



Miscellaneous Cladistics

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Review/Commentary

Miscellaneous Cladistics. *Cladistics: Perspectives on the Reconstruction of Evolutionary History* edited by Thomas Duncan and Tod F. Stuessy. 1984. 312 pp. New York: Columbia University Press. \$35.00.

This volume contains all but four of the papers originally presented at a workshop on cladistics held at the University of California, Berkeley, March 22–28, 1981 (for reviews of the workshop see Coombs et al. 1981, and Funk and Brooks 1981). The 14 papers are arranged in four parts entitled "Philosophical Concerns," "Character Evaluation," "Cladogram Construction," and "Applications," each preceded by a brief introduction by the editors.

The book-jacket indicates that the primary mission of the editors and authors was "to present contrasting viewpoints and differences of opinion currently prevailing in cladistics." In my view they have been only partially successful. It is true that a variety of views are presented, but some issues that have occupied cladists are conspicuously missing. For example, almost no mention is made of the role of fossils in phylogeny reconstruction, of coevolution, or of species concepts. Some other issues are not given the coverage they would probably receive if the book were written today, such as the controversy over "pattern cladism." Some parts of the book are now rather badly out-of-date, especially the appendix by R. Arnold and T. Duncan on computer-assisted analysis, wherein no mention is made, for example, of either PHYSYS (written by J. S. Farris and M. F. Micevich) or PAUP (by D. L. Swofford), the latter now available for some microcomputers. The views that are represented in the book are not always easy to compare. Taken as a group the contributions yield a frustration similar to that produced by species descriptions that fail to give information on the same characters. This is exacerbated by major variation in style and depth of coverage. For all of these reasons I would not recommend the book for courses on phylogenetic systematics; however, for the most part it makes interesting reading, and it does provide insight into some of the problems that cladists have been grappling with.

In the first paper D. Hull contends that in order to understand the history of ideas it is necessary to adopt a genealogical approach, classifying scientists by common ancestry rather than by possession of similar views on particular issues. He also points to the importance of distinguishing scientific groups, delimited by cooperation (not agreement), from conceptual systems, delimited by their unique historical developments. All of this seems right as regards the study of ideas and scientists, but how should scientists classify themselves and their colleagues if they

want, for example, to predict who will be sympathetic when they submit their next grant proposal? It strikes me that ideas held in common at the moment may be more important in this context than the way in which those ideas were reached by the individuals involved. This is not to imply that ideas and scientists should not be classified genealogically—I think they should be. Instead it suggests that the entities being classified may have their own day-to-day classifications based directly on current interaction, which might include, for example, predators and prey.

P. Ashlock restates his preference that, based on traditional usage, the word monophyly should be used for both paraphyletic and monophyletic groups sensu Hennig (1966), and urges that the latter be called holophyletic. Even if his interpretation of history were entirely accurate, why should we be so concerned with tradition in cases like this? The concepts associated with words should change as we learn more and as theories that make use of them change. The word "species" provides a good example. The main issue should be what definitions best serve the development of science. If we now think the distinction between paraphyly and strict monophyly is important, as it certainly seems to be from the standpoint of understanding evolution, then we should choose words that emphasize the difference as much as possible. R. Phillips apparently finds the distinction important, as he argues in his contribution for strictly genealogical classification and rejection of paraphyletic groups.

D. Kaplan's paper on homology will be especially interesting to systematic botanists. He gives examples from his work on *Acacia* to show the necessity of sound developmental morphology for character analysis. I agree with this completely; in fact, ideally, characters should be ontogenies rather than instantaneous morphologies (de Queiroz 1985). Kaplan retains the word homology for "structural correspondence regardless of its phylogenetic implications" (p. 53), and uses homogeny for homology inherited from a common ancestor. Cladists have mostly taken another route, equating homology directly with synapomorphy. B. Baum's comparison of compatibility and parsimony methods as applied to grasses provides a stunning example of the fruitlessness of cladistics without critical character analysis. I marvel at transformation series involving up to 16 ordered character states. How were these obtained? And is it any wonder that the largest cliques in compatibility analysis of such data sets contain so few characters?

The paper by T. Stuessy and J. Crisci on polarity assessment is a great disappointment. They seem to have paid no attention to criticisms by Stevens (1981)

and Wheeler (1981) of their previous paper on the same topic (Crisci and Stuessy 1980). They continue to defend their earlier view that ingroup and outgroup analysis have the same logical basis and that both are acceptable, although, predictably, they note that exactly when these approaches will be appropriate depends on the group under consideration. They still seem to have given very little thought to how polarity criteria should be evaluated. Here are two examples of their "reasonable (eclectic)" approach to the problem.

"... in our own experience, polarities derived from in-group analysis usually correlate with those from out-group comparison, which again suggests that the former *are* giving useful information." (p. 77)

"The out-group criterion is a very useful check on the results of the in-group analysis, because it represents an independent assessment of primitiveness." (p. 79)

The root of many of the problems in this paper may be a misunderstanding of parsimony in general and its role in polarity assessment in particular. Consider the following:

"Almost any cladogram shows some reversals or parallelisms. Parsimony, therefore, can be used as an approximation if no other data exist to the contrary." (p. 81)

The implication is that character conflicts can be resolved without the use of an extra-evidential criterion such as parsimony (see Farris 1983, for a critique of such claims). Judging by analyses I see in the literature, most systematists appreciate the role of parsimony and reject ingroup comparison.

G. Estabrook and C. Meacham both discuss character compatibility methods. Estabrook shows that more than one phylogeny may be consistent with a given cladogram, an observation already widely discussed (e.g., Eldredge 1979). He also considers character state trees and their addition, and the notion of character compatibility and incompatibility. I find nothing new here, but this may be a good overview for those unfamiliar with these ideas. Meacham presents a method for determining if the observed frequency of compatibility of a character is significantly different from the expected number of random compatibilities, and gives examples of the application of this calculation (see also Penny and Hendy 1985). He suggests that this may be useful in identifying and weeding-out characters that contain little phylogenetic information. Although absurd characters can be invented that appear random by his measure, it is unclear that all apparently random characters contain no phylogenetic information. But this reasoning is consistent with the compatibility approach to building cladograms, wherein characters are discard-

ed if they show any conflict. Curiously, neither Estabrook nor Meacham explicitly defends using character compatibility in cladogram construction, leaving the strong impression that they are retreating from compatibility in tree construction and now wish to emphasize its possible uses in character evaluation.

A. Kluge gives a brief account of the relevance of parsimony in phylogenetic inference, distinguishing between evolutionary parsimony, which "assumes that some quality of nature, say the process of evolution, is economical" (p. 25), and methodological parsimony, which "urges acceptance of the proposition that best fits all relevant observations and hypotheses." He argues that methodological parsimony is critical to cladistics, as it is to all science, and contends that compatibility methods, which often discard character data, are not properly cladistic or scientific. Helpfully, a number of recent discussions of parsimony are cited by Kluge in a short addendum to his article. This kind of up-date would have benefited other contributions to the volume.

D. Brooks gives a useful step-by-step account of the mechanics of a quantitative parsimony method, including additive binary coding and optimization. Much of his explanation is based on Farris (1970), but includes a brief and not entirely satisfactory discussion of the now outdated WAGNER-78 computer program. In the last few years there have been several important advances in algorithms for finding parsimonious trees, including the development of "branch and bound" methods guaranteed to find most parsimonious solutions (Hendy and Penny 1982). Although these are not yet efficient with most data sets containing more than about a dozen taxa, they represent a major advance over exhaustive enumeration of all topologies.

I find it interesting that W. Wagner's paper is included in the section on parsimony methods, considering that one of the editors (Duncan 1984) contends that Wagner's groundplan-divergence method is not a strict parsimony procedure (see Churchill et al. 1985, and Farris and Kluge 1985, for objections to this and other claims in Duncan 1984). Wagner himself is little help in clarifying whether he condones parsimony, compatibility, or some combination of the two. I was especially happy to read his short discussion of cladograms in the study of adaptation, wherein he emphasizes the need to determine the direction of character transformation and suggests that cladograms might be used in designing appropriate functional experiments.

J. Felsenstein's very clearly written paper combines an overview of alternative approaches to resolving character conflict in constructing trees with a summary of his use of maximum likelihood in comparing parsimony and compatibility. As Farris (1983) has pointed out, the use of maximum likelihood in this kind of evaluation depends on acceptance of the

process model that underlies it. If the process model is unrealistic, as Felsenstein readily admits that it is for most data, then the conclusions may not be warranted. Nevertheless, I think that Felsenstein's explicitly statistical approach, and the discussions that it has generated, are helping us explore the assumptions of available numerical methods and may point the way toward better approaches. I agree with him that "it may be more useful to have available robust methods that are not sensitive to small departures from one biological model than to have maximum likelihood methods if these are not robust" (p. 187). In this regard it is worth noting Sober's (1985) arguments that the use of parsimony in choosing among competing cladograms requires very few assumptions and that parsimony is more robust than maximum likelihood methods, which effectively choose among phylogenetic trees. I share Felsenstein's enthusiasm about exploring confidence intervals on phylogenies (e.g., Felsenstein 1985). Although such calculations are still in their infancy, the direct relationship to character analysis, especially character independence, is already obvious.

In what seems to be a direct transcript of his oral presentation, W. Fitch compares parsimony to matrix methods and shows that the former give the most information about tree structure. He argues that although matrix methods lose historical information contained in a data set, they may be necessary if we wish to treat data that come in the form of pairwise distances, such as DNA hybridization data. In the end he urges that we "adopt a spirit of discriminating eclecticism" (p. 247). In particular, he agrees with Felsenstein that different methods are appropriate for different kinds of data, and proposes that we find ways of deciding which characters should be analyzed by which methods. Now all we need are some good suggestions as to how this might be done.

In the final paper G. Nelson considers historical biogeography, asking "whether cladograms for different groups of organisms interrelate areas in the same way or ways" (p. 275). He points out that this is difficult to judge due to lack of relevant cladograms to compare, and because it is not entirely clear how congruence should be assessed in real data owing to lack of occurrence of relevant organisms in areas of interest, widespread taxa, and redundant taxa within an area. He suggests that we may find a surprisingly high level of congruence between area cladograms when we look at these in the right way. In any case it is abundantly clear that phenetic approaches to historical biogeography are a dead-end and that comparison of cladograms will allow a much finer resolution of the history of areas and distributions.

Nelson's paper drives home the point that cladograms are critical to the study of evolutionary history. It seems to me that this is why cladistics has

generated so much excitement and why its future looks so bright. The present volume documents a stage in its development—a stage characterized by necessary (if not always very pleasant) debate over appropriate methodology. This debate will and should continue, but I hope we will see increased attention paid to the uses of cladograms in helping to answer basic questions in evolutionary biology.

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