

- Is the commonness of a phenotype the result of many independent evolutionary events or of substantial speciation (or lack of extinction) in clades possessing that trait (Fig. 5.1e)?

Without a phylogeny, these questions are unanswerable.¹⁰⁷ A great deal of work over the past 25 years has been devoted to developing new methods to answer questions like these in a phylogenetic framework and the result has been a vastly enhanced understanding of evolutionary patterns and processes. In many respects, what we have learned about anole evolution is an exemplary case study of the power of a phylogenetic perspective, as I will describe shortly.

Before delving into the anole specifics, though, it's worth considering the limitations of phylogenetic studies. The following discussion is not meant to disparage phylogenetic approaches, but rather to recognize that phylogenies are useful for answering some questions, but less useful, at least sometimes, for answering others. In particular, I will suggest that in some situations, the ability to use a phylogeny to reconstruct ancestral character states will be limited. Importantly, however, this conclusion cannot be reached without evaluating patterns of character evolution on a phylogeny. Thus, phylogenetic approaches are essential, even if sometimes they will reveal their own limitations.

DIFFICULTIES WITH PHYLOGENETIC APPROACHES

PROBLEMS WITH ANCESTOR RECONSTRUCTION

Probably the biggest disappointment in the development of phylogenetic approaches has been the realization that attempts to infer ancestral character states often will be highly problematic. The reason is that when rates of change are high relative to the frequency of cladogenesis, then the confidence that can be placed in any ancestral reconstruction is bound to be low.

Consider first the simplest case, when ancestral character states are reconstructed by parsimony, which is an approach that minimizes the number of evolutionary transitions inferred to have occurred on a phylogeny. When only a few evolutionary transitions are required on a phylogeny, then the ancestral trait reconstructions may seem reasonable (Fig. 5.2a). However, when the minimum number of inferred transitions is great, then it would be unreasonable to strongly prefer one reconstruction over others that require a slightly greater number of transitions (Fig. 5.2b).

107. One might think that an alternative avenue for answering questions of this sort would be through examination of the fossil record. However, fossils do not come with labels on them, and so interpretation of fossils must be conducted within a phylogenetic framework as well. Moreover, for many taxa, certainly including anoles, Darwin's (1859) reservations about the imperfections of the fossil record still ring true. Finally, fossils can inform about some aspects of morphology, but insights about other aspects of the phenotype, such as ecology, behavior, and physiology, are far less reliable. Bottom line: fossils are great when you have them, but for many types of evolutionary ecological study, they usually are not a major source of information or insight.

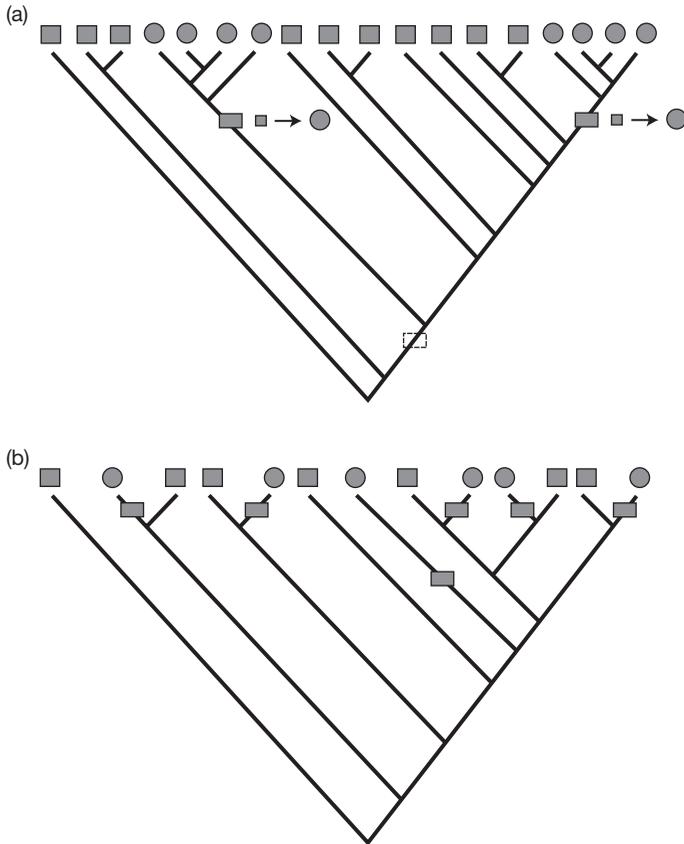


FIGURE 5.2

The reliability of ancestral reconstructions using parsimony. Parsimony reconstructs ancestral character states to minimize the number of evolutionary changes. In (a), parsimony would infer two transitions from square to circle. Of course, other reconstructions are possible. For example, the circle phenotype could have arisen independently in each of the eight species currently exhibiting that phenotype, or it could have arisen once at the point indicated by a dashed box deep in the phylogeny, followed by five instances of evolutionary reversal in each of the descendant clades that exhibit the square phenotype. Nonetheless, parsimonious inference of few evolutionary transitions, with each clade inferred to have experienced no evolutionary reversal, suggests that evolutionary change has been infrequent and that we might place high confidence in a parsimony reconstruction. By contrast, in (b), the square phenotype is again inferred to be ancestral, with six evolutionary transitions to the circle phenotype. However, a very different scenario, in which the circle phenotype is ancestral and squares are derived, requires only seven evolutionary transitions. In situations such as this, we can safely conclude that evolutionary change must have been frequent, occurring at least six times, but we probably wouldn't want to place much confidence in particular scenarios; given that evolutionary change has occurred at a high rate, a scenario requiring six transitions wouldn't seem to be much more strongly supported than another scenario requiring seven evolutionary events.

In recent years, sophisticated methods have been developed to quantify uncertainty in ancestral reconstructions (e.g., Schluter et al., 1997; Garland et al., 1999; Martins, 1999; see reviews in Ronquist, 2004; Garland et al., 2005; Hardy, 2006; Vanderpoorten and Goffinet, 2006). These methods use a model of trait evolution—often some variant of Brownian motion, which assumes that the amount of expected change is a function of time (as represented by branch lengths of the phylogeny)—to estimate the rate of change of a character based on the values of extant taxa and their phylogenetic relationships. With this rate, the methods can estimate not only the character state of ancestral taxa, but also the variance around that estimate. These methods generally produce the same conclusion arrived at for simple parsimony approaches—the more frequently character change occurs, the greater the uncertainty on estimates of ancestral character states (Fig. 5.3; Schluter et al., 1997; Oakley and Cunningham, 2000).¹⁰⁸

But the news gets even worse: these models generally assume that evolutionary change has been non-directional. However, evolutionary trends, in which taxa all evolve in the same direction, are common in the fossil record. No method for reconstructing ancestral taxa can account for such trends; indeed, in the absence of fossil data, trends are undetectable. Several studies have shown that when evolutionary trends exist, ancestral reconstructions are highly inaccurate (Oakley and Cunningham, 2000; Webster and Purvis, 2002; but see Polly, 2001).

The unhappy conclusion is that we probably shouldn't have much confidence in ancestral reconstructions, except when the rate of character evolution is low relative to the frequency of cladogenesis. This exception is an important caveat, however, because many traits do, in fact, evolve slowly enough for ancestor reconstructions to be reliable. For example, the sorts of morphological characters used by systematists are often of this sort. Nonetheless, many of the characters that evolutionary ecologists work on do not evolve slowly (Frumhoff and Reeve, 1994). In particular, many studies are driven by the observation that certain traits evolve repeatedly. Although convergence is a fascinating phenomenon of great importance to evolutionary biology in general, and anole studies in particular, its widespread occurrence indicates that attempts to infer ancestral character states will often produce ambiguous outcomes.¹⁰⁹

This is unfortunate, because many of the questions we would like to ask require estimation of ancestral character states: What was the ancestor like? Where did it live? How

108. Of course, there is a middle ground. Traits often evolve convergently many times in some parts of a phylogeny, and not in others; in cases such as this, ancestral reconstructions may be reliable in those parts of the tree experiencing relatively little trait evolution, but unreliable where levels of trait evolution and convergence are high.

109. A related point concerns the incorporation of phylogenetic information into statistical comparative analyses. This approach has become *de rigueur* for good reason, as many studies have shown that ignoring phylogenetic information can lead to inflated Type I error rates (Martins and Garland, 1991; Purvis et al., 1994; Díaz-Uriarte and Garland, 1996). Nonetheless, the underlying rationale for these methods is that closely related taxa are likely to be phenotypically similar because they have inherited their phenotype from a common ancestor and, consequently, possession of the same trait by two species experiencing the same environment does not constitute evidence that the trait has evolved multiple times in response to the same selective pressure.

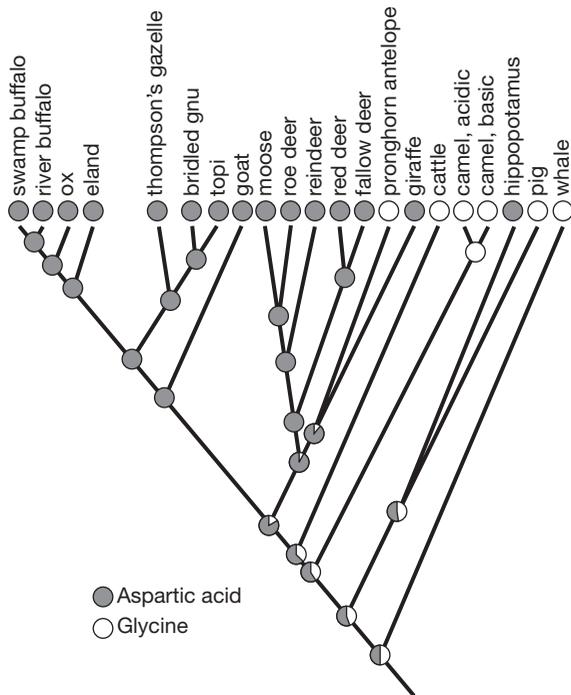


FIGURE 5.3
 Maximum likelihood method for assessing support for ancestral reconstructions. Pies represent the relative strength of support for reconstructing the state of an ancestral node as one of two types of amino acid residue (note that this figure predates reconsideration of the phylogenetic position of cetaceans vis-à-vis artiodactyls). Parsimony reconstruction would infer that glycine was the ancestral state, with two transitions to aspartic acid (one on the branch leading to hippos and the other on the branch leading to the major clade in which all but pronghorns have aspartic acid) and one reversal back to glycine in the pronghorn antelope. By contrast, maximum likelihood methods reconstruct aspartic acid as the ancestral state throughout the tree with five transitions to glycine. However, these reconstructions are not strongly supported for ancestral nodes deep in the tree, as indicated by the pie charts (modified from Schluter et al. [1997] with permission).

However, if character change has been sufficiently rapid relative to the rate of speciation, then closely-related species would not necessarily be expected to be phenotypically similar. Consequently, if no relationship exists between phenotypic similarity and degree of phylogenetic relatedness, then there may be no benefit to incorporating phylogenetic information into statistical analyses. Given that using such information comes with a potential cost resulting from errors in phylogeny estimation or in misspecification of the model of evolution of the trait under study, incorporating phylogenetic information into statistical analyses might not be the best course in such situations (Gittleman and Luh, 1994; Björklund, 1997; Losos, 1999). This view, however, is not universally shared; some workers contend that phylogenetic information always should be used in comparative analyses (see discussion in Garland et al., 2005; Carvalho et al., 2006). Moreover, this view does not argue against the importance of a phylogenetic perspective, for only with a phylogeny can one investigate whether trait variation among species is correlated with phylogenetic relatedness (i.e., whether a “phylogenetic effect” exists [Losos, 1999]).

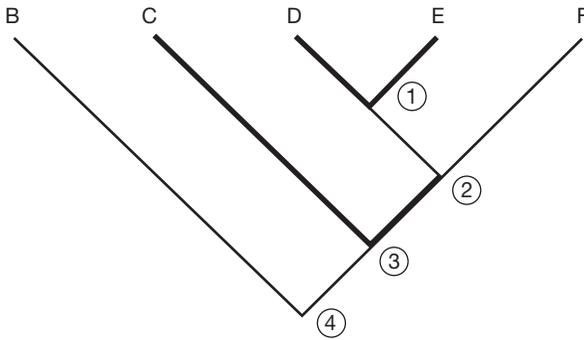


FIGURE 5.4

The difference between ancestor reconstruction and non-reconstruction approaches. In the former, ancestral character states are inferred for each node in the phylogeny and then the amount of change that occurred along each branch is calculated by subtracting the value of the ancestor from that of the descendant. In the independent contrasts approach, the difference between each pair of sister taxa—termed a “contrast”—is calculated. Pairs of sister taxa can be extant species, ancestral nodes, or one of each. The four contrasts are indicated by line shading in the figure. Note that the contrasts method includes as part of its algorithm a step in which a value is assigned to an ancestral node in the phylogeny, but this occurs solely for algorithmic purposes and should not be interpreted as an estimate of the ancestral character state (Felsenstein, 2004).

many times did the trait evolve? Evolutionary ecologists will have to accept that some questions may be unanswerable, at least with any confidence, the data erased in the fog of time.¹¹⁰

One way of getting around this problem is to ask questions in a way that does not require ancestor state reconstruction. Many (but not all) questions can be rephrased such that they only need consider a phylogeny and the character values of the taxa included in it—this is Harvey and Purvis’s (1991) distinction between directional and non-directional approaches.¹¹¹ The clearest example of this is in determining whether evolution in one trait is correlated with evolution in a second trait. The ancestor reconstruction approach is to estimate ancestral traits, calculate the amount of change in both traits on each branch of the phylogeny, and then ask whether changes in one trait are correlated with changes in the second trait (e.g., Huey and Bennett, 1987; Losos, 1990b). The non-reconstruction approach is exemplified by the independent contrasts approach, which calculates the amount of difference between each pair of sister taxa—both extant species and internal nodes of the phylogeny—in a phylogeny (Fig. 5.4).

110. This highlights the major advantage of a fossil record: it provides a direct view of the past, as opposed to the inferences that must be drawn from phylogenies when one only has data on extant taxa. Of course, establishing that a fossil taxon is actually the ancestor of either another fossil taxon or a modern taxon can be problematic (see discussion in Wagner and Erwin, 1995).

111. So named because in ancestor-to-descendant comparisons, the direction of change is specified, from the ancestral state to the descendant one. By contrast, when sister taxa differ, evolution must have occurred, but such comparisons do not imply the direction in which the change occurred.

PROBLEMS WITH PHYLOGENY ESTIMATION

A second shortcoming of phylogenetic approaches has received detailed attention only recently. A phylogeny represents the best hypothesis for evolutionary relationships of the group under study. As such, the phylogeny likely is incorrect to some extent, and a battery of methods has been developed to assess the strength of support for different clades within a phylogenetic tree (Felsenstein, 2004).

Most comparative studies employing a phylogenetic perspective, however, take the preferred phylogenetic hypothesis as a given and base analyses and conclusions on this single phylogeny. Yet, the obvious possibility is that results would change if the analysis were performed on other, slightly less preferred, phylogenetic hypotheses.

The solution is to integrate over the universe of possible phylogenetic hypotheses, weighting the results from each phylogeny by how strongly it is supported (Felsenstein, 1988; Losos and Miles, 1994; see also Swofford, 1991; Maddison and Maddison, 1992). Although the idea has been around for more than a decade, its implementation was ad hoc and somewhat arbitrary (Richman and Price, 1992; Losos, 1994b; Martins, 1996; Donoghue and Ackerly, 1996). Now, however, the analytical and computational methods are in place to implement this approach in a sophisticated and statistically rigorous manner (e.g., Huelsenbeck et al., 2000, 2003; Pagel et al., 2004; reviewed in Ronquist, 2004).

The drawback to this approach is that it is still computationally intense, and computer programs are just now being developed. As a result, these approaches are just beginning to be used, but I predict they will become routine and expected within a few years.

ANOLIS PHYLOGENY

A BRIEF HISTORY

With these considerations in mind, I now turn to the phylogeny of *Anolis* and what we can learn from it. I first review anole phylogenetics in this chapter, and then in the next two chapters discuss the inferences we can draw about anole evolutionary history by taking a phylogenetic perspective.

Anole systematics represents in many respects a microcosm of the systematic world: as new types of data and methods have become available over the past four decades, they have been quickly put to use by anole systematists.¹¹² What follows in the next few paragraphs is the CliffsNotes® version; a more complete history can be had by consulting Guyer and Savage (1986), Williams (1989), Jackman et al. (1999), and Poe (2004) and working back from there.

112. I do not intend to review methods of phylogenetic data collection or analysis. Good entrées to the literature on these topics can be found in Hillis et al. (1996) and Felsenstein (2004).