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"UNORDERED" VERSUS "ORDERED" CHARACTERS

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Abstract.—Multistate morphological characters have generally been treated as either "unordered" or "ordered" in phylogenetic analyses using parsimony. Because ordering relations do not apply to the states of characters treated under these methods, I prefer "maximally connected" character to "unordered" character and "minimally connected" character to "ordered" character. This paper formally defines the two character types, compares their properties, and considers the consequences of the two methods for both resolution and congruence. The results demonstrate that minimally connected characters increase resolution relative to maximally connected characters. Minimally connected characters do not, however, necessarily increase congruence among data sets. Because both methods produce nonrandom congruence among data sets, both character types constitute valid phylogenetic methods. A mixed-parsimony approach is advocated, wherein multistate characters are treated as minimally connected whenever reasonable but treated as maximally connected otherwise. [Multistate character; ordered character; unordered character; parsimony.]

Since the introduction of parsimony methods for inferring phylogenies, various ways to treat multistate characters have been developed (reviewed by Swofford and Maddison, 1992), each of which makes assumptions about the evolution of characters. Of these, the relatively unrestrictive method of treating character-state relationships as undirected, such that the number of steps in the transformation from any state to another is equal to the number of steps in the reverse transformation, has been the most popular. Several variations of this method exist, the most restrictive of which assumes that the states of a character are related according to a treelike transformation series, which constrains the transformation between any pair of states to proceed through any intermediate states defined by the transformation series. The least restrictive method places no such constraints on a character, assuming that any state can transform directly into any other. The most restrictive method results in what are traditionally termed "ordered" characters; the least restrictive method results in what are traditionally termed "unordered" characters. However, for the reasons discussed below, I prefer "minimally connected" to "ordered" character, and "maximally connected" to "unordered" character. A third method, which results in "moderately connected" characters, imposes constraints that are intermediate between those imposed by the maximally and minimally connected methods by assuming transformation series with one or more closed circuits (Mabee, 1989; Swofford and Maddison, 1992). These three methods form a continuum in terms of the evolutionary constraints imposed on characters. The present paper, however, focuses only on the two extremes for the simple reason that these are the only character types that have been commonly employed in parsimony analyses.

Given that there is a choice between treating multistate characters as minimally or maximally connected, the question naturally arises whether one method is preferable to the other. Resolution and accuracy are important criteria to use in answering this question. By "resolution," I mean the extent to which relationships can be recovered; by "accuracy," I mean the extent to which the recovered relationships are correct. Only one paper (Hauser and Presch, 1991) has addressed the relative merits of the minimally and maximally connected character methods. Hauser and Presch tested the assumption that minimally connected characters result in greater resolution by reanalyzing each of 27 published data matrices twice, once

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with the multistate characters treated as minimally connected and again with the multistate characters treated as maximally connected. Their results indicated that minimally connected characters do not necessarily result in more resolution than do maximally connected characters. Although Hauser and Presch did not attempt to empirically assess the relative accuracy of the methods, they did consider the potential effect of the two methods on accuracy from first principles. They concluded (p. 262) that "if one accepts that the most reliable criterion for determining the evolutionary sequence of a multistate character is the cladogram itself . . . , then hypotheses of order are unnecessary." Thus, Hauser and Presch seem to recommend that multistate characters should generally be treated as maximally connected.

Unfortunately, Hauser and Presch's (1991) comparison of the merits of maximally and minimally connected characters is inadequate for two reasons. First, they ignored the original treatment of the multistate characters sampled, choosing instead to linearly connect all multistate characters in their reanalyses. However, many of the multistate characters were originally maximally connected. Any study that purports to compare maximally and minimally connected characters must use the original hypotheses of character state relationships.

Second, a consideration of phylogenetic resolution, although important, is insufficient by itself to evaluate the relative merits of the maximally and minimally connected methods. An empirical evaluation of the accuracy of the methods must be made. After all, accuracy should ultimately be the most important consideration when deciding between competing phylogenetic methods; what good is improved resolution if the results are inaccurate?

The present paper has two major parts. The first formally defines maximally and minimally connected characters and compares their properties. The second part empirically reexamines the rationale for choosing between maximally and minimally connected characters by considering the consequences of the two methods for both resolution and accuracy. Parsimony analyses were performed on 21 published data matrices (three of which were also analyzed by Hauser and Presch [1991]) using the original (minimally connected) hypotheses of character-state relationships and again with the characters maximally connected. Phylogenetic resolution was measured as the number of clusters minus one on the strict consensus trees resulting from each set of most-parsimonious trees. Obviously, it is impossible to directly assess the accuracy of a phylogeny. Instead, I assessed accuracy indirectly by the method of taxonomic congruence (Mickevich, 1978), which examines the extent to which phylogenetic trees based on different data sets are similar. Congruence among different data sets may provide the best evidence available bearing on the accuracy of phylogenies (e.g., Penny et al., 1982; Miyamoto and Cracraft, 1991). In practice, however, perfect congruence is seldom achieved. Nonetheless, it is reasonable to assess competing phylogenetic methods by their ability to produce congruence (Penny and Hendy, 1985a, 1986).

TERMINOLOGY

The characters discussed in this paper are undirected or symmetrical characters (Swofford and Maddison, 1992), for which the number of steps in the transformation from any state to another is equal to the number of steps in the reverse transformation. (My usage of "undirected" and "directed" with reference to characters is equivalent to Swofford and Maddison's [1992] usage of those words. Others [e.g., Meacham, 1984] have used "undirected" and "directed" character synonymously with "unpolarized" and "polarized" character, respectively.) Undirected characters whose states are related according to a tree-like transformation series or "character state tree" (sensu Farris et al., 1970) are commonly referred to as "ordered." If the tree is linear, the character is said to be "fully ordered"; if the tree is branching, the character is said to be only "partially ordered" (Swofford and Olsen, 1990). Un-

directed characters whose states are allowed to transform directly into any other state are commonly referred to as "unordered." However, under the strict mathematical definition of ordering relations between pairs of elements (e.g., Roman, 1986), the terms "unordered" and "ordered" do not apply to undirected characters. For a character to be ordered, $i \geq j$ or $j \geq i$ must be true for some or all pairs of character states i and j under some appropriate sense for the binary order relation "$\geq$." In the present context, the appropriate sense for $\geq$ is "is derived from" (see Estabrook, 1972). Thus, $i \geq j$ means "i is derived from j." However, by definition, no state of an undirected character can be considered to be unequivocally derived from another for the simple reason that both forward and reverse transformations are allowed; relations between pairs of states are unordered. Ordering relations do apply to directed characters, e.g., to Camin–Sokal or irreversible characters (Estabrook, 1968), because the relationships between states are directed. For these reasons, I prefer "minimally connected" character, meaning that the states of the transformation series are connected with the minimal number of branches, rather than "ordered" character. Similarly, I prefer "maximally connected" character, meaning that the states of the transformation series are connected with the maximal number of branches, rather than "unordered" character.

DEFINITIONS AND PROPERTIES OF MAXIMALLY AND MINIMALLY CONNECTED CHARACTERS

A character used in parsimony analysis, regardless of how it is treated, can be defined as an exhaustive partition of m taxa (including all outgroup or hypothetical ancestral taxa) into n nonoverlapping subsets corresponding to the character states, together with a set of "rules" that specify the number of units ("steps") in the transformation between each ordered pair of character states. Generally, the character states are a set of distinct features that are hypothesized to have transformed into each

other. The characters discussed in this paper are types of undirected (or symmetrical) characters (Swofford and Maddison, 1992), for which $D(i, j) = D(j, i)$ for all character states i and j, and where $D(i, j)$ is the number of steps in the transformation from i to j. This independence from direction facilitates phylogenetic analysis because algorithms for finding shortest trees based on undirected characters can manipulate unrooted trees because tree length is independent of the position of the root. Directed characters are more restrictive than undirected characters because the number of steps in the transformation between any pair of character states depends on the direction of the transformation (Camin–Sokal or irreversible characters are examples of directed characters [Swofford and Maddison, 1992]).

The rules specifying the number of steps between pairs of character states can be conveniently represented by connected graphs (Swofford and Maddison, 1992). (A graph is a set of nodes and branches; a connected graph is one in which every pair of nodes is connected by at least one path; a path is a connected sequence of nodes and branches. All graph theory terminology herein follows Harary [1969].) A graph used in this fashion is a character state graph (CSG), which generalizes the notion of a character state tree (sensu Farris et al., 1970). On a CSG, the nodes correspond to character states and the branches represent the transformations between pairs of character states. The branches of CSGs can be directed or undirected to indicate whether the character is directed or undirected. CSGs can be weighted by assigning a positive integer to each branch. For a character represented by a CSG, the number of steps between any pair of states is the sum of weights along the shortest path (path of fewest branches) connecting the two states. Typically, the branches of maximally and minimally connected characters are equally weighted with 1's. Hence, the number of steps between any pair of states for a maximally or minimally connected character is simply the number of branches along the shortest path connecting the
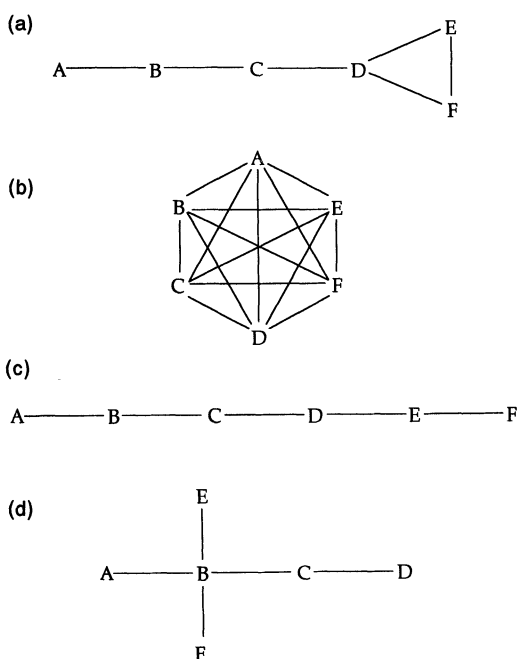
FIGURE 1. Character state graphs (CSGs) for several hypothetical undirected equally weighted characters. (a) A CSG for a moderately connected character. (b) A CSG for a maximally connected character. (c) A linear CSG for a minimally connected character. (d) A branching CSG for a minimally connected character.

states. Figure 1 depicts CSGs for several hypothetical undirected equally weighted characters.

The number $R(n)$ of undirected equally weighted CSGs for n character states is counted by a recursive formula:

$$R(n) = 2^{\binom{n}{2}} - \frac{1}{n} \sum_{k=1}^{n-1} \binom{n}{k} 2^{\binom{n-k}{2}} kR(k)$$

(Harary and Palmer, 1973), where $\binom{r}{s} =$ $r!/(r - s)!s!$. For $n = 2$–9, $R(n)$ is 1, 4, 38, 728, 26,704, 1,866,256, 251,548,592, and 66,296,291,072, respectively. This subsumes all undirected equally weighted characters, including maximally and minimally connected characters and characters whose CSGs contain one or more but fewer than $\binom{n}{3}$ cycles (a cycle is a path that begins

and ends with the same node). Figure 1a is a CSG of the latter type. Characters of this nature, termed "reticulate" by Mabee (1989) and "nexus" by Mickevich and Weller (1990), place constraints on the evolution of characters that are intermediate between those of the maximally and minimally connected methods. The maximally and minimally connected methods are the end points of a continuum of possible undirected methods, with reticulate/nexus characters occupying the middle. Reticulate/nexus characters are often formed during "transformation series analysis" (e.g., Mickevich and Weller, 1990) but have been neglected as an a priori way to treat characters for phylogenetic analysis. This neglect is unfortunate because such characters could be used in situations where the relationships between the states of a character are only partially known.

Maximally Connected Characters

A maximally connected character is one for which every state on the CSG is directly connected to every other state. Thus, $D(i, j) = 1$ if $i \neq j$; $D(i, j) = 0$ otherwise (the "trivial metric" of Kluge and Farris [1969]). Figure 1b illustrates a CSG for a maximally connected character. Construction of a maximally connected character merely entails identifying the character states; specifying the number of steps separating pairs of states is trivial. In this paper, only "phylogenetically informative" characters are of interest. Phylogenetically informative characters are characters that require different numbers of steps on different trees. A maximally connected character is informative when two or more character states are each present in two or more taxa (Fitch, 1977).

Maximally connected characters were first formalized by Fitch (1971) as his "minimum mutation model" but were apparently first suggested by Kluge and Farris (1969). Although Fitch (1971) presented an algorithm for optimizing maximally connected characters to phylogenetic trees and developed the computer program ANCESTOR to do so, very few or possibly none of the phylogenetic analyses of morpho-

logical characters published in the 1970s and early 1980s employed maximally connected characters, probably because of a mistrust by systematists of maximally connected characters as too "agnostic" with respect to evolution and, hence, less informative. For example, Mickevich (1982: 475) labeled the maximally connected method as "the nihilistic method." Recently, however, opinion seems to be changing, and maximally connected characters are being increasingly used.

Minimally Connected Characters

A minimally connected character is one for which the CSG contains $n - 1$ branches, the minimal number for a connected graph. A CSG with $n - 1$ branches contains no cycles and is, by definition, a tree. A tree used in this way is a specific type of CSG called a character state tree (CST). Figures 1c and 1d are linear and branching CSTs, respectively.

Minimally connected characters were originally formalized by Kluge and Farris (1969) and Farris (1970). Any minimally connected character for $m \geq 4$ is phylogenetically informative, unless the character possesses a state with r taxa incident on $m - r$ branches on the CST.

The polarity of a minimally connected character and the relationships of its states are distinct concepts (Mabee, 1989; Swofford and Olsen, 1990). Polarization of a CST entails identifying the ancestral state. The resulting CST, however, is not rooted. Rooting a polarized CST and, therefore, directing its branches, would imply irreversibility of the transformations, contrary to the definition of undirected characters. To avoid confusion, polarized CSTs should not be drawn as rooted CSTs, contrary to the usual practice. It is preferable to illustrate a polarized CST as unrooted, but with an asterisk (or some other symbol) included to denote the hypothesized ancestral state.

The number $T(n)$ of unpolarized CSTs is found by a simple formula:

$$T(n) = n^{n-2}.$$

This equation is often attributed to Cayley (1889) but has an earlier history (see Moon, 1970). Because a CST is polarized by denoting one of its n nodes as ancestral, the number of polarized CSTs is $n(n^{n-2}) = n^{n-1}$. The number of CSTs rises very quickly with increasing number of states. For example, for $n = 3-8$, $T(n)$ is 3, 16, 125, 1,296, 16,807, and 262,144, respectively. The corresponding number of polarized CSTs is 9, 64, 625, 7,776, 117,649, and 2,097,152, respectively.

An important distinction exists between linear CSTs, i.e., CSTs with no states connected to three or more branches, and branching CSTs, i.e., CSTs with at least one state connected to three or more branches (Figs. 1c, 1d). This distinction is important because linear CSTs can be represented by a sequence of integers or letters for direct use in computer-aided parsimony analysis, whereas branching CSTs must be decomposed into two or more sequences of integers or letters that are jointly equivalent to the original character (version 3.0s of PAUP [Swofford, 1991a], however, allows the states of a branching CST to be entered directly into a matrix). By this definition, a polarized CST on which the primitive state is an interior node and the remaining states are connected to one or two branches is not a branching CST. The number of unpolarized linear CSTs is $n!/2$, because each unpolarized linear CST corresponds to two permutations of n states taken n at a time. The number of unpolarized branching CSTs is simply the difference between the number of unpolarized linear CSTs and the total number of unpolarized CSTs (i.e., $n^{n-2} - n!/2$). The number of polarized linear CSTs is $n(n!/2)$ because there are n ways to polarize an unpolarized linear CST. The number of polarized branching CSTs is the difference between the number of polarized linear CSTs and the total number of polarized CSTs (i.e., $n^{n-1} - n[n!/2]$).

Differences between Maximally and Minimally Connected Characters

Maximally and minimally connected characters differ in several respects. The most obvious is the greater degree to which a single character constrains the number of most-parsimonious trees when the char-

acter is minimally connected (Mabee, 1989). The number of shortest unrooted dichotomous trees based on a single maximally connected character of n states for m taxa is

$$N(m - 1)N(a_1)N(a_2)\cdots$$
$$\cdot N(a_n)/N(m - n + 1), \qquad (1)$$

where $N(r) = (2r - 3)(2r - 5)\cdots 1$ and a_k is the number of taxa possessing the kth state (Carter et al., 1990: based on theorem 2). The number of shortest unrooted dichotomous trees based on a minimally connected character is

$$N(a_1 + f_1 - 1)N(a_2 + f_2 - 1)\cdots$$
$$\cdot N(a_n + f_n - 1), \qquad (2)$$

where f_k is the number of branches connected to the kth state on the CST. This equation derives from the observation that for any single minimally connected character, the shortest trees are exactly those derived from completely resolving a strict consensus tree of the same form as the CST with the terminal taxa substituted for the character states. Equation 2 counts the number of ways to resolve an unrooted strict consensus tree with the same form as the CST. Using Equation 1, the number of shortest trees for a maximally connected character of three states, wherein $a_1 = 3$, $a_2 = 2$, and $a_3 = 2$, is 27. If the states are related 1—2—3, the number of shortest trees from Equation 2 is 9. If $a_1 = 4$, $a_2 = 3$, and $a_3 = 3$, the number of shortest trees under the maximally and minimally connected methods (states related as before) is 2,025 and 675, respectively.

This difference is due to the different ways the two character types treat transformations between pairs of states. With a maximally connected character, every transformation is treated equally as comprising one step, resulting in a much larger number of trees than if the same character is treated as a minimally connected character. As correctly argued by Hauser and Presch (1991), however, this reasoning does not necessarily extrapolate to collections of characters; a matrix of maximally connected characters will not necessarily result in less resolution, hence the need for empirical tests of the present nature.

Still another difference between maximally and minimally connected characters relates to tree length: the shortest trees based on a set of minimally connected characters will be at least as long and usually longer than those based on the same characters treated under the maximally connected method. This is a simple consequence of the different way that the characters are defined, and I agree with Hauser and Presch (1991) that it does not constitute a valid criticism of minimally connected characters.

METHODS

The systematics literature was surveyed for morphological data matrices containing minimally connected multistate characters. To be included in the analysis, a matrix had to be comprised of at least 10% minimally connected multistate characters whose state relationships were explicitly described.

Two analyses were performed on each matrix. The first was designed to compare the resolution produced by treating the characters as minimally and maximally connected. The second analysis was designed to compare the congruence produced by treating the characters as minimally and maximally connected.

For the resolution study, each matrix was analyzed twice, once with the multistate characters minimally connected according to the author(s)'s CSTs and again with the characters maximally connected. The degree of resolution was measured simply as the number of interior nodes minus one on the strict consensus tree (SCT) of the shortest trees from each matrix. This index of resolution ranges from a minimum of 0 to a maximum of $m - 3$, where m includes all outgroup or ancestral taxa. Several authors (e.g., Swofford, 1991b) have pointed out an undesirable property of SCTs; two trees that differ only in the placement of one taxon can result in a highly or completely unresolved SCT. This difficulty with SCTs was not considered a problem, however, because the goal of this study was to assess resolution in a relative sense, not in some absolute sense, i.e., are SCTs based

on minimally connected characters better resolved than SCTs based on maximally connected characters?

The congruence study utilized halfling analysis (Penny and Hendy, 1985a, 1986). Each matrix was randomly divided once into two disjoint submatrices of equal sizes ("halflings"), and the two halves were analyzed separately, once with the characters maximally connected and again with the characters minimally connected. The resulting SCTs from the shortest trees based on each submatrix, analyzed by either the maximally or minimally connected method, were compared with the partition metric, which counts the number of interior branches not shared between two trees (see Penny and Hendy, 1985b). Two interior branches on different trees are considered equivalent if their deletion partitions the taxa into the same subsets. If trees are rooted, the partition metric counts the number of unshared clades. One problem with the partition metric is that a pair of trees differing only in the placement of one taxon can have a large dissimilarity value (Penny and Hendy, 1985b; Swofford, 1991b). Again, because only relative congruence is of interest in this study, the partition metric is appropriate. Furthermore, the partition metric is available in PAUP 3.0s (Swofford, 1991a) and is easily interpreted, and its probability distribution is known for up to 16 taxa for dichotomous trees (Penny et al., 1982; Hendy et al., 1984).

When two trees contain polychotomous nodes, application of the partition metric will result in a low dissimilarity value, which implies a high degree of similarity, when in fact the dissimilarity is low simply because the trees lack interior branches that might conflict. One solution is to convert the value of the partition metric, d, to the maximum value, d_{max}, possible if the polychotomous nodes on two trees are considered to represent unresolved relationships. This conversion is done by adding to d the number of interior branches that would be gained on two trees by resolving the polychotomous nodes. This strategy is employed in this study. The formula $d_{max} = 2m + d - t_1 - t_2 - 6$, where t_i is the res-

olution index for tree i, was used to calculate d_{max} from d.

The usefulness of halfling analysis for assessing phylogenetic accuracy depends on character independence, and especially with morphological characters, this condition is probably often not met. Nonetheless, halfling analysis is the best method available for comparing the accuracy of competing phylogenetic methods. Other investigators may wish to compare the minimally and maximally connected methods using other measures of reliability (e.g., bootstrapping, etc.).

All parsimony analyses were carried out with PAUP 3.0s (Swofford, 1991a) on a Macintosh computer using the branch and bound (for $m \leq 15$) or general heuristic search (for $m > 15$) commands together with the collapse zero-length branches option. Before each branch-and-bound run, an upper bound to the number of steps was estimated from the results of a general heuristic search to reduce run times. Characters treated as maximally connected by the author(s) were treated that way in all analyses. The original outgroup(s) or hypothetical ancestral taxa were included to root the trees.

For the congruence study, the tree-to-tree distances command of PAUP 3.0s was used to calculate d for pairs of SCTs based on the halflings. The equation described above was then used to calculate d_{max}.

RESULTS

Twenty-one published matrices were analyzed (Table 1). Three of the sampled matrices were also analyzed by Hauser and Presch (1991): Crother et al. (1986), Ladiges et al. (1989), and Churchill et al. (1984) (cited as Humphries [1981] by Hauser and Presch). It was difficult to find acceptable matrices for this study because many published studies do not explicitly describe the CSTs for minimally connected characters; some studies do not even mention how the characters were treated, i.e., whether maximally or minimally connected. Hauser and Presch (1991) noted the same problem.

Resolution typically was greater for the minimally connected analyses. The SCTs

TABLE 1. Resolution and congruence (d_{max}) for 21 published data matrices reanalyzed treating characters as maximally (max) or minimally (min) connected.

Data source	No. taxa[a]	No. char- acters[b]	Resolution[c]		d_{max}[d]	
			Max	Min	Max	Min
Hulbert and MacFadden, 1991: table 1	14	39 (24)	7	8	18 (1.9E − 2)	12 (1.2E − 5)
Heyer, 1974: table 2	30	50 (33)	23	22	52 (1.2E − 1)	54 (1.0)
Crother et al., 1986: table 1	5	30 (6)	1	1	4 (1.0)	4 (1.0)
Smith and Koehn, 1971: table 1	17	30 (19)	3	11	24 (1.6E − 2)	26 (1.2E − 1)
Crumly, 1982: table 4	15	26 (11)	2	2	24 (1.0)	24 (1.0)
Ladiges et al., 1989: appendix	16	26 (12)	10	7	24 (1.6E − 1)	20 (1.3E − 3)
Beehler and Swaby, 1991: table 2	7	17 (12)	4	4	4 (5.6E − 2)	2 (9.5E − 3)
Eckenwalder and Barrett, 1986: appendix 1	37	42 (16)	25	15	60 (2.0E − 4)	64 (1.6E − 2)
Taber, 1990: table 1	24	33 (11)	17	21	36 (1.9E − 3)	40 (1.2E − 1)
Hood and Smith, 1982: table 2	11	6 (3)	5	6	16 (1.0)	14 (1.9E − 1)
Jensen and Barbour, 1981: table 1	7	26 (11)	4	4	4 (5.6E − 2)	4 (5.6E − 2)
Trueb and Cannatella, 1986: table 3	7	27 (6)	3	4	4 (5.6E − 2)	2 (9.5E − 3)
Thiele and Ladiges, 1988: table 3	12	29 (19)	0	5	18 (1.0)	18 (1.0)
Nussbaum, 1979: appendix 2	14	43 (10)	9	10	20 (1.7E − 1)	14 (1.0E − 3)
Duellman and Trueb, 1983: table 2	8	8 (3)	2	5	10 (1.0)	10 (1.0)
Davis, 1986: table 1	15	8 (4)	1	3	22 (1.7E − 1)	22 (1.7E − 1)
Montanucci, 1987: table 6	13	36 (12)	7	9	12 (2.0E − 4)	16 (2.0E − 2)
Deharveng and Bedos, 1991: table 1	15	15 (8)	6	8	24 (1.0)	22 (1.7E − 1)
Thewissen, 1992: table 1	8	10 (4)	2	2	8 (2.4E − 1)	10 (1.0)
Churchill et al., 1984: table 4	10	47 (5)	5	7	14 (1.0)	12 (2.0E − 1)
Page et al., 1992: table 8	11	9 (6)	5	6	14 (1.9E − 1)	14 (1.9E − 1)

[a] Includes all outgroup or ancestral taxa.
[b] Numbers in parentheses are number of multistate characters.
[c] Number of interior nodes minus one on the strict consensus tree of the shortest trees.
[d] Maximum possible value of the partition metric between the strict consensus trees from each pair of halflings. Numbers in parentheses represent cumulative probabilities of d_{max} values (based on Hendy et al., 1984: table 4; $aE − b = a \times 10^{-b}$). For $n > 16$, these probabilities were calculated using the asymptotic equation of Hendy et al. (1988).

based on minimally connected analyses were better resolved for 13 matrices, the SCTs based on maximally connected analyses were better resolved for 3 matrices, and the remaining analyses resulted in ties. This pattern is statistically significant, using a two-tailed binomial test ($P = 0.021$). The greater resolution of the minimally connected analyses resulted from the fact that, on average, matrices analyzed under this method resulted in fewer shortest trees than did the same matrices analyzed under the maximally connected method.

The results of the congruence study indicate that minimally connected characters do not necessarily result in greater congruence. The minimally connected analyses resulted in greater congruence for eight matrices, the maximally connected analyses resulted in greater congruence for six matrices, and the remaining analyses resulted in ties. For each d_{max}, a cumulative probability was calculated using table 4 of Hendy et al. (1984). For matrices of $n > 16$,

it was necessary to use the asymptotic equation of Hendy et al. (1988) because table 4 of Hendy et al. (1984) only applies for $n \leq 16$. The probabilities (Table 1) represent the chance that two randomly chosen dichotomous trees will share at least as many clades as they do. The inverse of each probability (P^{-1}) was calculated, and the 21 pairs of probabilities were compared using a Wilcoxon signed-rank test. The result was not significant ($P > 0.10$), indicating no significant tendency of either character method to produce greater congruence.

DISCUSSION

The question of how multistate characters should be treated in phylogenetic analysis is obviously important. The recent trend seems to be one of an increasing preference for maximally connected characters over the more traditional minimally connected characters. This preference seems to be motivated by a conviction that min-

imally connected characters entail a risk of error that should be avoided, that of misconnecting character states. But, as Page et al. (1992) correctly pointed out, useful information is lost when a correct "ordering" is discarded. Hence, "there is a tradeoff between the increased information gained by assuming an order versus the more severe consequences suffered if the assumption is wrong" (Page et al., 1992:639). The best way to resolve the dilemma posed by this trade-off is through an empirical evaluation of the ability of each method to produce resolution and congruence (as an indirect estimator of accuracy).

The results of this study demonstrate that minimally connected character analysis results in greater resolution than does maximally connected character analysis. Minimally connected character analysis does not, however, necessarily increase congruence; congruence was greater for minimally connected analyses in some cases but not in other cases (see Table 1). The cumulative probabilities for the d_{max} values for both character methods were generally low (see Table 1). Only 12 halfling comparisons (out of a total of 42) resulted in complete dissimilarity ($d_{max} = 2n - 6$). If the 42 pairs of SCTs used to generate the d_{max} values had been chosen randomly, the majority would show complete dissimilarity. I tested the hypothesis that each column of d_{max} values could have come from 42 randomly chosen pairs of trees, using Fisher's combined probability test (Sokal and Rohlf, 1981). Both columns of values were highly significant (maximally connected d_{max} values: $P \ll 0.0001$; minimally connected d_{max} values: $P \ll 0.0001$), which means that the SCTs generated from the halflings analyzed under both methods shared more clades than expected by chance. More to the point, neither method can be rejected outright based on congruence; both methods have the potential to produce nonrandom congruence and are valid phylogenetic methods.

Considering the above, I recommend a "mixed-parsimony" approach, whereby a multistate morphological character is minimally connected when one CST is clearly superior to the others (e.g., as with the morphocline small—medium—large) but treated as maximally connected otherwise. When one CST is clearly favored, useful information is gained by constraining the character's evolution according to that CST. Several methods exist for determining CSTs. The most commonly used method—which might be termed the "classical" method—chooses the CST that implies the least amount of change between states, but other methods exist as well, including the ontogenetic criterion (reviewed by Hauser and Presch [1991]).

A Caveat on Choosing CSTs

Although I have supported minimally connecting characters when feasible, I caution against the tendency to linearly connect all characters with four or more states. The majority of multistate characters in the literature (as well as the characters used in the present study) are three-state characters, for which only linear CSTs are possible. However, for characters with four or more states, branching CSTs are also possible. Yet, in conducting the survey of literature for this study, I noticed that characters with more than three states were usually connected in a linear fashion. I can think of no reason why an individual character state could not give rise to two or more descendant states. In fact, if every possible unpolarized CST is considered equiprobable, the probability that a CST of n states will be branching, which is $1 - (n!/2n^{n-2})$, rises very rapidly. For example, when $n = 4$, the probability that a CST will be branching is 0.25, but when $n = 6$, the probability is 0.72. It might be informative to investigate the predictions of a more realistic model, such as one where every state has an equal probability of giving rise to the next descendant state. These considerations are offered as a warning that nonlinear CSTs should also be considered for characters with more than three states.

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