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POLARITY ASSESSMENT IN PHYLOGENETIC SYSTEMATICS: A RESPONSE TO MEACHAM

In the February 1984 issue of *Taxon,* Christopher Meacham argued that too much emphasis has been placed on the need to assess the polarity of characters prior to cladistic analysis. We agree wholeheartedly with his suggestion that more emphasis be placed on the initial division of characters into character states, for, as he showed, most character conflicts are probably created during stages of character analysis other than polarity assessment (i.e., "membership" and "ordering"). However, we disagree with his conclusion that an unrooted network for the ingroup should be constructed first and rooted afterwards.

In the approach recommended by Meacham outgroup information is considered only after the ingroup network is resolved (if it is considered at all), and we will therefore refer to it as the "outgroups-after method." The alternative "outgroups-during method" uses outgroup information throughout the resolution of the ingroup cladogram. Maddison et al. (1984) demonstrated that the outgroups-during method is superior to outgroups-after methods such as Meacham's from the standpoint of global parsimony. Here we reiterate and elaborate on their explanation with special reference to Meacham's paper in order to clarify the importance of considering outgroups throughout the analysis. We also discuss methods for coping with uncertainty about outgroup relationships, parsimony and the analysis of character evolution, and the definition of cladistics.

Polarity Assessment and Parsimony

Meacham supposes that cladists assess character polarities "in the hope that this will remove conflicts from the data" (p. 33). He argues that this will never be true—that establishing polarities can only add character conflicts because "only directed characters can conflict because of direction" (p. 29). Thus, he concludes that a priori polarity assessment is an unnecessary "restriction" (p. 30).

Meacham's argument that establishing polarities adds character conflicts takes the following form. An analysis performed with undirected characters yields an unrooted network for the ingroup. An analysis performed with directed characters is equivalent to performing the analysis with a hypothetical ancestor added to the ingroup. New conflicts may be added because the directed data set effectively contains an additional taxon, and different characters of this taxon may disagree as to which ingroup taxa should be placed closest to it. Thus, directing characters can only increase character conflicts, that is, decrease parsimony.

We agree with this reasoning, but does it mean that we should avoid directing characters initially? Directing characters amounts to considering extra information, namely about the outgroups. Taking this information into account may necessitate accepting a more complex theory of character evolution in the ingroup. But ignoring information just because it forces us to accept a more complex theory is hardly justified. Conflicts may disappear from our view when we ignore the outgroups, but they do not cease to exist. The outgroups are still there, as are any conflicts spanning the outgroups and ingroup.

Since the data about the outgroup must be faced eventually if our theories are to account for the available information, any comparison of the merits of the outgroups-during method and the outgroups-after method should assess how well these techniques minimize conflicts over both the ingroup and outgroups. Meacham doesn't do this. When he considers the outgroups-during method he measures conflicts over the ingroup plus outgroups, but when he considers the outgroups-after method he measures conflicts over the ingroup alone. When the outgroups-after method is judged using the ingroup plus outgroups it is seen to be inferior to the method considering outgroups throughout the analysis.

As a demonstration of this point consider the data set in Table 1, in which an ingroup consisting of terminal taxa A–E and an outgroup O have been scored for 22 characters. In the outgroups-after method favored by Meacham the most parsimonious network for the ingroup alone is constructed

Table 1. Five ingroup taxa and an outgroup scored for 22 characters.

Characters	Ingroup taxa					Outgroup
	A	B	C	D	E	O
1–10	b	b	a	a	a	a
11–20	a	a	b	b	b	a
21	b	b	b	a	a	a
22	a	b	b	b	a	a

(Fig. 1a), and then the outgroup is attached to this network in the most parsimonious position. In this case, the most parsimonious attachment of the outgroup is between AB and CDE, and this yields the cladogram in Fig. 1b. In contrast, in the outgroups-during method the outgroup is used initially to assess polarities, and a hypothetical ancestor (with all *a*'s) is included in the analysis from the start. In this case the cladogram shown in Fig. 1c is obtained. Notice that this cladogram differs in topology from the first one (Fig. 1b), the position of taxon D having shifted.

Within the ingroup alone fewer character state transitions are required by the outgroups-after cladogram (Fig. 1d; 23 steps) than by the outgroups-during cladogram (Fig. 1e; 24 steps). However, over the ingroup plus outgroup fewer transitions are required by the outgroups-during cladogram (24 steps) than the outgroups-after cladogram (25 steps). There are, of course, several other ways that the characters could be arranged on these cladograms, but in no case will the cladogram in Fig. 1d require fewer than 25 steps overall.

Focusing on the ingroup in isolation and constructing an unrooted network without considering outgroups or a hypothetical ancestor appears, at first, to minimize conflict and improve parsimony, but this approach simply ignores conflicts that exist outside of the study group. To ensure a cladogram that is parsimonious globally—over the ingroup plus outgroups—information about the outgroups must be included throughout the analysis (Maddison et al., 1984: 94).

Outgroup Analysis and Uncertainty

Meacham's recommendations seem to stem in part from skepticism about outgroup polarity assessment. He is concerned that outgroup analysis hinges on initial assumptions regarding the broader cladistic relationships of a group, about which there may be considerable uncertainty. Because he wishes to avoid making unjustified ancestral state estimates solely to allow an analysis to proceed, he advocates making polarity decisions a posteriori. Lundberg (1972) apparently had the same concern and his solution was basically the same as Meacham's. Both authors recognized that when outgroup relationships are poorly resolved one should not make a strong a priori commitment to a particular polarity assessment, but, as shown above, both proposed a solution that fails to account adequately for outgroup information. Nevertheless, uncertainty about outgroup relationships is a real problem in many cases and must be dealt with.

If outgroup relationships are well resolved, globally parsimonious results can be obtained by assessing character polarities a priori and including a hypothetical ancestor in the analysis (Maddison et al., 1984). But when outgroup relationships are poorly resolved, and different ancestral state estimates could be yielded by different outgroup arrangements, one should not attempt to arrive at a single polarity assessment. Polarity assessment based upon common-among-the-outgroups-is-primitive or other such criteria will lead one astray in some percentage of cases. There are, however, several approaches that consider outgroups from the beginning and are consistent with global parsimony. One of these is to resolve ingroup and outgroup relationships simultaneously (Maddison et al., 1984: 97). This will yield maximally resolved and globally parsimonious results, but if character distributions among the outgroups are poorly known then the outgroup resolution might be based on unacceptably scanty evidence. In the outgroup substitution approach (Donoghue and Cantino, 1984) a hypothetical ancestor is constructed for each plausible outgroup arrangement and only the strict consensus ingroup cladogram is accepted. This is a conservative approach yielding ingroup cladograms that will not conflict with the globally most parsimonious results but that may not be very highly resolved. Using either of these two methods, one is not committed prematurely to a polarity determination and yet attention is paid to the outgroups throughout.

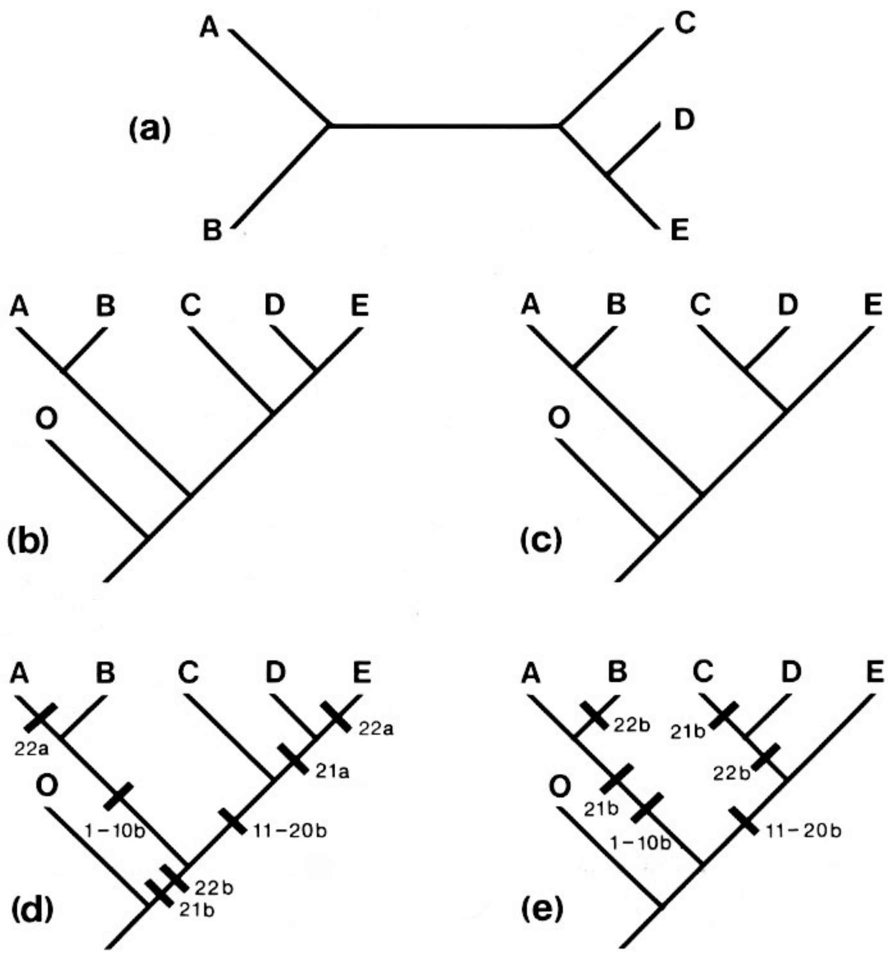

Fig. 1. Branching diagrams derived from the data matrix of Table 1. (a) The most parsimonious unrooted network for the ingroup; (b) Cladogram obtained by the outgroups-after method; (c) Cladogram obtained by the outgroups-during method; (d) The outgroups-after cladogram with characters added—23 steps are required within the ingroup portion and 25 steps over the ingroup plus outgroup; (e) The outgroups-during cladogram with characters added—24 steps are required both within the ingroup and over the ingroup plus outgroup.

Parsimony and Character Evolution

As we have discussed, information about outgroups should be considered throughout the analysis if one's goal is to construct the globally most parsimonious ingroup cladogram. Cladogram construction was Meacham's primary concern and has been ours above. However, character polarity assessments may be sought for reasons other than constructing cladograms, and in such cases Meacham's concerns about a priori polarity assessment are relevant. If one wished to pinpoint exactly where in a cladogram a particular state transition occurs most parsimoniously, as, for example, in a study of the adaptive significance of a trait, then it would be best to wait until the ingroup is fully resolved (Maddison et al., 1984: 88–89). This follows from the fact that the most parsimonious state assignment to any node in a cladogram is affected by character conditions all around that node.

This point can be demonstrated by adding a 23rd character to Table 1, with states *b,b,b,b,a* in the ingroup and state *a* in the outgroup. According to the outgroups the ancestral state of this character for the ingroup is *a*. Based on this information alone one might have proceeded to formulate a hypothesis to explain why state *b* was derived from state *a* within the ingroup. However, this would be premature. After the most parsimonious ingroup cladogram has been constructed (Fig. 1e) it can be seen that there is no longer clear evidence that *a* is ancestral and *b* derived. Other characters have arranged the ingroup in such a way that either *a* or *b* can be placed equally parsimoniously at the base of the ingroup portion of the cladogram. Thus, it might be that *a* changed to *b* sometime before the ingroup came into existence and that *b* reversed to *a* during the evolution of the ingroup. This sequence of character state changes, presumably requiring a different set of explanations, would not have been considered if outgroup analysis alone had been used.

Networks and Cladistics

Meacham expressed several times his opinion that undirected methods "have as much right to be called cladistic" (p. 35) as directed techniques. He argued that because "the logic for inferring the tree from the data is the same for both directed and undirected techniques" (p. 32), the derivation of an undirected network is as much a cladistic analysis as is the construction of a rooted cladogram. In our opinion, this view of cladistics obscures several very important distinctions.

Hennig (1966) made very clear the distinctions between his phylogenetic systematics and both phenetics and evolutionary taxonomy. He insisted that only strictly monophyletic groups be recognized in classifications and demonstrated that only shared derived characters (synapomorphies) provide evidence of monophyly. It is widely acknowledged that what we now call cladistics is more or less directly derived from Hennig's phylogenetic systematics, and cladists and others have consistently distinguished cladistics from alternative approaches on the basis of monophyly and synapomorphy. Given this standard outlook, the construction of an unrooted network might be *part* of a cladistic analysis, but could not be considered a *complete* cladistic analysis because monophyly and synapomorphy cannot be ascertained from an unrooted network. A cladist would not know how to construct a classification from an unrooted network—a cladistic classification can be derived only from a rooted cladogram. Moreover, although the position of a character state change can be determined from a network, the direction of character change cannot be established until the network is rooted. Thus, networks are insufficient, and rooted cladograms are necessary, for the study of evolution.

What can be gained by leaving aside monophyly and synapomorphy as diagnostic characteristics of cladistics and substituting in their place the common operations of computer algorithms designed to implement cladistic logic? The word monophyly never appears in Meacham's paper, but elsewhere (Meacham, 1980) he dismissed the distinction between monophyly and paraphyly and opted instead for "convexity," a concept that effectively combines the two (Duncan, 1980). If convex groups are acceptable in a classification, then an unrooted network is sufficient since convex groups can be obtained from it directly. Considering Meacham's skepticism concerning polarity assessment and his ambivalence about monophyly it is not surprising that his redefinition of cladistics does not require the recognition of synapomorphy or of monophyletic groups. However, in our view, the distinctions between plesiomorphy and apomorphy, and paraphyly and monophyly, are important ones, and we should adopt definitions that keep these ideas clearly separated in our minds. A definition of cladistics that blurs these concepts, and lumps Meacham with Hennig, would only conceal very real and very fundamental differences.

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