

EXACT INDICES, CRITERIA TO SELECT FROM MINIMUM LENGTH TREES

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Abstract—Modifications of the consistency, retention and rescaled consistency indices are introduced. These apply to particular transformations of a character state rather than all of the transformations of a character. For example, if one observes relatively many losses in a character state over a suite of minimum length trees, a low weight is applied to the transformation to a loss; however, these observations infer nothing on the probability of the character state being gained independently. If the same character state shows few or no convergent gains on the suite of minimum length cladograms, then gains receive a relatively high weight. Conversely, if for a particular character state, convergent gains are common and losses rare, the transformation to a loss is given a higher weight than the transformation to a gain. For multistate characters, each possible transformation is weighted independently. Three indices are proposed, i.e. the exact consistency index, the exact retention index and the exact rescaled consistency index. The consistency index is modified to deal with characters with unknown entries.

The methods outlined not only select (or generate) preferred tree topologies but they also choose character optimizations, even for trees of identical topology.

Introduction

One can think of numerous examples in which the loss of a particular character state is more common than independent gains of the character state. Digits in vertebrates have been lost in many lineages, yet relatively few examples of convergent digit gain have been documented. Similarly, the ability to fly has been lost thousands of times in the Coleoptera but there are no known instances of flight being regained (Wagner and Liebherr, 1992).

Conversely, character states may be gained independently many times but once acquired rarely reversed or lost. For example, abdominal terga three and four of the Hymenoptera (Insecta) have fused independently in many lineages, but there is no parsimonious argument suggesting that once fused they reverse to the freely articulating condition (personal observation). Current applications of, *a posteriori*, tree-dependent, weighting functions are insensitive to the reality that gains, losses and other character state transformations may be independent. The consistency index (Kluge and Farris, 1969), the retention index [Archie, 1989a,b (HERM); Farris 1989a,b, 1991] and the rescaled consistency index (Farris, 1989a), as presently utilized, fall into this category when used as weighting functions.

The idea to weight different character state transformations of the same character differentially is not new. As well as proposing his own weighting scheme with this quality (combinatorial weighting), Wheeler (1990) briefly discussed most other methods, i.e. Fitch optimization (Fitch, 1971), transformation series analysis (Mickeych, 1982; Mickeych and Lipscomb 1991; Mickeych and Weller, 1990), maximum likelihood (Felsenstein, 1978, 1979) and dynamic weighting (Williams and Fitch, 1990). Most of these methods are, *a priori*, weighting procedures. Transformation series analysis is vaguely similar to the method outlined here only in that they are both tree-dependent.

Three indices modified from the consistency, retention and rescaled consistency indices are introduced. Generally, the indices are analogous to one of the aforementioned indices, except that they apply to particular character state transformations instead of all character state transformations of a character. That is, each character state transformation (loss, gain, etc.) is indexed separately instead of being measured under the "umbrella" of one character.

In this paper I suggest that exact indices be used to select from minimum length trees. Current tree-dependent weighting techniques are not usually employed to select from a suite of minimum length trees; rather, they are routinely applied to the original data set to obtain one or more trees that are minimum length for the weighted data set. A problem with this approach is that trees longer than the minimum length for the unweighted data may be generated (Carpenter, 1988; Alexander, 1990). This renders the approach logically deficient. That is, if for any given data set, a tree longer than the minimum unweighted length may be considered the best tree, then minimum step trees are not necessarily the best hypotheses, and if minimum step trees are not the best hypotheses then the method is in paradox by only considering the indices based on character state distributions in the suite of minimum step trees. I am not raising the issue here of whether or not trees that are parsimonious for the unweighted data are best, I simply submit that if the original suite of trees does not include what is later considered to be the best tree, then either the original suite is incomplete or the result is in error.

Some differ with me in the views expressed in the previous paragraph; for example, the opposite opinion is expressed by Platnick et al. (1991). For readers sharing their conviction, exact indices may be incorporated as weights in the standard fashion, by utilizing the stepmatrix option of PAUP 3.0 (Swofford, 1990; Maddison and Maddison, 1992). One can use the minimum value of these indices, the maximum value or the average value, just as one can when weighting with the consistency, retention or rescaled consistency index.

The Indices

THE EXACT CONSISTENCY INDEX (ECI)

The ECI is based on the consistency index (Kluge and Farris, 1969).

ECI^i is the unit exact consistency index of the transformation from character state i to j , and the formula for binary characters is as follows: m^i is the minimum number of steps possible for the transformation from state i to j , s^i is the observed number of steps from state i to j .

$$ECI^i = \frac{m^i}{s^i}$$

If j is the root state then add 1 to m and s .

The values for m and s are root-dependent. If a particular state is the root, no transformations to that state need occur on any tree, whereas, if a state is not the root the minimum number of steps is equal to one on any tree. For characters with unknown polarities it is possible that different trees will have different root states. Therefore, for unrooted characters one must check the root state of each tree before calculating m and s values.

To obtain a value for a transformation over a suite of minimum length trees, the unit exact consistency indices are summed and this value is divided by the number of trees. This value is the average exact consistency index (AECI), which may be used to measure the reliability of character state transformations.

The consistency index (CI) has been criticized (Meier et al., 1991) because unknown data may not be handled properly by some computer programs. e.g. Hennig86 (Farris, 1988), PAUP 2.4 and 3.0 (Swofford, 1985, 1990). In these cases unknown states are made to conform to other characters such that no extra steps are inferred and "(T)hus, missing-data character states will inflate the consistency index" (Meier et al., 1991: 75). In other words, the consistency index does not incorporate the notion that if the states of a character were known for all taxa, there would be greater potential for conflict with other characters. This criticism may also be applied to the ECI. To correct this weakness for either the consistency index or the ECI when there are unknown entries, one may extrapolate the number of observed steps (s) over the entire suite of taxa to obtain a predicted s value. The corrected formula for s follows. t = number of terminal taxa and t'' = number of terminal taxa with an unknown entry for the character state in question.

$$s = s \text{ observed} + [s \text{ observed} \times (t''/t)].$$

The predicted value of s is substituted in the standard formula for the consistency index or the exact consistency index.

For multistate characters the calculation of the AECI is somewhat more involved. This is because for any transition to a particular state that has more than one origin, e.g. $i > j$ and $h > j$, the minimum number of steps for any one transition on any one tree is zero. With m equal to zero the simple formula for ECI will always yield a value of zero. The problem is solved by averaging the minimum number of steps possible over all transitions that are allowed on the suite of minimum length trees. For example, if there were four different origins of character state j over a suite of four trees, and if each tree had one transition to state j , then the $\sum m$ value for each transition is $0.25 \times 4 = 1$, and the AECI of each transition is equal to 0.25. The formula for the minimum number of steps expected, $\sum m(\text{exp})$, follows. y is the number of distinct transitions to j that are observed on all minimum length trees. $\sum m(\text{exp})^{i-j}$ is the expected minimum number of transitions $i > j$ under the null hypothesis that all transitions observed on the minimum length trees are equally likely. n = number of minimum length trees.

$$\sum m(\text{exp})^{i-j} = \frac{n}{y}$$

The formula for AECI which follows applies to binary and multistate characters. AECI^{ij} = the average exact consistency index for the transition from state i to state j .

$$\text{AECI}^{ij} = \frac{\sum m(\text{exp})^{i-j}}{\sum s^{i-j}}$$

if j is the root add n to $\sum m(\text{exp})^{i-j}$ and add n to $\sum s^{i-j}$.

The Exact Retention Index (ERI)

The exact retention index is based on the retention index [Archie, 1989a,b (as HERM); Farris, 1989a,b)]. The ERI is a measure of the observed number of steps

(s) a character state transformation has relative to the maximum number that are possible (M) on any tree. The formula for the unit exact retention index (ERI) for binary characters is as follows. ERI^{ij} is the exact retention index of the transition from state i to state j .

$$ERI^{ij} = \frac{M^{ij} - s^{ij}}{M^{ij} - m^{ij}}$$

If j is the root state then add 1 to m and s . If i is the root then $M^{ij} = \min(t_j, t_i, ch - 1)$. If j is the root then $M^{ij} = \min(t_j, t_i - 1, ch - 1)$. ch is the number of characters states for all characters in the data set exclusive of those of the character with the state in question. t_j is the number of terminal taxa with the state j . t_i is the number of terminal taxa with the state i .

The measure used to select from the suite of minimum length trees is the average ERI (AERI). This is equal to the sum of the unit ERI values divided by the number of trees.

As with the AECL, the formula for AERI must be modified for multistate characters because when a state is derived from two or more different origins, e.g. $i > j$ and $h > j$, the minimum number of steps for any one transformation on any one tree is 0. The problem is solved by setting m^{ij} proportional to M^{ij} , under the constraint that $\sum m$ for all transitions to state j , over all trees, is equal to the number of trees. The formula for the minimum number of steps expected for the transition from state i to j follows. $\sum M^{i-j}$ is the sum of the maximum possible number of transitions to state j on any tree (not just the universe of minimum length trees) that are not $i > j$. $\sum m(\text{exp})^{i-j}$ is the sum of the expected minimum number of transitions $i > j$. $\sum m(\text{exp})^{i-j}$ is the sum expected minimum number of transitions to j that are not $i > j$.

$$\begin{aligned} \sum m(\text{exp})^{i-j} &= n - \sum m(\text{exp})^{i-j} \\ \frac{\sum M^{i-j}}{\sum M^{i-j}} &= \frac{\sum m(\text{exp})^{i-j}}{\sum m(\text{exp})^{i-j}} \end{aligned}$$

Substituting for $\sum m(\text{exp})^{i-j}$:

$$\sum m(\text{exp})^{i-j} = \frac{n \times \sum M^{i-j}}{\sum M^{i-j} - \sum M^{i-j}}$$

The formula for $AERI^{ij}$ for multistate or binary characters is found by substituting $\sum m(\text{exp})^{i-j}$ for $\sum m$ in the equation for $AERI^{ij}$ that applies to binary characters, viz.

$$AERI^{ij} = \frac{\sum M^{i-j} - \sum s^{i-j}}{\sum M^{i-j} - \sum m(\text{exp})^{i-j}}$$

The ERI measures the amount of homoplasy a character state transformation has as a function of the amount of homoplasy that is possible; it varies between zero and one. For example, if a derived character state is present in only two of 20 terminal taxa and it has a convergent gain on a tree, the unit ERI for the transformation to a gain is 0. The character state transformation could not be more homoplastic, and there is no retained potential for homoplasy. Similarly, if a derived character state is present in 10 of 20 terminal taxa and there is only one convergent gain the unit ERI for the transformation to gains is 0.8. This transformation is considered to be a relatively reliable indicator of relationship since 10 independent gains are possible

whereas only two have occurred. Because of its sensitivity to the frequency of character state occurrence, the average ERI is my preferred weighting function.

Besides being sensitive to the frequency of occurrence of a character state, the exact retention index has a practical advantage over the exact consistency index in that it is easy to incorporate missing entries. Of course, the same applies to the (non-exact) retention index when compared with the (non-exact) consistency index. The exact retention index is a measure of character fit as a function of total possible homoplasy, which in turn is a function of the number of taxa. Unknown entries are not a problem since the variable t (number of terminal taxa) in the equation for the maximum possible number of steps (M), is simply reduced for the character in question by a number corresponding to the number of taxa with unknown entries.

THE EXACT RESCALED CONSISTENCY INDEX (ERCI)

The exact rescaled consistency index (ERCI) is analogous to, and based on, the rescaled consistency index of Farris (1989a), except that the ERCI is applied to particular character state transformations rather than to all transformations of a character. The unit exact rescaled consistency index is the product of the ECI and the ERI. The ECI is rescaled as a product of the ERI, or vice versa. The average ERCI may be used as a measure of the reliability of character state transformations in phylogenetic analysis.

I could not find a justification for the use of the rescaled consistency index, although Farris (1989a) stated (p. 418) that "for assessing the fit of a character to a tree, it might be desirable to use a measure that reaches 0 when a character fits a tree as poorly as possible". Since the retention index already has this property, why not simply use the retention index? A possible rationale for the rescaled consistency index is that it is often a relatively stronger weighting function than the retention index. Farris (1969) demonstrated that strong "unbounded concave" weighting functions are the most efficient when a data set is composed of random data and a subset of perfectly congruent cladistic data. If a stronger weighting function is desirable then why not multiply the retention index by the square or cube of the consistency index? Of course, resolving power may not be the justification, but whatever it is, it is not obvious to me.

Despite the lack of a definite justification, the rescaled consistency index appears to be in common use, especially in conjunction with the successive approximations approach; therefore, the analogous index for particular character state transformations (ERCI) is presented as a possible weighting function.

Applying the Indices

APPLYING THE AECI AS A WEIGHTING FUNCTION

The following example will illustrate the use of the AECI in selecting from among equally parsimonious trees. In the following examples only characters with homoplasy are considered. All non-homoplastic character state transformations take on a value of unity and are superfluous to the weighting procedure.

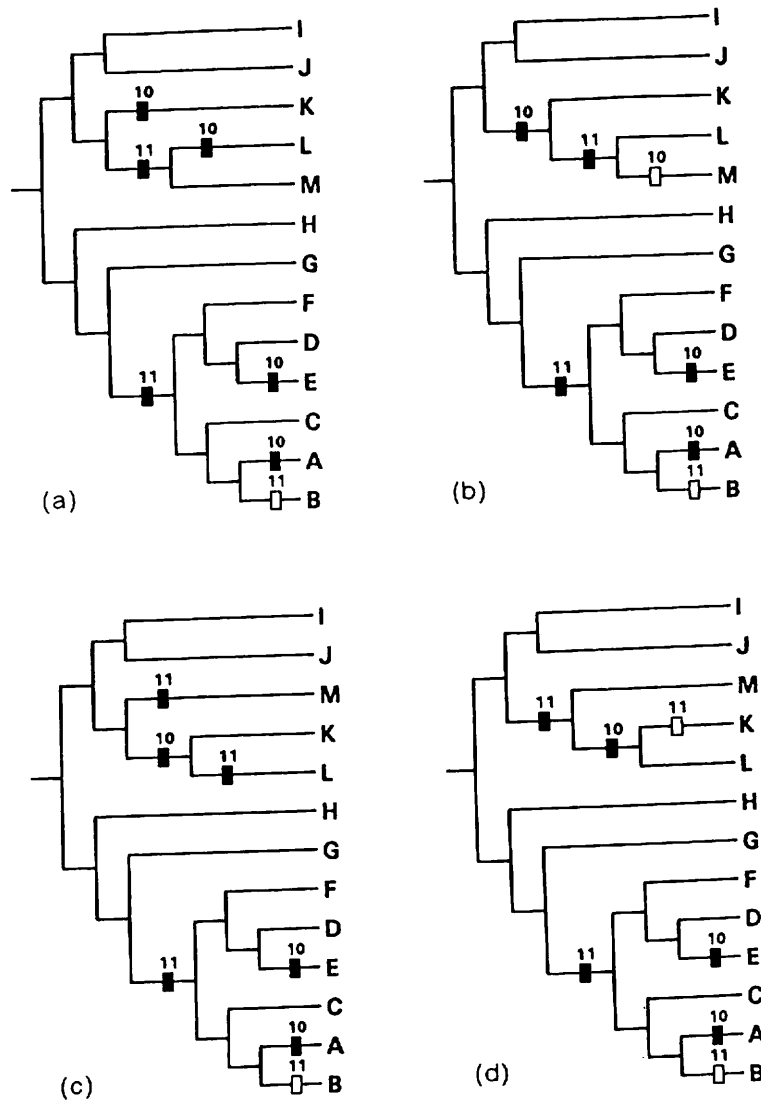


Fig. 1. The four minimum length trees based on the hypothetical data set of Table 1. ■, gains; □, losses.

Step 1. Obtain the set of minimum length trees [Fig. 1(a)–(d)]

The set of minimum length trees includes all different topologies and all unique character state distributions. There may be several trees with the same topology but with different character state optimizations. From the hypothetical data set of Table 1, observe that the topologies of trees a and b [Fig. 1(a) and (b)] are identical, and those of trees c and d [Fig. 1(c) and (d)] are identical, but all trees have unique character state distributions.

Step 2. Construct a homoplasy matrix (Table 2)

Here the number of observed steps (s) for each character state transformation on each tree is tabulated independently and summed over all trees ($\sum s$). Exact

Table 1
Hypothetical data set to demonstrate use of the average exact consistency index (AECI).

	11 12345678901
OUT	0000000000
A	11100110011
B	11100110000
C	11100100001
D	11111000001
E	11111000011
F	11110000001
G	11000000000
H	10000000000
I	00000011000
J	00000011000
K	00000010110
L	00000010111
M	00000010101

consistency indices are calculated and summed, and these values are divided by n (the number of trees) to obtain an AECI for each transformation. Note that for transformations to root states $n (= 4)$ is added to the $\sum s$ value.

Step 3. Construct a weights matrix (Table 3)

The AECI values from Table 2 are used as weights and applied to each step on each tree. For example, character 10 has four $0 > 1$ transitions in tree a [Fig. 1(a)] and the AECI for this character state transformation (from Table 2) is 0.308. The weighted value of these four steps is $0.308 \times 4 = 1.232$, and this is the value presented in column 1 of the weights matrix (Table 3). The net (minus those lengths that are equal to one in all trees) weighted length for each tree is presented in the bottom row of the matrix.

Step 4. Select a tree

The tree of choice is that with the lowest weighted length; in this case tree a [Fig. 1(a)] is preferred. END.

The average (non-exact) consistency indices of characters 10 and 11, as conventionally measured, are equal, i.e. 0.29; therefore, using this value as a weight

Table 2
Homoplasy matrix based on the data set of Table 1 and the four minimum length trees of Fig. 1.

		s				$\sum s$	AECI
		Tree					
		a	b	c	d		
10	0 > 1	4	3	3	3	13	0.308
10	1 > 0	0	1	0	0	1 + 4 = 5	0.800
11	0 > 1	2	2	3	2	9	0.444
11	1 > 0	1	1	1	2	5 + 4 = 9	0.444

$n = 4.$

Table 3
Weights matrix based on the average extra exact consistency indices (AECI) of Table 2.

		Tree			
		a	b	c	d
10	0 > 1	1.232	0.924	0.924	0.924
10	1 > 0	0	0.800	0	0
11	0 > 1	0.888	0.888	1.332	0.888
11	1 > 0	0.444	0.444	0.444	0.888
Total		2.564*	3.056	2.700	2.700

applied to all transformations of each character, one cannot choose from among the four cladograms, even in conjunction with the successive approximations approach. This points to a general property of all exact indices, which is that they have high resolving power. The number of tree topologies selected is usually half or less than half the number generated by the analogous non-exact index, furthermore the precise character transformations are specified, thereby decreasing ambiguity.

In this example there are only two different topologies, but there are two different character optimizations for each topology. To obtain the average exact consistency indices, each optimization and each topology is treated equally. Whether the topology changes or character distributions change, the fact is that the trees are fundamentally distinct and should be regarded as such in the analysis.

Applying the AERI as a Weighting Function for Multistate Characters

Table 4 is a hypothetical data set in which character 1 is an unordered multistate character. Figure 2 shows the six minimum length trees generated from the data and the transformations of the two homoplastic characters (1 and 2). Note that there are only two distinct topologies; the topologies of trees a–d are identical as are those of trees e and f. The homoplasy matrix (Table 5) illustrates the number of observed steps in each tree (s), the sum of the number of observed steps ($\sum s$), the sum of the maximum number of steps possible ($\sum M$), the expected average

Table 4
Hypothetical data set to demonstrate use of the average exact retention index (AERI) when applied to multistate characters.

	1234567890
OUT	000000000
A	1111001100
B	0111001100
C	0011001000
D	3011110000
E	3011110000
F	0011100000
G	1010000000
H	3000000010
I	2000000011
J	2100000011
K	3100000011

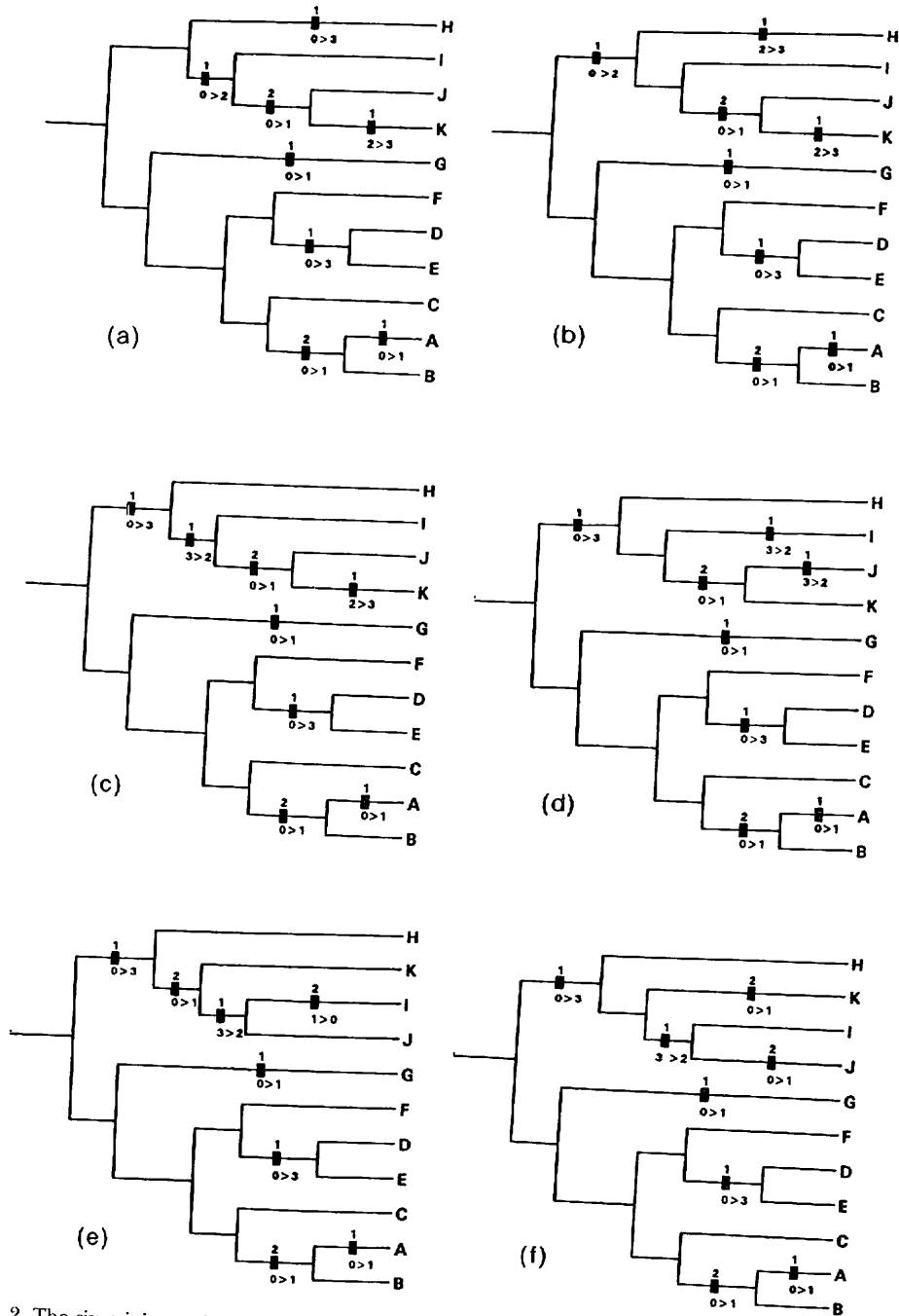


Fig. 2. The six minimum length trees based on the hypothetical data set of Table 11. 1 > 2 means character state 1 changes to state 2.

Table 5
Homoplasy matrix based on the data set of Table 4 and the six minimum length trees of Figure 2.

	s						Σs	ΣM	Σm^{exp}	AERI
	Tree									
	a	b	c	d	e	f				
1 0 > 1	2	2	2	2	2	2	12	12	6	0
1 0 > 2	1	1	0	0	0	0	2	12	3	1.10
1 0 > 3	2	1	2	2	2	2	11	24	4	0.65
1 2 > 3	1	2	1	0	0	0	4	12	2	0.80
1 3 > 2	0	0	1	2	1	1	5	12	3	0.78
2 0 > 1	2	2	2	2	2	3	13	24	6	0.61
2 1 > 0	0	0	0	0	1	0	6 + 1 = 7	18	6	0.92

$n = 6$.

number of steps for each state if the character shows no homoplasy (Σm^{exp}) and, finally, the average exact retention index (AERI) for all of the transformations of the two homoplastic characters, characters 1 and 2.

The AERI values are incorporated into a weights matrix (Table 6) and that tree with the net minimum weighted length is preferred, in this case tree f [Fig. 2(f)]. Different results obtain if the (non-exact) retention indices are employed. Trees a, b, c and d [Fig. 2(a)-(d)] would be selected instead of tree f [Fig. 2(f)]. Once again, the resolving power of exact indices is manifested.

Discussion and Summary

Sharkey (1989) referred to weighting procedures as hypothesis dependent or independent, but the more specific expression, tree-dependent, is used here because it specifies the dependent hypothesis. The weighting technique described here is tree-dependent; that is, a set of trees are obtained and the weights of character transformations depend on character state distributions over a suite of trees. Like other *a posteriori* weighting indices of this type, weights are based on the character state distributions over the suite of all minimum length trees. The view that tree dependency may be a deficiency is discussed in Neff (1986), Swofford and Olsen (1989) and Sharkey (1989).

Table 6
Weights matrix based on the average exact retention indices (AERI) of Table 5.

	s	Tree					
		a	b	c	d	e	f
1 0 > 1	0	0	0	0	0	0	0
1 0 > 2	2.20	2.20	0	0	0	0	0
1 0 > 3	1.30	0.65	1.30	1.30	1.30	1.30	1.30
1 2 > 3	0.75	1.5	0.75	0	0	0	0
1 3 > 2	0	0	0.78	1.56	0.78	0.78	0.78
2 0 > 1	1.22	1.22	1.22	1.22	1.22	1.22	1.83
2 1 > 0	0	0	0	0	0.92	0	0
Total	5.47	5.57	4.05	4.08	4.22	3.91*	

The indices introduced here have two advantages over non-exact weighting indices. First, they discriminate between different character state transformations even when presented with identical tree topologies, and second, when choosing from among minimum length trees, exact indices have a higher power of resolution.

As the examples in this paper demonstrate, exact indices may be used to select from the suite of trees that are minimum length for the unweighted data. Alternatively, one may employ exact indices as weights for raw data, resulting in a new suite of trees that may or may not be minimum length with respect to the original data. For reasons explained in the introduction, I prefer the former approach.

If one is using exact indices by applying weights to the raw data, as opposed to using the indices to select from minimum length trees, then one may do well to consider the successive approximations approach (Farris, 1969). This may also be true when using the indices to select from minimum length trees. If more than one tree remains after the first run, then the selection procedure can be repeated using the remaining trees to obtain exact indices. In the dozen or so (rather simple) examples that I have worked through, one or two trees have always resulted in the first run, and a second run would not deliver further resolution. I only suppose that more complex data sets may be further resolved after the first run.

Farris (1988), in his software package Hennig86, uses best fit values to obtain an "s" value (number of steps) when weighting using the successive approximations approach in conjunction with the rescaled consistency index. One may also use best fits for formulating exact indices. Best fits will generally give more conservative results than average fits, but an examination of the attributes of the two alternatives has not been conducted and remains beyond the scope of this paper.

Ascertaining all possible transformations can be a rather tedious practice. In this regard, I have found the `xx` command of Hennig86 (Farris, 1988) to be useful. For Apple computer users, a superior option is MacClade's Equivocal Cycling calculations which "find each of the equally parsimonious reconstructions of character evolution" (Maddison and Maddison, 1992: 107).

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