species A, B, C, D and E. The appearance of female-only care is an autapomorphy for species F.

Formulating the Question

Ecologists frequently strive to understand "why" the members of one species act the way they do. For example, suppose you were interested in studying a hypothetical species of fish, C for short, in which both the male and the female guard their offspring. Question: Why does C show biparental care? Traditionally, you would seek the answer to this question by performing a series of sophisticated cost/benefit analyses on populations of C. Now, let us consider the question within the larger framework of phylogeny. When the distribution of parental care behaviors is mapped onto the phylogenetic tree for the genus to which C belongs, the pattern shown in figure 5.15 emerges.

Biparental care occurs in the outgroup (X) and taxa A, B, C, D, and E. Since its distribution is correlated with the phylogenetic relationships of these taxa, its presence in species C represents the persistence of an ancestral trait in that species. The answer to the question, Why does C show biparental care? is thus, because its ancestor did. Although cost/benefit analyses will uncover valuable information concerning the maintenance of biparental care (**plesiomorphic** trait) under **current** environmental conditions, such analysis does not address why that character was originally successful. In order to explain this, we need two additional pieces of information: an expanded phylogenetic analysis incorporating additional genera of fishes to establish the evolutionary "point of origin" of the biparental trait and an assessment of that *ancestor's* biology in *its* environment. But this is a different question alto-

gether, and takes us on an excursion into the past, both genealogical and environmental. From an adaptationist perspective, the pertinent question for this clade is, Why does species F show female care only? Since female care represents the evolution of a **derived** character state in conjunction with **current** environmental conditions, cost/benefit analyses in this case would address the question of character origin, the more relevant component of the "why" of evolution to the adaptationist program.

Why are there one- and two-horned species of rhinos?

The preceding hypothetical example demonstrates the dangers of addressing evolutionary "why" questions within the context of a single species. However, omitting the historical component from evolutionary explanations will generate similar problems in formulating the relevant evolutionary hypothesis, regardless of the number of species investigated (Ridley 1983; Wanntorp 1983; Brooks 1985; Brooks and Wiley 1988). Coddington (1988) provided an excellent example of this in his reanalysis of the adaptationist explanation for the presence of one-horned and two-horned species of rhinos. Lewontin (1978) postulated that the one-horned condition and the two-horned condition represent independently achieved, equally functional, adaptive peaks in the evolution of antipredator defense structures. This scenario implies that both conditions arose *de novo* from a hornless condition. Coddington investigated this hypothesis by mapping horn number onto a phylogenetic tree for the rhinoceratids (fig. 5.16).
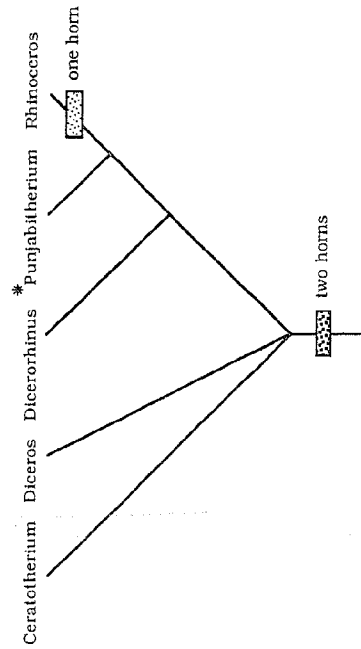

Fig. 5.16. Phylogenetic tree of rhinoceratids based upon dental and osteological characters, mapping distribution of horn number. * = an extinct genus. (Based on Groves 1983; redrawn from Coddington 1988.)

The distribution of horn numbers on the phylogenetic tree suggests that the two-horned condition is plesiomorphic for the group, including extinct species. The single-horned condition is derived from the two-horned condition through the loss of the frontal horn. Since the two conditions were not achieved independently from a nonhorned condition, and thus do not represent two alternative adaptive peaks, it is difficult to postulate an equally adaptive, antipredator function for each character state. Nor is it possible to state that two horns are better than one, because the plesiomorphic condition is two horns. However, as in the preceding example, placing the problem within a phylogenetic framework generated at least two new questions. The "whys" of two horns must be examined within the context of the ancestor and the environment in which the trait originated. Although difficult, this call for a detailed knowledge of past environments should excite students of paleoecology (a discipline also called "historical ecology" [Rymer 1979] or "zooarchaeology" by archaeologists). A more tractable question concerns the reduction in horn number from two to one in the genus *Rhinoceros*. If we cannot unequivocally postulate that horn number represents adaptive antipredator responses, perhaps we should consider other possibilities. Ample opportunities exist for students of behavior and ecology to collect data, map them onto the phylogeny, and investigate associations between changes in, for example, sexual behavior, habitat preference, or predation pressures, and changes in horn number.

The Temporal Sequence of Evolutionary Change

Lorenz (1941) cautioned, "The similarity of a series of forms even if the series structure arises ever so clearly from a separation according to characters, must not be considered as establishing a series of developmental stages." In his opinion, without reference to phylogenetic relationships the criterion of similarity was, of itself, a dangerously misleading evolutionary marker. The last two decades have witnessed a rise of a new methodology based, in direct contrast to Lorenz's warning, upon arranging characters as a "plausible series of adaptational changes that could easily follow one after the other" (Alcock 1984:432). Although intuitively pleasing, this method relies heavily on subjective, a priori assumptions concerning the temporal sequence of evolutionary modifications and dissociates character evolution from underlying phylogenetic relationships. The reintroduction of "history" into our evolutionary perspective has prompted researchers to seek alternate methods for uncovering the direction and sequence of character change (for an excellent discussion of this area, complete with additional examples, see Donoghue 1989).

The evolution of Dioecism in Lepechinia *section* Parviflorae

Hypotheses concerning the evolution of breeding systems in plants are currently a hot topic among botanists (see references in Hart 1985b). Various adaptive pathways have been proposed, based upon mathematical models of changes in gene frequencies in populations and studies at either the population level or across broad taxonomic categories. Hart (1985b) pointed out that, since these hypotheses were generally not formulated within a phylogenetic context, questions concerning the evolutionary transitions from one breeding system to another were difficult to address. He focussed his attention on one particular area of the debate: the evolution of dioecism (separate sexes) in the *Lepechinia* section *Parviflorae* (Lamiaceae). Among members of *Lepechinia* some species are monoecious, some are gynodioecious, and some are dioecious. Originally gynodioecism was viewed as a stable strategy that would not give rise to dioecism (Darwin 1877; Lewis 1942). This view was expanded by Ross (1978) to include two forms of gynodioecism, "stable" and "unstable," in which only the latter form allowed the possibility of dioecism evolving. Within the Lamiaceae, the stable form was thought to predominate. Hart investigated this problem by mapping the character "breeding system type" onto a phylogenetic tree depicting the relationships within three Lamiaceae sections (fig. 5.17). He was particularly interested in the relationships within the section *Parviflorae*, a group of small, white-flowered shrubs inhabiting the Andean regions of South America, which we have already discussed in chapter 4.

The phylogenetic relationships within this group of plants indicate that gynodioecism is the plesiomorphic condition for members of the monophyletic section *Parviflorae*. Within this section, dioecism is a derived state that has arisen independently at least twice. Hart cautioned that robust conclusions concerning the number of times dioecism has arisen in *Parviflorae* cannot be drawn based upon his phylogenetic tree, since characters involved in this type of breeding system were incorporated in the original systematic analysis. It is important to note, however, that (1) apomorphic characters independent of breeding-system type confirm the monophyletic status of this section and (2) outgroup comparisons have demonstrated that gynodioecism is plesiomorphic for the clade. Given this, the phylogenetic hypothesis of an evolutionary sequence from gynodioecism to dioecism is a valid one based on the available data. Hart's caution involves the resolution of the number of times the transition occurred, not the sequence in which it occurred. This result weakens the hypothesis that gynodioecism is "stable" within this section, and highlights some potentially interesting areas for further research. Hart noted that the gynodioecious outgroups occurred in mesic upland sites
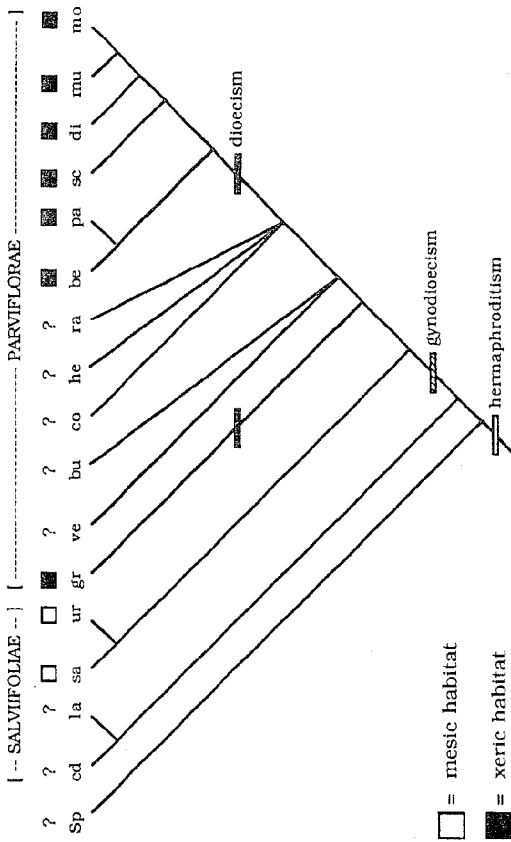
|-- SALVIIFOLIAE --| |------ PARVIFLORAE ------|

Fig. 5.17. Distribution of breeding-system type mapped onto a phylogenetic tree for three sections *Lepechinia* sections. *Speciosae, Salviifoliae,* and *Parviflorae.* be = *Lepechinia betonicaefolia; bu* = *L. bullata; cd* = *L. codon; co* = *L. conferta; di* = *L. dioica; gr* = *L. graveolens; he* = *L. heteromorpha; la* = *L. lancifolia; mo* = *L. mollis; mu* = *L. mutica; pa* = *L. paniculata; ra* = *L. radula; sa* = *L. salviifolia; sc* = *L. scobina; Sp* = *Speciosae; ur* = *L. urbanii; ve* = *L. vesiculosa.* The *boxes* above the phylogenetic tree represent habitat preference for each species where known. (Redrawn and modified from Hart 1985b.)

☐ = mesic habitat

▨ = xeric habitat

in the Andes, while the dioecious species preferred xeric habitats and demonstrate higher degrees of weediness. If further analysis of the ecology of the gynodioecious species within the *Parviflorae* demonstrates that preference for mesic habitats is the plesiomorphic condition in this section, then the hypothesized correlation between breeding-system shift and habitat shift would represent a correlation between apomorphic traits about which investigations of adaptation could be profitable.

In the preceding example, we used a phylogenetic analysis to establish the sequence of evolutionary changes for one character. We can also use this method to evaluate the evolutionary relationships between two or more different traits (see also Resh, Morse, and Wallace 1976; Morse 1977; Morse and White 1979). There are three general hypotheses concerning such relationships: (1) The traits neither co-originate nor co-occur in any members of the study group (fig. 5.18a). (2) The traits do not co-originate, but they do co-occur in some members of the study group. In this case the researcher is primarily interested in examining the sequence of origins for the different

Fig. 5.18. Examining the phylogenetic relationships between two different characters. (*a*) Traits x and y arose independently in different species; the traits neither co-originate nor co-occur. (*b*) Trait x arose before trait y; the traits do not co-originate, but they do co-occur in some members of the group. (*c*) Trait y arose before trait x; the traits do not co-originate, but they do co-occur in some members of the group. (*d*) Both characters originated in the same ancestor; the traits co-originate and co-occur.

traits. For example, the hypothesized sequence "trait x arose first, followed by trait y," is refuted by the phylogenetic patterns depicted in figures 5.18a and 5.18c and supported by the pattern depicted in figure 5.18b. Interestingly, the relationships outlined in figure 5.18d offer no resolution of the problem. These associations can only fail to refute hypothesis 2 because phylogenetic analysis cannot determine the sequence of trait origins within a species. (3) The traits co-originate and co-occur in members of the study group (fig. 5.18d).

The evolution of gregariousness in aposematic butterfly larvae

Although most butterflies are solitary ovipositors, there are species that lay their eggs in clusters. Once hatched, larvae from these egg aggregations tend to remain clustered. This observation requires an explanation because groups of small, relatively immobile but tasty prey items should be highly susceptible to predation, and thus be at a strong selective disadvantage. Closer examination reveals that (1) the larvae of many butterfly species are unabashedly aposematic, displaying vivid combinations of black, red, orange, yellow, or white against the brown-and-green backgrounds of the surrounding

Fig. 5.19 Temporal sequence of the evolution of larval clustering and warning coloration mapped onto a phylogenetic tree for the butterfly tribe Papilionini. A = *Pterourus* (5 species groups); B = *Heraclides thoas*; C = *H. torquatus*; D = *H. anchisiades*; E = *Chilasa elwesi*; F = *C. clytia*; G = *C. veiovis*; H = *C. agestor*; I = *C. laglaizei*; J = *Eleppone anacus*; K = *Papilio machaon*; L = *Princeps xuthus*; M = *P. demolion*; N = *Princeps* (9 species groups); O = *Princeps* (6 species groups); P = *Princeps* (10 species groups). The distribution of the two larval-aggregation and color characters is mapped above the taxa and optimized onto the tree. 1 = warning coloration present; 2 = gregariousness present; 3 = reversal to crypsis.

☐ = solitary larvae

▨ = gregarious (clumped) larvae

▥ = cryptic coloration

■ = warning coloration

vegetation; (2) there is a correlation between larval clustering (gregariousness) and aposematism; and (3) there is a correlation between larval distastefulness and aposematism. Based on these observations, Fisher (1930) proposed that the development of prey unpalatability required the involvement of kin selection. Turner (1971) and Harvey et al. (1982) extended the kinselection hypothesis to include the development of aposematic color patterns. The idea was straightforward; some bad-tasting mutants with warning coloration would be eaten, predators would associate bad taste with the mutant's color pattern, and those predators would avoid their last meal's similarly colored siblings. Under this hypothesis, gregariousness should either (1) evolve first, providing a context in which kin selection could work, followed by the evolution of distastefulness/aposematic coloration, or (2) appear at the same time as warning coloration/distastefulness. The former evolutionary sequence provides the strongest corroboration for the hypothesis of a causal link, provided by kin selection, between gregariousness and the appearance of "taste bad/look bad" traits. Sillen-Tullberg (1988) examined this hypothesis by referring to phylogenies (and, in cases where phylogenies were not available, through reevaluation of taxonomic information by optimization techniques) for a number of butterfly lineages. She compiled data from the literature concerning larval aggregation habits (solitary versus gregarious) and color (cryptic versus aposematic). Her focus was on the order of events: Did gregariousness evolve before, with, or after warning coloration? Her results were startling. For example, consider the tribe Papilionini (fig. 5.19).

In this particular clade, the ancestral condition was determined by outgroup analysis to be "larvae solitary and larvae cryptic." Diversification within the clade involved the evolution of gregariousness in three separate lineages and the transition from crypsis to warning coloration in two lineages. Although all four possible combinations of the grouping and color traits exist in these butterflies, in no case did the evolution of gregariousness precede the evolution of warning coloration. This example is representative of the results found for all the butterfly groups examined phylogenetically by Sillen-Tullberg: of the twenty-three independent appearances of gregarious larval interactions during the course of butterfly evolution, three evolved in conjunction with the appearance of warning coloration, fifteen evolved after warning coloration, and five evolved without the subsequent development of aposematism. Gregariousness did not evolve before warning coloration in any lineage. Based upon the temporal sequence of trait appearance, Sillen-Tullberg concluded that "kin selection is of minor importance for the evolution of both unpalatability and warning coloration" and suggested that researchers turn their attention to hypotheses of individual selection for explanations of the evolution of these characters.

Evolutionary Associations of Traits: Coadapted Trait Complexes within a Clade

Observations of correlations among traits in extant species have been used as the basis for adaptive hypotheses concerning the evolutionary relationship between the traits. For example, consider the distribution of two behavioral characters, number of mates per male and male nuptial plumage, among a taxonomically "closely related" yet hypothetical group of birds (table 5.2).

The nonhistorical explanation for this distribution might be that the characters are "travelling together" evolutionarily, acting as coadapted trait complexes (Mayr 1963). Advocates of this hypothesis would turn their attention to the special case, species C, in an attempt to discover the current environmental pressures that have led to a change in the relationship between the traits. Now consider an alternate method for examining the relationships be-

Table 5.2 Distribution of nuptial plumage and polygyny in a hypothetical, but monophyletic, group of birds.

Taxon	Characters	
	1 Nuptial Plumage	2 Polygyny
A	absent	absent
B	absent	absent
C	present	absent
D	present	present
E	present	present
F	present	present

□ = nuptial plumage absent

▨ = nuptial plumage present

▦ = polygyny absent

▨ = polygyny present

Fig. 5.20. Phylogenetic trees, differing in the placement of species C, for the hypothetical birds (table 5.2). Derived states of the two characters are mapped onto each tree. *1* = nuptial plumage present; *2* = polygyny present.

tween the two traits. Figure 5.20 depicts two phylogenetic trees for this clade of birds.

Both trees indicate that the correlation of "nuptial plumage absent" with "polygyny absent" and "nuptial plumage present" with "polygyny present" is the result of common phylogenetic history. While this in itself is interesting, it does not help us to distinguish between a coadaptive and a coincidental phylogenetic association between the two characters. The critical piece of evidence is provided by examining species C *within the phylogenetic frame-*

work. The relationships depicted in figure 5.20a reveal that, given the evolutionary "placement" of C, the presence of "polygyny absent" and "nuptial plumage present" in that species indicates different rates of evolutionary divergence in the two characters. This provides support for a hypothesis of relative evolutionary *independence* of male plumage development and number of mates in this group. The rel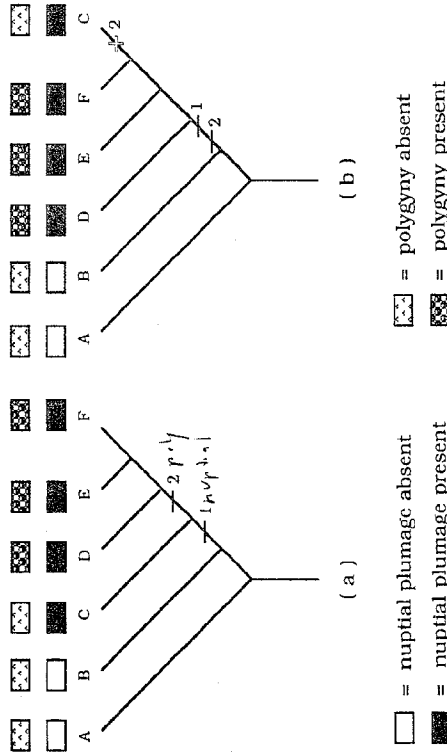ationships depicted in figure 5.20b corroborate the hypothesis that traits 1 and 2 are acting as a coadapted unit. This tree further suggests that species C seems so anomalous because it has undergone an evolutionary reversal to the plesiomorphic mating system, monogamy, while retaining the derived trait of "nuptial plumage present." In this case, as suggested by a nonphylogenetic approach, the change in the relationships between male plumage and number of mates could be examined within the context of current environmental selective pressures.

The association between ritualization of behavior and increasing levels of aggression in stickleback fishes

Tinbergen (1953) predicted that the evolution of increasing levels of aggression in any group should be accompanied by increased ritualization of agonistic behaviors. He proposed that the evolutionary ritualization of aggression was adaptive because threat and intense, but noncontact, fighting would permit the establishment of dominance/territorial relationships with a minimum amount of physical injury to the combatants. McLennan, Brooks, and McPhail (1988) examined this prediction using a fascinating and widespread family of north temperate fishes, the Gasterosteidae, or sticklebacks. Subjective observations have placed *Spinachia spinachia* (the sea stickleback) and *Gasterosteus aculeatus* (the famous three-spined stickleback) at opposite ends of a continuum of "aggressiveness," with *G. aculeatus* being the most pugnacious of the sticklebacks (Wootton 1976). Bearing this in mind, McLennan et al. mapped aggressive and submissive behaviors onto a phylogenetic tree for the Gasterosteidae (fig. 5.21). Since the analysis was not based on any a priori coupling of aggression and ritualization, examination of the relationship between the two on a macroevolutionary level provided a rigorous test of Tinbergen's hypothesis.

Inspection of figure 5.21 reveals that the directional change in levels of "aggressiveness" is correlated with both the phylogenetic diversification of aggressive behaviors through the predicted sequence of "chase/bite" to "threat" to "circle fight" and the simultaneous appearance of aggressive and appeasement behaviors (broadside and head-down "threat" coupled with "head up" submission; "circle fight" coupled with "dorsal roll"). This analysis thus provides corroboration for Tinbergen's hypothesis from the perspective of the evolutionary origins of agonistic characters, their associations dur-

The relationship between preferred environmental temperature and optimum sprinting temperatures in skinks

Skinks are hyperactive, predominantly terrestrial lizards. They generally eat insects and other arthropods, but large skinks will sometimes eat baby mice or birds, or small bird eggs (Conant 1975). As is the case with many middle-level predators, skinks are themselves tasty morsels for larger animals. They often sprint to avoid predators, and this running speed is, in turn, strongly influenced by environmental temperature because lizards are poikilotherms. Since predator avoidance is such a highly desirable outcome in the life of a lizard, the evolution of a species' habitat/body-temperature preference should be tightly coupled with the evolution of the temperature that produces its optimum sprinting speed. Huey and Bennett (1987) examined this expectation within both comparative/nonhistorical and comparative/phylogenetic frameworks. Statistical analysis of the relationship between thermal preference and optimum running temperature revealed a significant association between the two traits; however, this resulted from a very strong association between the characters in species with high thermal preferences and a weak association in species with low thermal preferences. The nonphylogenetic approach thus uncovered some flaws in the original expectation that thermal preferences and thermal sprinting optima would be tightly coupled in all species of skinks. Huey and Bennett then examined the relationship between thermal preference and optimum body temperature for sprinting speed within a phylogenetic framework. This was a difficult proposition because the states of the two characters are quantitative, with each species having a range of variation. Huey and Bennett based their analysis on the mean value of the character states for each species. Figure 5.22 depicts a simplified version of their results.

With an eye to both the direction and magnitude of evolutionary change, the authors delved further into the question of coadaptation. Phylogenetic examination corroborated the statistical conclusion that coadaptation was stronger in genera with high thermal preferences (*Egernia* and *Ctenotus*: same rate and direction of character changes) than in genera with low thermal preferences (*Leiolopisma, Sphenomorphus, Eremiascincus,* and *Hemiergis*). Skinks of the genera *Leiolopisma* and *Sphenomorphus* display moderate levels of partial coadaptation based upon similar directions in character change coupled with slightly different rates of evolution. The two weakest associations were displayed by *Hemiergis* and *Eremiascincus,* which, interestingly, have greatly reduced limbs. Huey and Bennett proposed that coadaptation was weak in *Hemiergis* because, although the direction of the thermal preference change was the same for both traits, the lowering of the thermal preference occurred at a
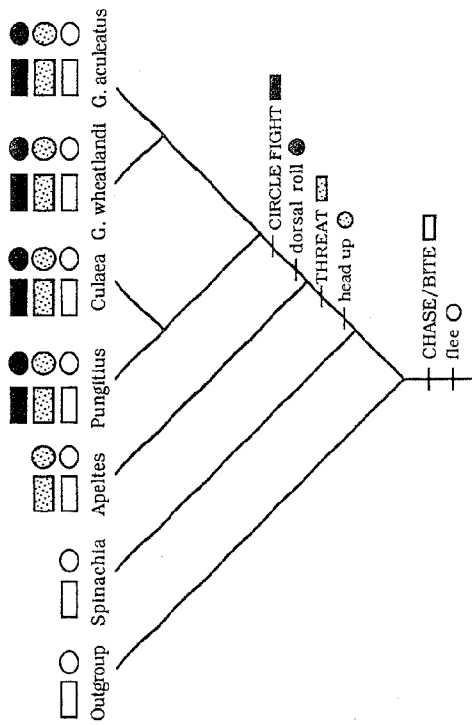
Fig. 5.21. Diversification of agonistic behaviors mapped onto the phylogenetic tree for the stickleback fishes, family Gasterosteidae. G = *Gasterosteus* Aggressive behaviors are in *uppercase letters,* submissive behaviors in *lowercase letters.* The figures above the tree are a visual representation of the character changes. *Rectangles* = aggressive behaviors; *circles* = submissive behaviors. The evolutionary diversification of the sticklebacks was accompanied by the simultaneous *addition* of aggressive/submissive behaviors to the repertoire of the new species.

ing their subsequent diversification, and the sequence of the diversification of the traits. The analysis also highlights an interesting and unexpected result. Experiments have demonstrated that *Pungitius pungitius* is substantially less aggressive than *G. aculeatus* (Wilz 1971; Wootton 1976); however, according to the phylogenetic hypothesis presented in figure 5.21, there has been no further diversification (ritualization) of agonistic behavior in this clade. The simplest explanation for this is that *Pungitius + Culaea + G. wheatlandi* retain the ancestral level of aggression (and the associated ancestral behaviors), and the increased levels detected in the three-spined stickleback (*G. aculeatus*) are derived. If this is so, then explanations for the increase in aggression without the simultaneous increase in the ritualization of agonistic behaviors must be sought for *G. aculeatus.* If all the members of this monophyletic group demonstrate some increase in aggressive levels, the interpretation would be more complex. Further resolution of the relationship between aggressiveness and ritualization awaits a more detailed analysis of levels of aggression in these fishes. In such studies, aggressiveness should be measured by using the plesiomorphic indicator of aggression in this family: the number of bites directed towards a test subject.

□ = same as ancestral

▨ = increase from ancestral

■ = decrease from ancestral

▦ = substantial decrease from ancestral

Fig. 5.22. Phylogenetic tree for Australian skinks, mapping thermal preference (*top line of bars*) and optimum sprinting temperature (*bottom line of bars*). Eg = *Egernia*; Le = *Leiolopisma*; Sp = *Sphenomorphus*; Er = *Eremiascincus*; He = *Hemiergis*; Ct = *Ctenotus*. The traits have been simplified to four categories based upon general trends in both the direction and magnitude of evolutionary change compared with the ancestral condition. Presumptive ancestral conditions were reconstructed based on outgroup comparison and a method called "the minimum-evolution method" (Huey and Bennett 1987).

substantially faster rate than the lowering of optimal sprint temperature. Within *Eremiascincus*, thermal preferences also underwent a major decrease from the ancestral preference; however, sprinting temperature remained at the ancestral high point. In this instance, both the rate and the direction of evolutionary change varied between the traits. So, rather than operating as a tightly coadapted unit in all cases, it appears that the relationship between thermal preference and optimal sprinting temperature can vary independently to some extent.

Convergent Adaptation

Convergent evolution of similar traits in different lineages is considered to be one of the strongest types of evidence for adaptation; however, convergence is often asserted without its demonstration by phylogenetic analysis. As we noted in chapter 2, phylogenetic systematics provides a strong test of homoplasy because the homoplasious characters are highlighted against a background of presumed evolutionary homology. Putative convergences are identified a posteriori from phylogenetic analyses based on a set of characters for which no postulate of convergence was proposed a priori. Convergences in quantitative or qualitative traits can be identified by optimizing such characters onto phylogenetic trees constructed using other data. Once convergence has been identified, adaptive hypotheses can be con-

structed by looking for similarities in environments inhabited by taxa exhibiting the convergent traits.

Run-jump behavior in Richardson's ground squirrels and black-tailed prairie dogs

Dobson (1985) documented the presence of an interesting "run-jump" flight behavior in Richardson's ground squirrels (*Spermophilus richardsonii*) and the black-tailed prairie dog (*Cynomys ludovicianus*), in which fleeing individuals "push the anterior part of the body off the ground with the forelegs, while continuing to run with the hind legs." Mapping the trait onto a phylogenetic tree reconstructed from the current classification scheme produces a disjunct and apparently convergent distribution of run-jumping (fig. 5.23a).

When the distribution is reanalyzed on a second tree, reconstructed from a different classification scheme, the appearance of run-jumping in both species is now hypothesized to be the result of common history (fig. 5.23b). Clarification of the problem resides in the resolution of the phylogenetic relation-

[------- SPERMOPHILUS -------]

(a)

(b)

■ = presence of run-jump behavior

Fig. 5.23. The presence of the run-jump trait mapped onto two hypothetical phylogenetic trees for ground squirrels and prairie dogs. (a) According to this tree, the genus *Spermophilus* includes the subgenera A, B, C, D, E, and Sp. (b) Under the second tree, subgenera *Spermophilus* (Sp) and *Cynomys* (Cy) are each other's closest relatives; therefore, if this is the correct phylogeny for the group, the genus *Spermophilus* is paraphyletic (i.e., it does not include all the species descended from the common ancestor).

159   Adaptation

Fig. 5.24. Simplified phylogenetic tree for members of the genus *Montanoa*, showing the distribution of the shrub and tree habits. Ploidy levels of the trees are listed above the trees. * = a case of hypothesized, but as of yet unconfirmed, polyploidy.

ships within the possibly paraphyletic genus *Spermophilus*. Dobson's analysis reiterated the importance of examining character evolution on phylogenetic trees reconstructed by phylogenetic systematic methodology, rather than equating taxonomy with phylogeny. It also emphasizes a critical aspect of the importance of phylogeny in the testing of adaptationist hypotheses. Consider the following scenario for the origin of run-jumping. Prairie dogs and ground squirrels live in tall grasses, which makes it difficult to detect terrestrial predators. When run-jumping appeared in each species, it became fixed because it increased an individual's detection of predators in that environment. Now consider an elaborate and lengthy series of field experiments that ultimately do not produce supportive data for the "predator perception" hypothesis. Result: rejection of the hypothesis. However, if figure 5.23b represents the true phylogenetic relationships within this group of rodents, then run-jump originated in the common ancestor of Richardson's ground squirrels and black-tailed prairie dogs. Since the presence of run-jumping in extant species is due to phylogenetic constraints on its evolution, there is no a priori reason to assume that the benefits conveyed upon the ancestor in which the trait originated will still be in effect in the descendants of that ancestor. It is possible that run-jumping was advantageous to the ancestor of *C. ludovicianus* and *S. richardsonii* in terms of predator perception, and that the environment has changed sufficiently to decrease or obscure that benefit, but not sufficiently enough to select against the trait. This study underscores the dangers of formulating hypotheses about convergence based upon studies of paraphyletic groups.

Daisy trees: convergent adaptations to living in cloud forests?

The Compositae genus *Montanoa*, or "daisy trees," comprises some thirty taxa living throughout Central America, extending as far north as central Mexico and as far south as central Colombia. All species are woody, possessing flowers with white to cream "petals" (rays) surrounding a central yellow to grey-green or black disc floret. Twenty-one of these species are shrubs, five are trees reaching twenty meters in height, and four share the vine "habit." Funk (1982) performed a phylogenetic analysis of the genus based on morphological characters, then mapped the habits of each species on the phylogenetic tree (fig. 5.24).

She discovered that the shrublike habit is plesiomorphic in daisy trees. If the common ancestor of the genus was a shrub, the presence of shrub forms in 70% of the known taxa indicates a rather ancient origin for, and considerable phylogenetic conservatism in, the diversification of the shrub habit. Therefore, studies involving the convergence of two or more species on the shrub habit are inappropriate for this genus. Seven out of forty-seven

branches on the phylogenetic tree (about 15%) demonstrate an evolutionary change in habit. These evolutionary events have given rise to the tree forms four times and to vines three times. It is the tree and vine forms for which studies of convergent adaptation in particular species of *Montanoa* might be appropriate.

Now let us consider the tree forms in particular. One species grows in cloud forests at higher elevations than other species in the genus in each of the following locations: Guerrero, Mexico; Chiapas, Mexico; and northern Guatemala; Costa Rica; Venezuela and Colombia; and the Santa Marta mountains, Colombia. All five species have a number of similar morphological and anatomical characters that allow them to survive in cloud forests, and none has ever been found at lower elevations. They are members of four different clades, their sister species in each case being shrubs living at adjacent lower elevations. They represent cases of convergent adaptation because they exhibit a convergent trait correlated with the same environmental variable. One could speculate that in each case natural selection had favored the evolution of the same kind of strategy for surviving in cloud forests, but we do not

know if this convergent adaptation was environmentally driven. In fact, an understanding of the development of tree forms within a phylogenetic context leads to a different interpretation.

Examination of the distribution of the *Montanoa* habit and ploidy level on the cladogram reveals a repeated pattern of association between the appearance of the tree form and increased ploidy levels (fig. 5.24). Although diploidy is the ancestral condition in *Montanoa*, all the tree species, and only the tree species, are high-level polyploids (Funk and Raven 1980; Funk 1982; Funk and Brooks 1990). Developmental studies have demonstrated that it is common for polyploids to be larger than diploids in the Compositae; hence, the distinction "tree versus shrub" may simply be a by-product of ploidy level. It is also common for diploids to produce polyploid seeds in this group, so the parallel and convergent appearance of polyploids is not a surprising phylogenetic pattern. Based on these data, it would appear that the repeated convergent evolution of treelike species is a result of developmental plasticity in polyploid production in this genus (something common among composites). What needs to be explained is the restriction of tree forms to cloud forests and the absence of shrub and vine forms from cloud forests. For this, we need to examine the adaptive **divergence** of each tree species from its shrubby ancestor and sister species.

Divergent Adaptation

Phylogenetic analysis of ecological diversification can be used to investigate hypotheses about mechanisms involved in evolutionary diversification within a clade. In contrast to convergent adaptation, *where we looked for evidence of distantly related species inhabiting similar habitats and exhibiting convergent traits associated with the habitat*, the evidence for divergent adaptation is the occurrence of apomorphic changes in ecological traits associated with the appearance of descendant species inhabiting new habitats.

Why don't tree and shrub forms of daisy trees occur together?

The Compositae genus *Montanoa* offers an example of the way in which this can be done. As noted previously, daisy trees, contrary to the name, exist in vine, shrub, and, fortunately, tree forms. The convergent evolution of the trees was hypothesized to be a result of the propensity for the diploid sister species to produce polyploid seeds, with concomitant changes in shape due to the increase in ploidy level. While this explains the convergence of tree forms, it does not explain the strict habitat divergence between each tree species and its sister shrub. The trees all grow in cloud forests at higher elevations than the other species in the genus, while their sister shrubs live at lower elevations. Prior to the phylogenetic analysis (Funk 1982), all the trees

were classified together in a single taxon, and their disjunct distribution was explained as either the remnants of a once widespread ancestral distribution or as the result of long-distance dispersal from mountaintop to mountaintop. The phylogenetic relationships within the group do not corroborate either of these hypotheses, because the tree forms do not form a monophyletic group. Rather, they suggest a possible alternative evolutionary explanation. The absence of sympatry between the tree forms and the shrub forms could have arisen repeatedly through interspecific competition between the derived tree forms and ancestral shrub forms, leading to divergent adaptation as the competition was resolved when the tree forms moved into cloud forests (fig. 5.25).

As we have noted previously, assumptions about particular evolutionary mechanisms are not intrinsic to a phylogenetic analysis. Such analyses are most useful in differentiating between those possibilities that are supported and those that are not supported by the phylogenetic evidence about macroevolutionary structuring of character appearance and divergence. In this case, it is possible that the adaptive divergence of the tree forms from shrub forms involved competitive exclusion. This hypothesis, in turn, can be examined within the larger framework of potential constraints on divergence. In gen-

= living high up in mountain cloud forests
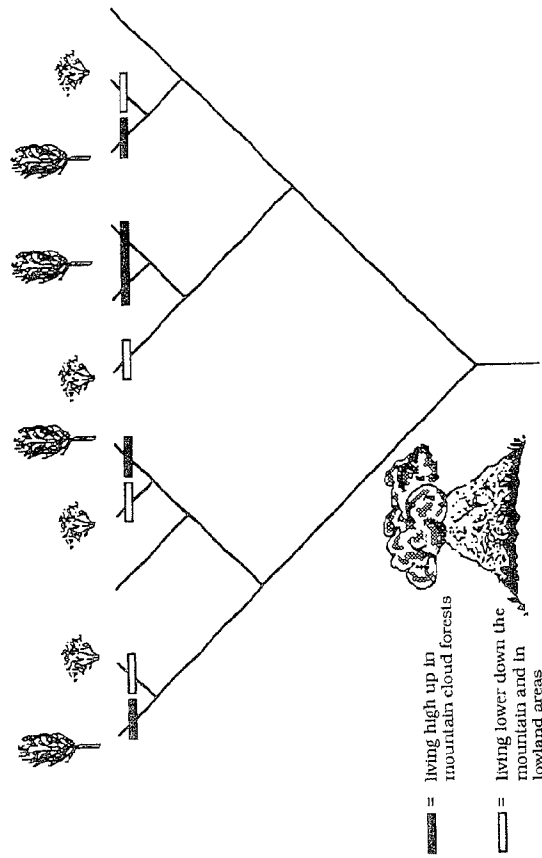
= living lower down the mountain and in lowland areas

Fig. 5.25. Habitat distributions of the tree species of the genus *Montanoa* and their shrubby sister groups. Tree forms only live high in the mountain cloud forests, while the shrub forms are located lower down the mountain sides and into lowland areas.

eral, this entails examining the system from several levels. For example, in the case of trees versus shrubs, developmental and physiological data bring an interesting new perspective to the question. Physiologically, composites are relatively inefficient water conductors, so it is unlikely that the large tree forms could survive outside of high-moisture habitats like cloud forests. On the other hand, greenhouse experiments (Funk, pers. comm.) indicate that the diploid seeds of shrublike species of *Montanoa* cannot survive under conditions of high moisture. The developmental constraints on size (ploidy), moisture requirements, and moisture tolerance lead to three conclusions: any polyploid seed that is produced too far from a cloud forest to disperse into a high-moisture zone will never germinate successfully; no diploid seed that disperses into a cloud forest will survive in the high-moisture conditions; and no polyploid seed that disperses outside a cloud forest will germinate successfully in the low-moisture conditions. The habitat segregation between trees and shrubs results from developmental constraints on moisture requirements/tolerances in the clade leading to strong selection against diploids in cloud forests and against polyploids in more mesic environments. No matter how many times the treelike polyploid forms evolve, they will never occur sympatrically with any diploid species, so the necessary initial conditions for interspecific competition will never be established.

Why don't all the snakes on Hispaniola eat the same things?

On the zoological side, snakes on Hispaniola exhibit a variety of feeding strategies, preying on local frogs and lizards. Some are generalists and some are specialists; some are active foragers and others are sit-and-wait ambushers. Traditionally, the differences in the foraging and feeding behaviors of each species have been explained as adaptive responses to interspecific competition. Henderson et al. (1988) provided ecological and phylogenetic data for some members of *Hypsirhynchus*, *Uromacer*, and *Alsophis*, using *Antillophis*, *Ialtris*, and *Darlingtonia* as outgroups (fig. 5.26).

Their analysis suggests that the active-foraging, generalist feeding mode employed by *Alsophis cantherigerus* is plesiomorphic in these snakes. The change to a sit-and-wait ambushing strategy occurred in the common ancestor of *Uromacer* and *Hypsirhynchus* and has been retained in all its descendants. These relationships emphasize the importance of historical constraints on foraging behaviors in these groups. *U. catesbyi* is reported to show both active and sit-and-wait behaviors. This raises some interesting points about the control of these two behaviors, which have been treated as alternative character states in the analysis. The most parsimonious phylogenetic explanation is that active foraging has reevolved in *U. catesbyi*. However, when this problem is examined in light of the snake's diet, a new explanation presents itself. All
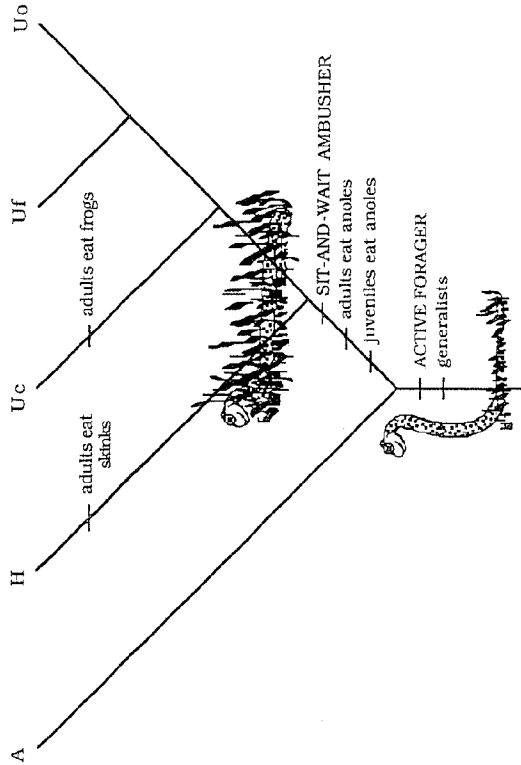
Fig. 5.26. Feeding habits of colubrid snakes on Hispaniola, mapped onto a phylogenetic tree for the group. A = *Alsophis*; H = *Hypsirhynchus*; Uc = *Uromacer catesbyi*; Uf = *U. frenatus*; Uo = *U. oxyrhynchus*.

the sit-and-wait species on the island feed predominantly on some type of anoline lizard, except for *U. catesbyi*, which eats frogs. Perhaps the appearance of active foraging is associated with this shift to such a novel prey item. Observations recorded in the literature also suggest that *U. catesbyi* is the worst sit-and-wait predator in the genus *Uromacer*, and that it is frequently seen chasing its prey, presumably after missing them by the first strategy! Further field observations are required to discover whether *U. catesbyi* does indeed display both foraging modes (which requires quite a complex phylogenetic explanation) or whether its chasing behavior is simply a by-product of its inability to capture frogs very efficiently. Additional resolution of the relationships among all the colubrid snakes in this area is also required before this problem can be adequately formulated. For example, three species of colubrids were not included in the study group because information on their feeding habits and behavior is lacking. Of these, all are active foragers; one feeds on frogs almost exclusively, one feeds on anoles primarily and frogs secondarily, and the feeding habits of the third are unknown. Interestingly, the most plesiomorphic member of the study group, *Alsophis*, is an active forager feeding on frogs among other things. Although the recurring association between active foraging and feeding on frogs is a tantalizing one, without

further phylogenetic analysis such a relationship is, for the moment, speculative.

Although foraging mode is phylogenetically conservative among these colubrid snakes, there has been moderate evolutionary divergence in the group with respect to the principal prey item. All species retain the plesiomorphic juvenile feeding preference for anoles, and *U. oxyrhynchus* and *U. frenatus* carry this preference into adulthood. *Hypsirhynchus ferox* becomes more specialized on teiid lizards (*Ameiva*) and *U. catesbyi* switches to frogs (*Osteopilus*). These species pinpoint profitable foci in the search for adaptationist explanations of ecological diversity in this group of snakes. Although there has been a trend within the group towards an increase in dietary specialization, only three of the eight branches on the phylogenetic tree are characterized by any shift in feeding mode. It is therefore unlikely that such diversification has been driven solely by competitive interactions favoring niche partitioning. Instead, phylogenetic analysis suggests that the observed ecological diversity is a reflection of more than one factor, only one of which might be competition.

Discovering Constraint: Is the Study Finished?

The belief that the evolution of ecological traits for a given species can be explained by studying only that species implies that ecological diversification occurs at a higher rate than speciation. In fact, many evolutionary biologists operate under the implicit assumption that new species form as a result of ecological diversification. Ross (1972a,b) was among the first of recent authors who have questioned this assumption. Now even more authors have begun to examine the question of overall degree of ecological diversity within a phylogenetic framework, with some interesting results.

The evolution of mating-behavior repertoires in stickleback fishes

Many biologists have voiced concern over the structural and temporal plasticity of behavior, arguing that it is far more environmentally sensitive than morphology and thus difficult to characterize (Parsons 1972; McClearn and DeFries 1973; Dunford and Davis 1975). On the surface, this concern seems valid. Verbs are intuitively more labile than nouns. These perceptions, however, are based on an assumption that variability within a species automatically disqualifies a character from examination of relationships among species. Consider the following example: All male three-spined sticklebacks court females with an elegant, horizontal zigzag dance. The frequency and duration of the dance is highly variable both within and among individuals. However, no male *Gasterosteus aculeatus* ever executes the semihorizontal zigzag of *G. wheatlandi* or the vertical zigzag dance typical of the related

X Spinachia Apeltes Pungitius Culaea G. wheatlandi G. aculeatus

⊚ = habitat generalists
☐ = marine habitat
▨ = brackish habitat
■ = freshwater habitat

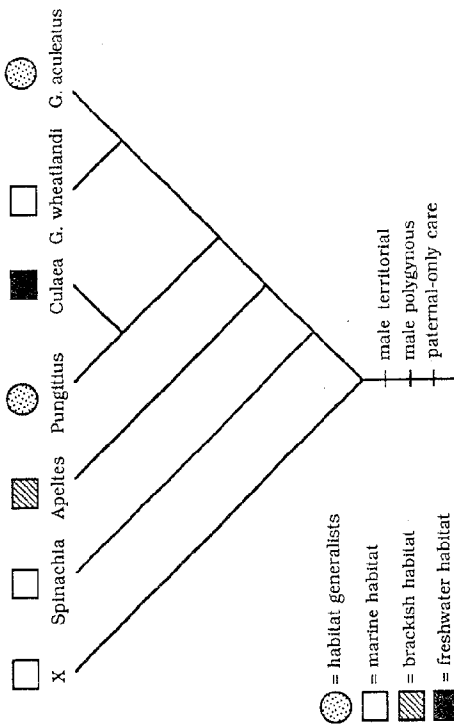male territorial
male polygynous
paternal-only care

Fig. 5.27. Distribution of general mating-system characteristics, mapped onto the phylogenetic tree for the sticklebacks. Habitat preferences are listed above each species. *G.* = *Gasterosteus*.

species *Pungitius pungitius*. So, although some aspects of the character "male courtship dance" show high intraspecific variability (i.e., frequency, duration), other aspects (orientation of the zigzag) are autapomorphic for the species, and still other components (presence of a zigzag dance) are synapomorphic for a larger clade and therefore are useful systematic tools at those levels (see also fig. 9.4). If this is true, then behavior, like any other biological system, should be a product of the interplay between constraints from the past and adaptations to the present.

McLennan, Brooks, and McPhail (1988) examined this prediction by performing a phylogenetic analysis for the stickleback family Gasterosteidae based solely upon twenty-seven behavioral characters. Traits were polarized using the sister group of the Gasterosteidae, the Aulorhynchidae, or tubesnouts, as the outgroup. One tree was produced from this analysis (fig. 5.27) with a very high consistency index (90.3%), indicating a high overall level of historical constraint and a low degree of evolutionary plasticity for the behavioral traits used to construct the tree. That tree, in turn, was congruent with trees based on morphological and genetical traits, and with a higher consistency index!

Having discovered that behavioral characters contain phylogenetic information, let us turn our attention towards an investigation of what phylogeny can tell us about the evolution of behavior. In a paper about mating systems and ecology, Vehrencamp and Bradbury (1984) stated, "One expects mating

behaviour to be a prime focus of selection for all sexual organisms. . . . One of the early important insights about mating system evolution was the recognition that the form of mating systems is more closely correlated with environmental contexts than it is with phylogenetic heritage." Is this statement corroborated by the distribution of mating behaviors on the gasterosteid tree?

Within the Gasterosteidae, *Pungitius* and *Gasterosteus* are habitat generalists. *G. aculeatus*, for example, exists as marine, estuarine, anadromous, and freshwater populations. Among the freshwater populations, habitats range from ephemeral, weed-choked ditches to large, oligotrophic lakes. At the other end of the spectrum, the fifteen- and five-spined sticklebacks are habitat specialists: *Spinachia spinachia* is restricted to marine habitats and *Culaea inconstans* to freshwater ones. *Apeltes quadracus* falls somewhere between these extremes, preferring brackish habitats but venturing into freshwater areas on occasion. Although they live in vastly different environments, all gasterosteids exhibit a male territorial, polygynous, paternal-care mating system. The presence of these behavioral patterns is thus a reflection of tight phylogenetic constraints on mating-system evolution within this family of fishes. So examination of the relationship between the form of the mating system and the environment on this coarse level of analysis reveals that this system is more closely tied to phylogeny than to the environment. However, the discovery of this phylogenetic influence is only the first step in developing a comprehensive evolutionary picture. We might next ask, What factors were responsible for the initial success of that mating system, and what factors are responsible for its current maintenance throughout the entire family? Answering this requires an analysis of the "fitness components" of the mating system for each species (i.e., female fecundity, adult survival rates, female encounter rate; see Vehrencamp and Bradbury 1984 for a detailed discussion). Once these have been optimized on a phylogenetic tree, we can investigate, for example: (1) whether there are any macroevolutionary correlations between the appearance of this mating system and a change in one (or more) of the fitness components; (2) which components appear to have been evolutionarily fixed throughout the family, and which are highly variable; and (3) the flexibility of the mating system (how many components can change and still maintain a male territorial, polygynous, paternal-care system). The results of such an analysis will provide a more robust estimate of the relative roles for the effects of *both* "phylogenetic heritage" *and* environmental factors in the evolution of this mating system.

Sexual dimorphism and social systems in lizards

Carothers (1984) investigated the relationship between sexual dimorphism and social organization in nine species of herbivorous iguanid lizards. Based
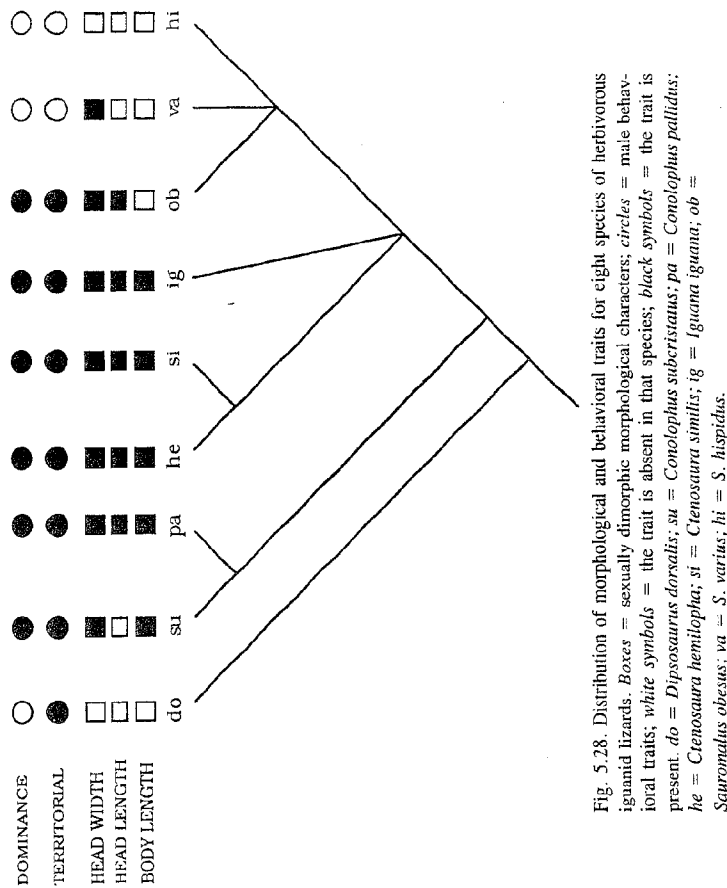
Fig. 5.28. Distribution of morphological and behavioral traits for eight species of herbivorous iguanid lizards. *Boxes* = sexually dimorphic morphological characters; *circles* = male behavioral traits; *white symbols* = the trait is absent in that species; *black symbols* = the trait is present. *do* = *Dipsosaurus dorsalis*; *su* = *Conolophus subcristatus*; *pa* = *Conolophus pallidus*; *he* = *Ctenosaura hemilopha*; *si* = *Ctenosaura similis*; *ig* = *Iguana iguana*; *ob* = *Sauromalus obesus*; *va* = *S. varius*; *hi* = *S. hispidus*.

on extensive experimental work and a search through the current literature, Carothers compiled data concerning sexual differentiation in three morphological characteristics: body length, head length, and head width. He also compiled data pertaining to two behavioral traits involved in the structuring of lizard social systems: the presence or absence of male territoriality and male dominance hierarchies. He examined the distribution of those five traits among the species in the context of their phylogenetic relationships (fig. 5.28).

Carothers did not designate outgroups for his study, so character polarizations could not be determined by outgroup comparison. Instead, he used *Dipsosaurus dorsalis* as the functional outgroup because, according to the phylogenetic relationships among the members of the ingroup, it is the sister group of the remaining eight lizard species considered. Based upon this, the characters displayed in figure 5.28 can be optimized onto the phylogenetic tree in the following manner (fig. 5.29).

do   su   pa   he   si   ig   ob   va   hi

no territoriality no dominance hierarchy

sexual dimorphism
dominance hierarchy

no sexual dimorphism
territoriality

SEXUALLY MONOMORPHIC CHARACTERS
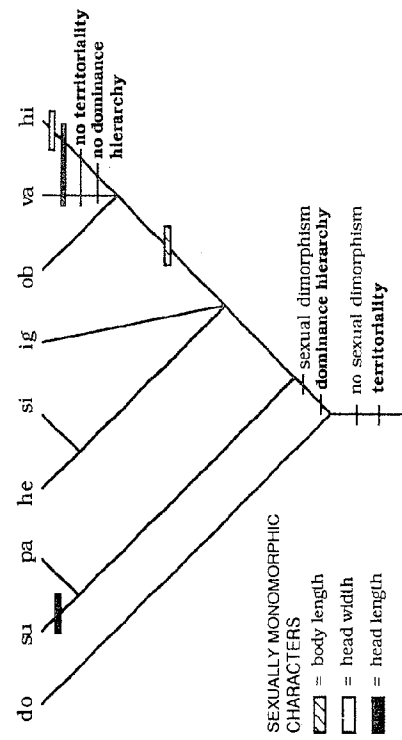= body length
= head width
= head length

Fig. 5.29. Optimization of characters onto the phylogenetic tree for eight species of herbivorous lizards. Three morphological characters involved in sexual dimorphism (head length, head width, and body length) and two behavioral characters involved in mating-system "type" (territoriality and dominance hierarchy) were polarized using *Dipsosaurus dorsalis* as the "outgroup." *do = Dipsosaurus dorsalis; su = Conolophus subcristatus; pa = Conolophus pallidus; he = Ctenosaura hemilopha; si = Ctenosaura similis; ig = Iguana iguana; ob = Sauromalus obesus; va = S. varius; hi = S. hispidus.*

This analysis demonstrates that the morphological/behavioral attributes of these species represent a mixture of past (historical constraints) and present (selection in current environments). The presence of male territoriality is primitive in this group, has been retained in the majority of species, and has been lost either once or twice within the chuckwallas, depending upon the phylogenetic relationships between *Sauromalus hispidus* and *S. varius*. In contrast to this, the consistency index for the three morphological characters on the phylogenetic tree is 37.5% (3/8 steps), demonstrating that these traits are highly labile (in this case easily reversed). However, trait vagility does not necessarily translate into lack of phylogenetic constraints. For example, four of the eight species in the ingroup, *Conolophus pallidus, Iguana iguana* (the green iguana), *Ctenosaura hemilopha,* and *Ctenosaura similis,* express the derived state for all three characters as a legacy of change that occurred in their common ancestor. Additionally, the loss of sexual dimorphism in body length occurred in the common ancestor of the genus *Sauromalus* and has been retained in all its descendants. The evolution of male dominance hierarchies is more tightly constrained, having appeared once, been retained in six of eight species, and, like territoriality, lost either once or twice within the chuckwallas.

The association between sexual dimorphism and social structure is a fas-

cinating one, according to this preliminary phylogenetic hypothesis. Male territoriality has not played a direct role in the appearance of sexual dimorphism, since it appeared before the change in morphology. On the other hand, the co-occurrence of the appearance of sexual dimorphism in all three morphological characters and the appearance of male dominance hierarchies suggests a possible link among the four characters. This relationship is maintained even when one of the characters reverses to a sexually monomorphic state—loss of head-length dimorphism in *Conolophus subcristatus* and loss of body-length dimorphism in *S. obesus*—suggesting that the characters are not perfectly coupled. However, the association cannot withstand the reversal of more than one character, and the loss of head-length dimorphism, in addition to the ancestral loss of body-size dimorphism in *S. hispidus* and *S. varius*, is associated with the loss of both male territoriality and dominance structure. Overall, then, the association between sexual dimorphism and dominance hierarchies is an old one maintained in five of the nine species considered. Studies involving the relationship between these characters should concentrate on comparing species that exhibit this ancestral association with sister species that exhibit evolutionary changes in the association. For example, questions about the relationship between head length and dominance structure might focus on comparisons between *Conolophus pallidus* (dimorphism present, dominance present) and *C. subcristatus* (dimorphism absent, dominance present). Investigations of the suite of correlated morphological and behavioral reversals demonstrated in *S. hispidus* and *S. varius* might also prove rewarding. If, as the distributions of characters on the phylogenetic tree suggests, these two chuckwallas are sister species, then these changes occurred in a relatively recent ancestor. If they are not sister species, then questions about convergent evolution would be exciting. Until the characters are analyzed by outgroup comparison, however, these conclusions are still in the preliminary stage. The hypothesized origin of male territoriality prior to the evolutionary divergence of these lizards will be retained regardless of the state in the sister group. Resolution by outgroup analysis will only tell us whether territoriality originated in the ancestor of this group (synapomorphic for the group) or at some point before that speciation event (plesiomorphic for the group). The conclusions regarding the evolutionary origins of sexual dimorphism and male dominance hierarchies may change depending upon the state of these characters in the outgroup. Further phylogenetic analysis, based upon adequate outgroups and including the species belonging in this group of iguanids that were not considered by Carothers (e.g., the Galapagos marine iguana; see Estes and Pregill 1988 for a current estimate of lizard phylogeny), are necessary before any robust hypotheses concerning the evolutionary relationships between sexual dimorphism and social structure can be drawn.