

Transition Confidence and Modified Mean Values: Confidence Measures for Hypotheses of Character State Transition between Nodes and Ancestral State Optimizations

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A measure is introduced to quantify the reliability of character state transitions and character state stasis (lack of character state change between nodes). The mean value of a character state at an internal node is altered to obtain a measure termed the modified mean. Modified mean values at connecting nodes are employed to determine the support for hypotheses of character state transition/stasis between the nodes. The lowest of the two neighboring modified mean values implied by an hypothesis of character state transition/stasis is used as a direct measure of support for that hypotheses of character state transformation or stasis between the respective nodes. © 1999 The Willi Hennig Society

INTRODUCTION

Various techniques have been suggested to measure the reliability of branches on a cladogram, e.g., Bremer

support (Bremer, 1988) and bootstrap (Felsenstein, 1985), and to measure the reliability of whole characters over an entire tree, e.g., the consistency index (Kluge and Farris, 1969) and the retention and rescaled consistency indices (Farris, 1989). There have also been attempts to measure the reliability of character state transitions over entire trees, for example, "dynamic weighting" (Williams and Fitch, 1990), "exact indices" (Sharkey, 1993), and "self-weighted optimization" (Goloboff, 1997). Finally, there are also methods proposed that might be inferred to be reliability measures of optimizations at internal nodes (Maddison, 1991; Yang *et al.*, 1995; Schluter, 1995; Schluter *et al.*, 1997; Pagel, 1997). Conversely, no cladistic tools have been proposed to measure of the reliability of hypotheses of character state transition or stasis between adjacent nodes. The object of this paper is to introduce a technique to effect this: to quantify degree of support for character state transitions and character state stasis between nodes. It is hoped that this gauge, termed transition confidence, will aid in the evaluation of hypotheses of character phylogeny and encourage the development of other measures for this purpose.

ANCESTRAL STATES AND CHARACTER STATE TRANSITIONS

Hypotheses of character state transition/stasis are inferred from hypotheses of ancestral character states at internal nodes. For example, Fig. 1 illustrates a cladogram (cladogram A) with seven terminal taxa A–G and a binary character with states “a” and “b”. The unique set of parsimonious character state optimizations at the internal nodes infers that state b is apomorphic and that it has appeared convergently three times. Despite the uniqueness of the internal node optimizations and the inferred character state transitions, they do not elicit much confidence since all appear to be

sensitive to change, such that a change in one internal node optimization may result in a change in the hypotheses of character state transitions throughout the tree. With the introduction of new evidence in the way of a previously unknown ingroup taxon or another outgroup, the ancestral states could change radically. A newly discovered outgroup with character state b would render all internal node optimizations equivocal, such that state b could be considered plesiomorphic and state a independently derived four times. A more dramatic example of a poorly supported unique solution is that of the cladogram of Fig. 2. The only parsimonious character phylogeny infers that state a gave rise to all other character states, but few

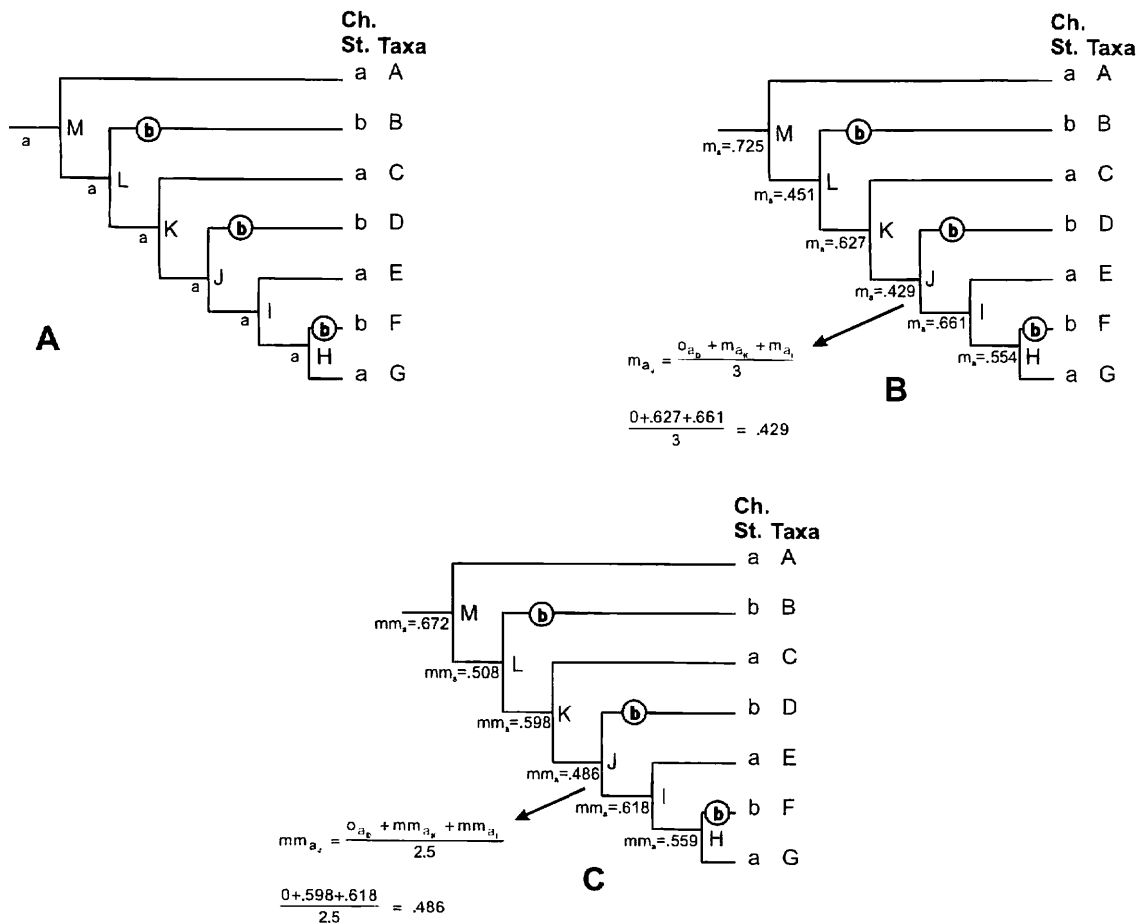


FIG. 1. Hypothetical cladogram (A) showing the unique, but poorly supported, optimizations for the ancestral states of a binary character using the parsimony criterion. Cladogram B shows the mean values for character state a at the internal nodes and an example calculation. Cladogram C shows the modified mean values for character state a at the internal nodes and an example calculation.

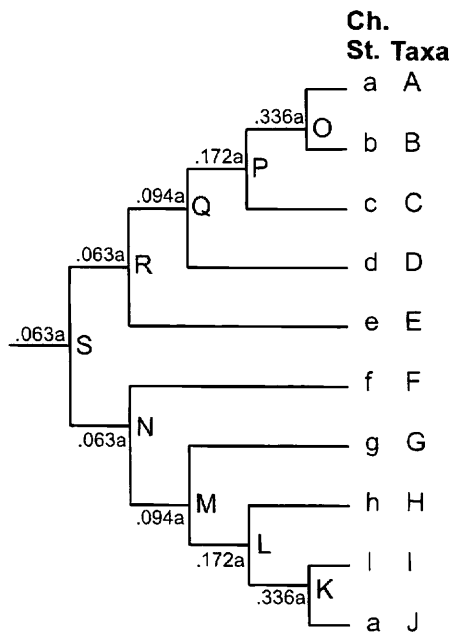


FIG. 2. Hypothetical cladogram showing unique, but poorly supported, optimizations for the ancestral states of a multistate character using the parsimony criterion. Numbers at internal nodes are modified mean values.

would place much confidence in this hypothesis. Though it may be the best hypothesis, it is not at all convincing.

In contrast to the previous examples, considerably more confidence would be reasonable for the ancestral state optimizations in the cladogram of Fig. 3 and the resulting hypothesis of character state transition ($a \rightarrow b$) between nodes K and J. Here again, there is only one parsimonious character state phylogeny, but it would be relatively stable to new discoveries. For example, the introduction of a new outgroup with character state b would have no effect on the character state phylogeny within the clade.

An example from the literature illustrates the potential usefulness of a reliability measure for character state transition/stasis. The cladogram of Fig. 4 is simplified from Sillén-Tullberg's (1988, Fig. 11) cladogram of the Helconiini (Insecta: Lepidoptera) by collapsing monomorphic clades [The tree was first proposed by Brown (1981)]. The cladogram traces Sillén-Tullberg's hypothesis of the evolution of gregariousness (g) and solitary living (s) in the larvae of these brightly colored butterflies. The conclusions drawn by Sillén-Tullberg

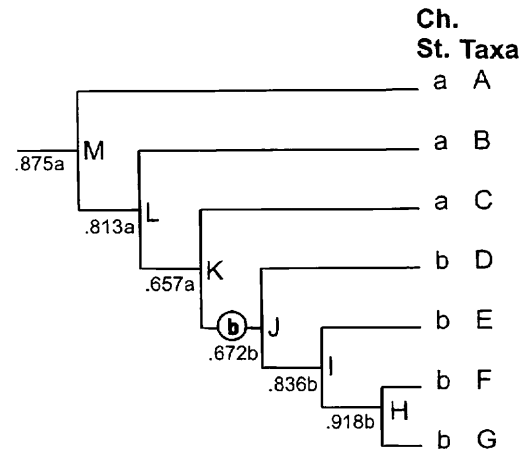


FIG. 3. Hypothetical cladogram showing unique, and well supported, optimizations for ancestral states of a binary character using the parsimony criterion. Modified mean values for character state a are illustrated at the internal nodes.

are that there were five independent origins of gregariousness and four reversals to solitary larval life (all illustrated on the cladogram of Fig. 4). A reliability or confidence measure for character state transitions might suggest which, if any, of Sillén-Tullberg's proposed character state transitions are well supported.

MEAN VALUES AT ANCESTRAL NODES

Before defining the modified mean which is the basis of my confidence measure, the following paragraphs will explain the concept of mean values and illustrate their weakness as confidence measures.

Mean character state values have long been used to obtain optimizations at internal nodes for continuous characters (Rogers, 1984; Huey and Bennett, 1987; Maddison, 1991). Cladogram B of Fig. 1 illustrates a simple example of how mean values may be calculated for a rooted tree. The two states (a and b) of a binary character are shown at the terminals. The terminal taxa are labeled A, B, C, D, E, F, and G and the ancestral nodes are H, I, J, K, L, and M. Mean values at internal nodes are found by averaging the values at the (usually three) neighboring nodes. This may be accomplished using a series of linear equations. For example, to find the mean value (m) of state a (m_a) at node J (m_{aj}) the

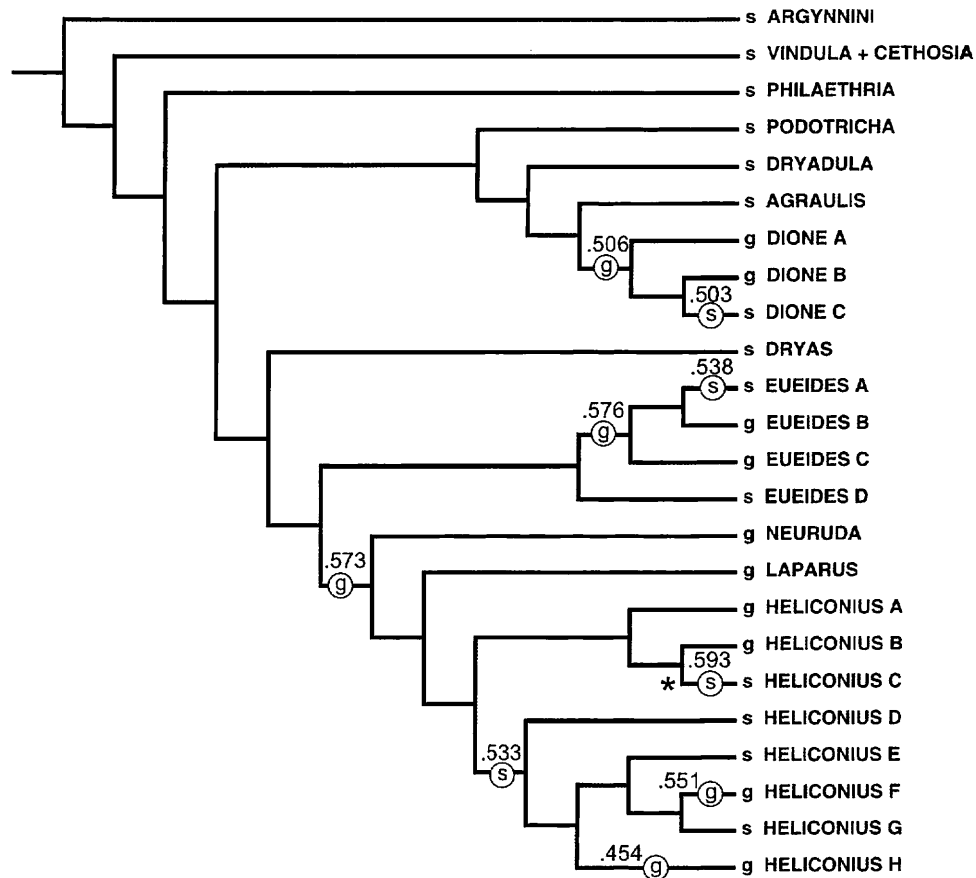


FIG. 4. Cladogram of the Helconiini (Insecta: Lepidoptera) (first proposed by Brown, 1981) simplified from Sillén-Tullberg's (1988) Fig. 11 by collapsing monomorphic clades. The cladogram traces Sillén-Tullberg's hypothesis of the evolution of gregariousness (g) and solitary living (s) in the larvae. Transition confidence (TC) values are reported for each internode at which a character state transition was proposed. The transformation indicated with asterisk is the only transformation that does not have an alternate equally parsimonious explanation.

mean values of state a at the two neighboring internal nodes and the observed value of state a at the neighboring terminal node are summed and divided by three. These three neighboring values are as follows: o_{aD} (the observed value of state a at terminal node D is zero since it is not the observed state at the terminal node), m_{aI} (which is calculated with a similar linear equation), and m_{aK} (also calculated with a similar linear equation). (See calculations on Fig. 1, cladogram B.)

To allow for polychotomies, a general equation (1) for the mean value (m) of a state at internal node i (m_i) for a rooted tree is equal to the quotient of the sum of the mean values, or observed values in the case of terminal nodes, at the neighboring nodes (m_k) and the number of neighboring nodes (P).

$$m_i = \frac{\sum_{k=1}^P (m_k)}{P} \quad (1)$$

A problem with mean states as confidence measures is best explained by referring to Fig. 5. The confidence value at the nodes indicated by an asterisk in cladograms A and B should be the same because the cladograms differ only in that cladogram A is a simplification of cladogram B; however, the mean values (m) at these nodes are not equal (0.20 in cladogram A, and 0.294 in cladogram B). Just about any terminal node could be expanded into a series of nested taxa that all possess the same state for the character in question. For example, a terminal node may represent a genus

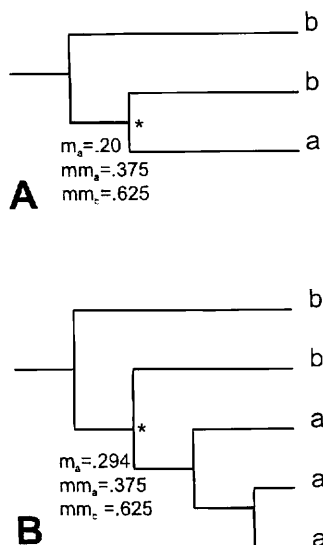


FIG. 5. Cladograms A and B showing mean (m) and modified mean (mm) values.

composed of species that are monomorphic for the character being examined, and for a given character, even species may sometimes be considered a nested set of monomorphic, monophyletic populations. The level of the analysis should not change the confidence value; moreover, the confidence value of the node indicated in cladogram B (Fig. 5) should most certainly not be lower than that of cladogram A (Fig. 5), since a character state surviving cladogenesis might elicit greater confidence. For these reasons mean values are not employed as confidence values.

MODIFIED MEAN VALUES

A solution to the aforementioned problem can be had by giving half the weight to terminal nodes when deriving a confidence value for internal nodes. Multiplying the observed values at the terminal nodes by 0.5 before entering them into the formula for mean values results in modified mean (mm) values of 0.375 for the nodes in both cladograms A and B of Fig. 5, demonstrating that the number of monomorphic terminal taxa (constituting a monophyletic group) does not affect the modified mean values. Although this demonstration is for only one example, I have not been

able to find an example to which it would not apply and expect that it applies universally.

The general formula (2) for the modified mean value (mm) at node i (mm_i) is equal to the sum of the modified mean values at the neighboring internal nodes (mm_k) plus half of the sum of the observed values at neighboring terminal nodes (n), divided by the sum of the number of internal neighboring nodes (A) plus the number of neighboring terminal nodes (T) divided by two.

$$mm_i = \frac{\sum_{k=1}^A mm_k + \left(\sum_{k=1}^T n_k / 2 \right)}{A + T/2} \quad (2)$$

The higher the modified mean value of a character state at an internal node, the more convincing is the hypothesis that it represents the ancestral state. The lowest possible value for a nonhomoplastic binary character is 0.625. This is the value for character state b (the complement of the value given for character state a) at the node marked with an asterisk in Fig. 5A. Since there is no homoplasy, and the character is binary, values of 0.625 and above are considered very convincing. The modified mean values for the states of a multistate character that represent the parsimonious optimizations at the internal nodes are illustrated in the cladogram of Fig. 6. These values are high relative to those found for the multistate character in the cladogram of Fig. 2. In the cladogram of Fig. 6 the lowest modified mean value for a parsimonious optimization is 0.584. In general the lowest modified mean values for states that are parsimonious optimizations are found at nodes that are nearest to character state transitions. This example is included to show that multistate characters may have rather convincing ancestral state optimizations.

Using the cladograms of Figs. 1, 3, and 6 as standards, modified mean values of approximately 0.58 and lower are not well supported, values of 0.625 and above are very convincing, and those values between 0.58 and 0.625 show increasing amounts support. Of course these are subjective standards and, just as in other cladistic measures such as the consistency and retention indices, readers must decide for themselves.

The modified mean values of character states a and b are presented at the internal nodes of the cladogram in Fig. 7. The modified mean values of state a jumps

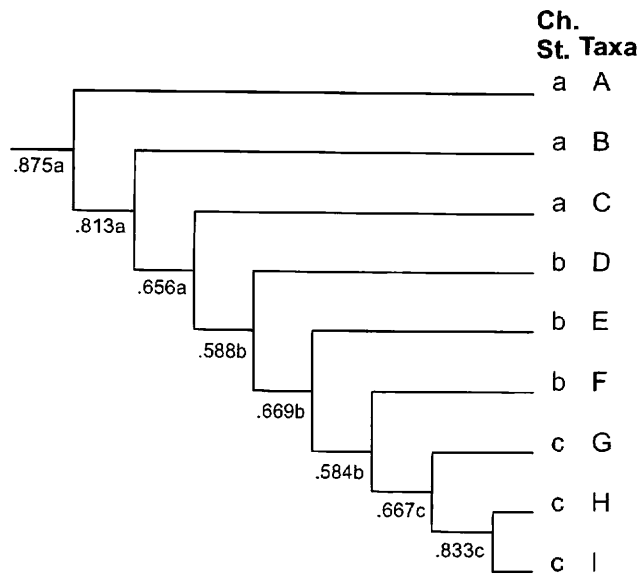


FIG. 6. Hypothetical cladogram showing the unique, parsimonious, optimizations for the ancestral states of a multistate character using the parsimony criterion, and illustrating the modified mean values for the character states that are optimum at the internal nodes.

from 0.328 to 0.656 between nodes T and S, which is the internode where the character transforms from state b to a. The further into the nested set of taxa with character state a on the cladogram, the higher the modified mean value of a is, and conversely, the further removed the internal node is from a terminal taxon with character state a, the lower the modified mean value of a. Modified mean values for character state b are highest near the base of the tree and decrease toward the apex of the tree. The hypothesis of stasis in state a, i.e., that character state a remains a, is increasingly supported as one moves from node T through to node M, although there are increasingly smaller increments of support. Modified mean values range between 0 and 1 inclusive. Values of 1 are obtained when all terminal nodes have the state being measured, and values of 0 obtain in the trivial case where the state in question is not present at any terminal node. For any binary character the modified mean value of a character state is equal to the complement of the modified mean value of the alternative character state. The summed mean values of all character states (regardless of the number) at any internal node equal unity.

Polymorphic terminal taxa are not difficult to analyze. In fact, the original paper employing mean values

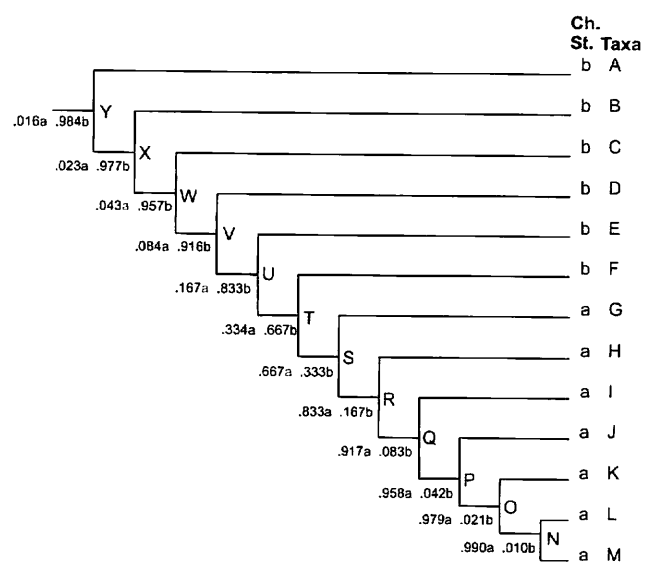


FIG. 7. A hypothetical cladogram showing convincing modified mean values for character states a (nodes N to S) and b (nodes T to Y) at the internal nodes.

in cladistic analysis (Rogers, 1984) is concerned with allele frequencies, and many of the terminal taxa investigated were polymorphic. Polymorphic terminals may be treated in several ways; the most simple is to divide the value at the terminal taxon by the number of states observed in that taxon. For example, if a terminal taxon had states a, b, and c, it would be assigned values of 0.33 for each state. These can then be introduced to the standard formula (2) to calculate the modified mean values at neighboring internal nodes.

CHARACTER STATE TRANSITION/STASIS CONFIDENCE MEASURES

Transition confidence (TC) or the reliability of character state transition/stasis between two nodes is equal to the lesser of the two modified mean values implied by the transition. For any binary character there are two modified mean values at each node, as exemplified in the cladogram of Fig. 7. The hypothesis that state b changes to state a between nodes T and S infers that state b is at node T and state a is at node S. The modified mean values for these states at the respective nodes are 0.672b and 0.656a. The transition confidence value

for the character state change $b \rightarrow a$ is equal to the lower of these two values (0.656) which is a convincing value. There is also a TC value for the transition $a \rightarrow b$ between these same nodes. The modified mean values inferred by this transition are 0.328a and 0.344b and the TC value is equal to the lower of these or 0.328, a value that indicates little support.

The low modified mean values illustrated in the cladogram of Fig. 2 demonstrate that, for a multistate character, transformation or stasis reliabilities can approach zero and still represent unique parsimonious transformations. The modified mean values of character state a vary between 0.336 and 0.063; all represent hypotheses of stasis for state a between nodes, and none is convincing. Obviously, a unique parsimonious character state transition/stasis does not necessarily equate to a convincing hypothesis.

Referring again to Sillén-Tullberg's (1988) hypothesis of the evolution of gregariousness (g) and solitary living (s) in the larvae of *Heliconiini* butterflies (Fig. 4), an examination of the modified mean values of the ancestral nodes on either side of the character state transitions suggested by Sillén-Tullberg shows that there are no well supported transitions. The transition from gregarious (g) to solitary (s) living between internal node E and terminal node *Heliconius c* with a TC value of 0.593 is the best supported and of all the transitions suggested it is the only one that is a uniquely parsimonious solution. Due to nearby convergence and ambiguity in character state optimizations even it has rather moderate TC support (Using the standards introduced in the previous section, values between 0.58 and 0.625 are moderately supported). All of the other character state transitions are poorly supported with TC values below 0.58.

DISCUSSION

Modified mean values are rather rough estimates of the robustness of optimizations at internal nodes (much like consistency and retention indices are rough measures of cladistic reliability) influenced by the proximity of convergent occurrences of the state and the number of parsimonious explanations.

For binary characters the conclusiveness of hypotheses of ancestral character states and character state transitions may be rather obvious to most cladists by simple examination of a cladogram. However, the measures introduced here may serve as an important guide for multistate characters in which unique parsimonious results may be very poorly supported (e.g., Fig. 2). Even for binary characters these measures will be useful to the uninitiated, those who do not have a background in cladistic theory, and who may think that all unique character state transitions are equally supported (compare again the cladograms of Figs. 1 and 3 if this is not clear).

PAST FAILURES AND FUTURE DIRECTIONS

I began this study hoping to find a method to optimize ancestral character states for discrete characters and/or choose between alternative parsimonious ancestral state optimizations. Although I investigated many different modifications of mean values, none gave satisfactory results. To illustrate the main problem of using mean states to optimize ancestral states for discrete characters consider cladogram B of Fig. 1. Here ancestral node optimizations based on mean values would give unparsimonious results with character state a jumping to state b and then back to state a on either side of ancestral node J, resulting in a total of four steps for the character over the cladogram instead of the minimum of three.

Mean state values have been used convincingly to estimate the ancestral states of continuous characters, but they may have greater utility, particularly in generating cladograms from continuous data or from data sets with a mixture of continuous and discrete data. There is fair agreement in the cladistic literature that much information is lost or corrupted when transforming continuous data into discrete character states for linear (standard) parsimony analysis (Chapphill, 1989; Stevens, 1991). Future research will investigate the usefulness of mean state parsimony (squared change parsimony) and modified mean state parsimony applied to data sets with both discrete and continuous characters. Perhaps mean state parsimony corrupts discrete characters less than linear parsimony

corrupts continuous characters or perhaps, as my preliminary studies suggest, it corrupts not at all, but rather weights discrete characters based on the incidence of homoplasy in neighboring clades.

Mean or modified mean values may show utility as a method of measuring and comparing the reliability of entire branches by averaging all characters at internal nodes. Also, averaging the absolute values of mean or modified mean values for one character over an entire tree may generate a measure indicative of the reliability of the character. For binary characters, these average values will approach 1 when there is no homoplasy and 0.5 when a character is showing the maximum amount of homoplasy on a tree (e.g., Fig. 1, cladogram C).

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