Symposium: Reconstructing Ancestral Character States

The Assumptions and Challenges of Ancestral State Reconstructions

KEVIN E. OMLAND[1]

James Ford Bell Museum of Natural History and Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108

Ancestral state reconstruction is at the center of a tremendous resurgence in interest in comparative methods in evolutionary biology. Also known as character optimization or character mapping, this set of methods is responsible for getting many nonsystematists to think about phylogeny and evolutionary history. This recent flood of interest can be traced to a series of important papers (e.g., Felsenstein, 1985; Coddington, 1988; Donoghue, 1989), two influential books (Brooks and McLennan, 1991; Harvey and Pagel, 1991), and the computer program MacClade (Maddison and Maddison, 1992). But although ancestral reconstructions have been embraced by both systematists and evolutionary biologists, the reliability and assumptions of these methods need continued examination. An increasing number of authors have discussed the assumptions and challenges of character mapping (Swofford and Maddison, 1992; Frumhoff and Reeve, 1994; Maddison, 1994; Ryan, 1996; Schultz et al., 1996; Cunningham et al., 1997; Omland, 1997; Cunningham et al., 1998).

Reconstructing ancestral character states is a tremendous challenge because of the inherent data limitations. As Maddison and Maddison point out, "...if one's goal is to reconstruct the precise sequence of evolutionary changes in the character, *realize that the precise sequence of changes requires the estimation of almost as many parameters as there are data points (observations in terminal taxa)!*" (Maddison and Maddison, 1992: 111, their italics; also see Swofford and Maddison, 1992; Cunningham et al., 1998). More specifically, a rooted bifurcating tree with N taxa has $N-1$ ancestral nodes, each requiring ancestral state reconstruction. However, reconstructing ancestral states is crucial to a wide range of research programs in systematics and evolution, so the challenges of ancestral reconstruction cannot be ignored.

This paper and many of the following six papers were part of a symposium on ancestral state reconstruction, with a special focus on unequal character state gain–loss probabilities. The first part of this paper discusses some of the assumptions of reconstructions based on simple parsimony. The second and third parts focus on the issue of asymmetric transformation probabilities and the need for independent cost estimates. The paper concludes with a brief overview of the other papers to follow.

Only one of the papers (Martins, 1999) examines the reconstruction of continuous characters. The other papers all discuss the reconstruction of discrete character states; however, many of the methods and topics discussed (e.g., asymmetric transformation probabilities: T. H. Oakley,

[1]Present address: National Zoological Park Genetics Laboratory, 3001 Connecticut Avenue NW, Washington, D.C. 20008-2598, USA; E-mail: komland@nzp.si.edu.

pers. comm.) also apply to continuous characters. The papers also generally focus on single, complex phenotypic or ecological characters, and not nucleotides or amino acids, for which ancestral state reconstruction has been more thoroughly studied (often based on whole classes of characters) (e.g., Schluter, 1995; Zhang and Kumar, 1997).

Assumptions of Ancestral State Reconstruction

The most widely used method for reconstructing ancestral states is parsimony, or more precisely, unordered or "simple" parsimony (Fitch, 1971; Swofford and Maddison, 1992; Maddison, 1994). Several assumptions, usually unstated, go into ancestral state reconstructions based on parsimony. I will address six of the most fundamental assumptions of these methods. The first three are relatively obvious assumptions: (1) that the tree being used is the true tree, (2) that all relevant extant taxa are included, and (3) that the characters are coded correctly. These first three assumptions all involve the fundamental goals of systematics and have been discussed frequently by other authors (e.g., Donoghue and Ackerly, 1996; Lanyon, 1985; Maddison and Maddison, 1992, respectively). These are also assumptions shared with other methods of ancestral reconstruction, including maximum likelihood (Schluter et al., 1997).

But even having the perfect tree, including all taxa, and having the characters coded exactly as they should be does not guarantee reliable reconstructions. Three less obvious assumptions made by simple parsimony can also affect the reconstructions: (1) that changes on all branches are equally likely, (2) that the rate of evolution is relatively slow, and (3) that the transformation probabilities (costs) are symmetric, i.e., that the probabilities of gains and losses of character states are equal.

These latter three assumptions of parsimony reconstructions are more subtle or implicit assumptions that for the most part have been neglected (but see Felsenstein, 1973; Maddison and Maddison, 1992; Swofford and Maddison, 1992; Collins et al., 1994; Frumhoff and Reeve, 1994; Schultz et al., 1996; Omland, 1997; Cunningham et al., 1998; Ree and Donoghue, 1998). There are probably many characters that do not meet one or more of these assumptions. I will next discuss these last three assumptions and detail the ways in which the importance of these assumptions have been addressed, especially the symmetric transformation assumption.

A crucial implicit assumption of simple parsimony is that changes on all branches are equally likely. This means that parsimony ignores all information about branch lengths (e.g., Schluter et al., 1997). Phylogenies based on analyses of DNA sequences offer estimates of branch lengths. Maximum likelihood methods can also be used to reconstruct ancestral states, and one of the advantages of this approach is that maximum likelihood can account for different branch lengths. For example, Schluter et al. (1997) showed that accounting for different branch lengths by using maximum likelihood methods can have dramatic affects on ancestral reconstruction (see Pagel, 1999).

Another implicit assumption of simple parsimony is that the rate of evolutionary character change is slow enough that evolutionary history can be recovered (Felsenstein, 1973; but see Felsenstein and Sober, 1986). A related point is that the time between successive nodes must not be too great for a given rate of character evolution. Schultz et al. (1996) showed that more-rapidly evolving characters are reconstructed with less accuracy. Schluter et al. (1997) confirmed the dependence of accuracy on rates by using maximum likelihood approaches. This effect of rates leads to an unfortunate trade-off in comparative biology, at least for discrete character methods that heavily rely on explicit ancestral state reconstructions (e.g., Ridley, 1983; Maddison, 1990; also see Cunningham et al., 1997). Statistical comparative methods (e.g., Harvey and Pagel, 1991) require repeated evolutionary transformations. More-rapid character-state change causes more transformations, thereby increasing the power of comparative tests. However, the same rapid

change simultaneously decreases the reliability of reconstructions, thereby decreasing the reliability of comparative tests. More studies of this problem and possible solutions are needed.

SYMMETRIC TRANSFORMATION ASSUMPTION

Perhaps the most crucial assumption of simple parsimony is the symmetric transformation assumption, which is the focus of this paper and of several of the other papers from the symposium. Simple parsimony assumes that the probability of change from character state A to B equals the probability of change from B to A. Thus, most reconstructions are based on a symmetric 1 to 1 transformation step matrix. Several studies have shown that reconstructions can be sensitive to different gain–loss ratios (e.g., Kohn et al, 1996; Omland, 1997; Lee and Shine, 1998; Ree and Donoghue, 1998).

An increasing number of studies have begun to question the equal gain–loss assumption (Cunningham et al., 1998). Many character states in diverse groups of organisms have long been thought to be more easily lost than gained (Dollo, 1893; Simpson, 1953), e.g., feeding larvae in marine invertebrates (Strathmann, 1978; Hart, 1996; Cunningham, 1999), wings in insects (Maddison, 1994), and functional wings in birds (Livezey, 1989). Most of these are complex character states that the authors argued could be lost repeatedly, but once lost, could not be regained easily. Several recent studies have used transformation weightings reflecting states that are more likely to be lost: for example, feeding larvae in starfish (Hart et al., 1997), plumage dimorphism in ducks (Omland, 1997), oviparity in reptiles (Lee and Shine, 1998), and tristyly in flowering plants (Kohn et al., 1996).

Kohn et al. (1996) reconstructed the history of three floral conditions related to adaptations for pollen transfer. Species with tristylous and enantiostylous flowers have different morphs with specific arrangements of stamens and styles to facilitate pollen transfer between morphs, whereas species with homostylous flowers are monomorphic. Kohn et al. considered the homostylous form to be simple and the other two forms to be relatively complex. Thus they considered changes from tristyly to the simple form more likely than the reverse. The reconstruction in Figure 1a uses a step matrix that makes changes to and among the complex forms more costly than changes back to homostyly. This reconstruction shows one gain of tristyly, with four subsequent reversals to homostyly. Kohn et al. (1996) considered this reconstruction to be more reasonable because of the complexity argument, as well as evidence from microevolutionary studies (Graham and Barrett, 1995; also see Barrett and Graham, 1997).

Maximum likelihood approaches offer some advantages when dealing with the possibility of asymmetric gain–loss probabilities. Maximum likelihood provides a framework for determining whether character states of extant taxa provide statistical evidence of asymmetric rates of change (Mooers and Schluter, 1999; Ree and Donoghue, 1999). However, strong directional biases that can mislead simple parsimony may also mislead maximum likelihood reconstructions. In some cases, using trees with large numbers of taxa (e.g., Ree and Donoghue, 1999) may help detect local biases in directionality. However, likelihood reconstructions on large phylogenies are still based on data from the single character being reconstructed. As Maddison and Maddison (1992:64) point out, "Clearly the assumed model of change can bias the reconstructed frequencies of change and thus the inferred model of change." How can this inherent data limitation of all ancestral state reconstruction be addressed? As Schluter et al. wrote, "[Maximum likelihood] conditions on rates of change that are themselves estimated from few data (species). This weakness could be remedied with realistic prior probability distributions for rate parameters" (Schluter et al., 1997:1708).

NEED FOR INDEPENDENT PROBABILITY ESTIMATES

Whether one uses generalized parsimony, maximum likelihood, or Bayesian methods, good independent probability estimates will
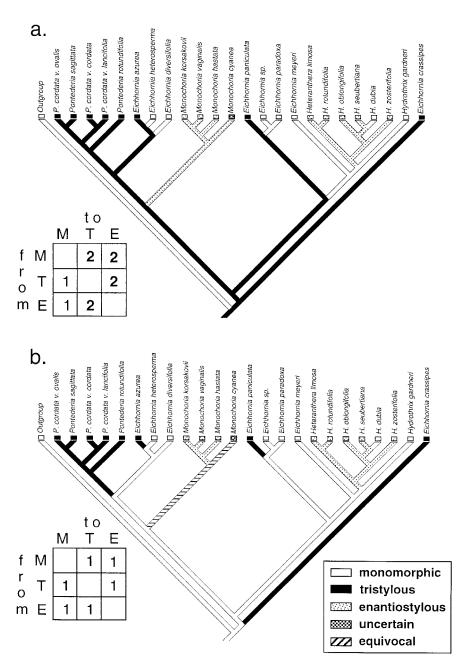
FIGURE 1. Reconstruction of floral form in the Pontederiaceae redrawn from Kohn et al. (1996) (their Figs. 4b and 4a). The step matrices to the lower left of panels a and b show the costs of transformations between the three floral forms (M = monomorphic, T = tristylous, E = enantiostylous). (a) The reconstruction favored by Kohn et al, which shows repeated losses of tristyly rather than independent gains. A cost-matrix favoring loss of the complex forms (tristyly and enantiostyly) at a ratio of at least 2:1 was sufficient to reconstruct a tristylous ancestor for the group.

help reconstruct character evolution. Such estimates can be used in cost-weighting matrices in parsimony algorithms, or as formal prior probability estimates in Bayesian approaches. How can we hope to get such estimates? Although independent probability estimates are indeed difficult to obtain for complex morphological or behavioral traits, this approach may be one of the only possible ways to improve the accuracy of ancestral reconstructions.

Several studies of plumage dimorphism in birds offer a hopeful case study that such an approach may be feasible. These studies were all done contemporaneously, without knowledge of the methods or conclusions of the other researchers. Studying plumage evolution in ducks, I concluded on the basis of several independent (nonphylogenetic) lines of evidence that losses of dimorphism in ducks had been more common than gains (Omland, 1997). Peterson (1996) studied dimorphism across all birds and also concluded that dimorphism was lost more frequently than gained. His conclusions were based on considerations of biogeography and taxonomic classifications, not explicit phylogenetic ancestral state reconstructions. Price and Birch (1996) used phylogenetic methods to study the frequency of gains and losses of dimorphism in passerine birds. They concluded that losses of dimorphism were more frequent than gains. Parsimony estimated that losses were 1.4 times more frequent, and maximum likelihood estimated that the rate of losses was 3 times higher than the rate of gains.

The similar findings among the three studies suggests that there may be a generality to transformation probabilities for plumage dimorphism in birds (although further study of all these groups is warranted). Therefore, any future studies on dimorphism in bird groups that include cryptic monomorphic species should at least test weightings that make losses more likely than gains. Such weighting also may be generalizable to integument color dimorphisms in other vertebrates or to sexual dimorphism in other types of characters. More study is needed of how generalizable such weight-

ing may be and what range of values should be tested. In addition, there has only been limited discussion of whether parsimony weights can be used to develop rate estimates for maximum likelihood models (see Maddison and Maddison, 1992; Mooers and Schluter, 1999). Schultz and Churchill (1999) address topics related to prior probabilities and sensitivity analyses for more-general cases.

Generalizing transformation costs from similar taxa and character types is one way to obtain independent cost estimates for ancestral state reconstruction. This approach seems to be the most promising, but much more research is needed. Detailed knowledge of the genetic and developmental bases of characters can inform character coding (e.g., DeSalle and Grimaldi, 1993) and in some cases may help estimate the costs of different evolutionary transformations (see Ree and Donoghue, 1998). In a few taxa, nearly complete fossil records (e.g., microinvertebrates: Prothero and Lazarus, 1980; Theriot, 1992) may help establish some general transformation costs. Finally, in some groups, microevolutionary studies (e.g., Graham and Barrett, 1995; Kohn et al. 1996; Omland, 1997), including artificial selection experiments, might give some indication of how easy it is to evolve character state A from B, and vice versa. Given the inherent statistical difficulty of reconstructing the states of a single character (Maddison and Maddison, 1992; Cunningham et al. 1998), it is important that researchers use all of the biological evidence available to increase the reliability of character optimization (also see Ryan, 1996; Cunningham et al. 1997; Lee and Shine, 1998).

It would be convenient if organisms possessed only two types of characters—a type for which transformations between character states were equally easy, and a second type for which transformations between states were irreversible. Such characters would enable us to avoid deciding on appropriate transformation weights and skirt the serious problem of allowing subjective biases to affect reconstructions (e.g., Hillis, 1998; Lanyon and Omland, 1998). However, the vast majority of characters

probably do not correspond to either of these two types. The examples of dimorphism in ducks (Omland, 1997) and tristyly in flowering plants (Kohn et al., 1996) are especially useful because they almost certainly fall in this difficult middle ground—there is no reason to believe that the character states in question are strictly irreversible.

Choosing a transformation weight or even a range of weights is indeed challenging, but choosing 1:1 weighting is no less of an assumption than choosing 4:1 weighting (e.g., Fitch, 1984; Swofford and Olson, 1990; Swofford and Maddison, 1992; Omland, 1997; Ree and Donoghue, 1998). When constructing phylogenies based on many characters, choosing specific transformation weights for each individual character is indeed problematic because biases can be introduced that are hidden from other systematists and even from the researcher. (Avoiding such hidden subjectivity is one of the strengths of modern quantitative tree-building methods.) However, when mapping a single character, the biases introduced by different weightings should be transparent, especially if a range of weights are used. For example, any researcher who has biological information that leads them to favor equal gain–loss costs for duck plumage dimorphism can use the reconstruction based on 1:1 weighting (Omland, 1997). Schultz and Churchill (1999) fully explore the issue of different prior beliefs in their paper on Bayesian approaches. If two different researchers use the same data and general methodologies, but different a priori transformation weights produce different reconstructions, then the researchers can argue about why they disagree about prior probabilities (Schultz and Churchill, 1999). This outcome focuses our attention to one of the central challenges involved in ancestral state reconstruction—understanding the biology of the characters in question.

FUTURE CHALLENGES OF ANCESTRAL RECONSTRUCTION

Three general challenges are facing ancestral state reconstruction, and these are addressed by the other papers from this symposium. The first challenge relates to the algorithms and statistics used to reconstruct ancestral states. Several papers explore alternative methods of reconstructing and assessing the uncertainty of ancestral states. Pagel (1999) presents a general maximum likelihood approach for inferring discrete ancestral states. Two papers use maximum likelihood approaches to explore in detail the issue of asymmetric transformation probabilities. Mooers and Schluter (1999) surveyed a range of examples from the literature and found that using models with different forward and backward rates is seldom justified statistically. However, Ree and Donoghue (1999) use a "supertree" of the Asteridae to explore a case in which there is statistical support for a two-rate model. Martins (1999) developed computer simulations to study the statistical performance of several methods for reconstructing continuous characters.

The second general challenge facing ancestral state reconstruction is biological. As mentioned above, better knowledge of the biological basis of the characters being reconstructed is needed (Cunningham et al. 1998; also see Ryan, 1996). Such information can lead to better models of character evolution, including prior information about transformation weights and rates of evolution. The present paper has dealt with this issue, as does the paper by Cunningham (1999).

A third challenge relates to the inherent uncertainties of ancestral reconstructions. Schultz and Churchill (1999) explore the role of subjectivity in ancestral state reconstructions in a Bayesian simulation study. Finally, given some of the uncertainties of ancestral reconstructions, how can reconstructions be used to test evolutionary hypotheses? Cunningham (1999) addresses this crucial topic in the final paper of the symposium.

In addition to the assumptions discussed here, many others that have yet to be explored in detail: e.g., that probabilities of character transformations do not change (Maddison, 1994; Mooers and Schluter, 1999), and that speciation is bifurcating (Ryan, 1996; Omland, 1997). Simulation studies are needed to test the sensitivity

of ancestral reconstructions to violations of each of the above assumptions. Future empirical and theoretical studies should be directed toward those assumptions to which ancestral state reconstructions are most sensitive. For some questions, the challenges of ancestral state reconstruction can be avoided by using comparative methods that do not require that ancestral states be reconstructed (e.g., see Schluter, 1997; Cunningham, 1999). Another solution is to draw general conclusions based on the reconstructions across the whole phylogeny (e.g., the overall ratio of gains to losses, Maddison and Maddison, 1992), although strong biases can mislead such general conclusions as well. Yet a third approach is to use ancestral state reconstructions to guide further detailed biological studies of different character states (e.g., Lee and Shine, 1998). However, explicit ancestral reconstructions are needed for progress on many interesting problems in systematics and evolution. For these cases, the challenges of ancestral state reconstruction must be addressed directly. In many cases better understanding of the biology of the characters and organisms being studied will lead to more-reliable ancestral state reconstructions.

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