More about Directed Characters: A Reply to Donoghue and Maddison
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————. 1984. The role of hypothesized direction of characters in the estimation of evolutionary history. *Taxon* 33: 26–38.

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MORE ABOUT DIRECTED CHARACTERS:
A REPLY TO DONOGHUE AND MADDISON

In the previous paper, Donoghue and Maddison raise a number of issues concerning the views I expressed in Meacham (1984). I intended that the arguments presented in my earlier paper would reduce the importance that is placed on hypothesizing the ancestral state of characters prior to phylogenetic analysis and hoped that the use of directed characters would no longer be considered a sine qua non of cladistics.

My arguments hinged on the observation that, with respect to two major phylogenetic methods: parsimony and compatible clique analysis, it is the pattern of conflicts among characters that determines the phylogenetic tree chosen by the method. If all of the characters in our analysis are true indicators of evolutionary relationships, then there are no conflicts among characters and both parsimony and clique analysis will choose the same tree, which in this case is the historically true phylogenetic tree. The two methods handle the resolution of character conflicts differently so that when conflicts occur, the trees chosen may differ. In general, as the level of character conflict rises, the trees chosen by parsimony and by clique analysis will tend to be less similar to each other. In a sense, it is the pattern of character conflicts that constitutes our real source of information, not only on the phylogeny of the group, but also on the validity of the characters themselves for inferring the phylogeny of the group. If we were to discover a new taxon in our study group that had exactly the same combination of character states as some other taxon we had already observed, the new taxon would not change the pattern of character conflicts and so would have no influence on the result of a parsimony analysis or a clique analysis. In a similar fashion, even if a new taxon does not possess the same combination of character states as some taxon already included in our study group, if it introduces no new conflicts, then it will not change the evolutionary history inferred for the original study group not including the new taxon.

I think that the pattern of conflicts we discover is very valuable. This pattern is obtained by direct observation and is as free as we can make it of the effects of our preconceived notions of how the world is. I do not think that we can observe nature entirely without bias, but unbiased observation is a goal to be strived for. Donoghue and Maddison argue that "[d]irecting characters to considering more information . . . ." As I pointed out, directing characters is equivalent to adding an hypothesized ancestor to the study collection. If we are as sure of the character states of the hypothesized ancestor as we are of the taxa in the study collection whose states we determined by direct observation, then I have no objection. I do not believe that this level of certainty can be attained by outgroup analysis. I do not ". . . [ignore] information just because it forces us to accept a more complex theory . . ." (Donoghue and Maddison, this issue). I ignore it because it is more likely to be incorrect than the information obtained by immediate experience.

Donoghue and Maddison point out the logical connection between my view that the need for a priori directing of characters should be deemphasized and my view that taxa in classifications need not be strictly monophyletic. However, it is not just because I accept paraphyletic taxa that I find undirected phylogenies acceptable as a final result. Instead, I find that the problems of determining the directionality of character state change are likely to make undirected phylogenies more reliable and thus a better basis for formulating classifications. It is the problem with directionality (among other considerations) that leads me to accept paraphyletic taxa, not that because I accept paraphyletic taxa, I have no need to use directed characters. (Thomas Duncan and I have a forthcoming paper that discusses at length the problems with strictly monophyletic classifications and the advantages of classifications that allow paraphyletic taxa [Meacham and Duncan, 1987].)

The use of outgroups to determine directionality is, in part, based on the assumption that either both the ingroup and the outgroup are monophyletic or that the ingroup is monophyletic with respect to a paraphyletic outgroup. In the terms of Estabrook (1978), the assumption is that the ingroup and

outgroup are convex on the actual phylogeny. This is an assumption that is not explictly tested within the "outgroups during" method described by Donoghue and Maddison. Instead, it is a restriction on the outcome of the analysis. It would seem more convincing to me if the possibility that the outgroup and ingroup were convex were a *result* of the analysis rather than a prior restriction on the analysis. The restriction can easily be removed by performing an undirected analysis on the outgroup plus ingroup. If the undirected parsimony analysis produces a tree on which the ingroup and outgroup are both convex, then the contention that both groups might be monophyletic or that the ingroup is monophyletic with respect to a paraphyletic outgroup is supported by global parsimony of ingroup plus outgroup. If the ingroup and outgroup are both convex, rooting the tree at the internode between the two groups will produce a tree on which both the ingroup and the outgroup are monophyletic. Rooting the tree within the outgroup will produce a tree on which the ingroup is monophyletic and the outgroup is paraphyletic. These rootings, in turn, will suggest the ancestral states of the characters. Again, this determination of the ancestral states depends on the assumption on the monophyly of the ingroup. (After all, it might be that the ingroup is paraphyletic with respect to a monophyletic "outgroup.") But in this case, the contention that the assumption is true is at least supported by the fact that the groups are both convex under the criterion of undirected parsimony rather than resulting from a restriction that is forced on the analysis from the beginning. On the other hand, if the ingroup and outgroup are not both convex, then at least one of the groups is polyphyletic under undirected global parsimony and the assumption that the two groups are sister monophyletic groups or that the outgroup is paraphyletic is called into question. I feel that this method of performing an undirected analysis on the ingroup plus outgroup is the best implementation of an "outgroups during" method of analysis.

I am not swayed by the argument that, because an undirected analysis performed on just the ingroup may result in a shorter tree than would be possible if the outgroup were included, global parsimony thus demonstrates the inferiority of undirected ingroup analysis. No matter how large the group of taxa chosen for parsimony analysis, the analysis can always be criticized on the grounds that if the next most closely related sistergroup were added, global parsimony might indicate a longer tree for the ingroup. The only truly global parsimony analysis that would be immune to this criticism would include all organisms (at least the eukaryotes). Any other level of analysis must be called "limited" and any limited analysis can possibly produce different results if the analysis were expanded. The "global" parsimony of outgroup plus ingroup is no more immune to criticism on this point than undirected ingroup parsimony analysis. (I point out in passing that for truly global parsimony, there is no outgroup!)

To further clarify my views, I stress that I have no objection at all to including an outgroup in a cladistic analysis. Each taxon in a cladistic analysis is essentially represented by a list of the taxon's character states. We know that the character states observed in a particular taxon co-occur because we have observed that they do so. Unobserved combinations of co-occurring character states may be inferred by cladistic analysis. That is one of the purposes of doing the analysis in the first place. My main point is that I object to including in a cladistic analysis an hypothesized taxon represented by a combination of character states that have not actually been observed to co-occur. Such unobserved combinations of character states should be the result of analysis, not a prior restriction on analysis. My second point is that if the characters are directed by designating as primitive those character states that are actually observed to co-occur in combination in some outgroup taxon, then the results obtained by directed analysis, both parsimony and compatibilty, are exactly equivalent to the results obtained by the corresponding undirected analysis on ingroup plus outgroup. My third point is that these considerations indicate that an undirected analysis can have an entirely appropriate role in developing a directed cladistic estimate and a monophyletic classification. And finally, because undirected methods have the very close logical correspondence to directed methods that I discussed in Meacham (1984), these methods cannot reasonably be thought of as "uncladistic."

This brings me to the last issue raised by Donoghue and Maddison: my use of the term *cladistics*. Donoghue and Maddison limit this term to a particular methodology. I hold an opposing view that the term should apply to a field of study: the scientific endeavor of reconstructing the evolutionary history of biological organisms. Similar terms like statistics, genetics, and physics indicate fields of science. It is clear that the "cladistics" of Donoghue and Maddison is markedly different from the "cladistics" espoused by Hennig. The methods have changed somewhat, but the field of interest is the same. As the field continues to develop and techniques continue to evolve, it is likely that the number of differences will increase. We already have terms for the elements that make up "cladistic" methodology: a "cladistic" tree is a cladogram, a "cladistic" classification is a monophyletic classi-

fication, and the "cladistic" criterion is parsimony. I acknowledge that, in a sense, the methodology of Hennig is the "type specimen" of cladistics, but I recommend that use of the term be broadened so that it is no longer restricted to a single methodology. As the field develops, I believe it will become more and more difficult to maintain a methodological definition of cladistics. Although Donoghue and Maddison object to a definition of cladistics that lumps me with Hennig, and presumably me with them, we all share an interest in reconstructing evolutionary history and in developing a rational foundation for classifying organisms. I feel that cladistics should be defined on the basis of these goals.

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REPLY TO W. H. WAGNER ON THE SPECIES QUESTION

Summary
   In a recent paper on taxonomic and biosystematic concepts, Wagner (1984) gives an inaccurate account of my treatment of the species in *Plant Speciation* (Grant, 1971, 1981).

Reply
   According to Wagner (1984, p. 645), "Verne Grant (1971, 1981) took over the word species from traditional taxonomy and proceeded to define it in six different ways . . . ."
   In the first place, I did not take the word species over from traditional taxonomy, and taxonomy did not own it. The species is a unit in ecology, genetics, population biology, and evolution theory, as well as taxonomy, and has been since the 19th century. Attempts to formulate a concept of species in plants trace back to the early naturalists of the 18th and 17th centuries, who were interested not only in classification but also in the reproductive and ecological aspects of species, as noted in *Plant Speciation*.
   With regard to the second part of the above quotation, my actual statement in the book (1981, ch. 7) was that the term species is used in various senses to refer to different units. In order to "reduce confusion in communication," therefore, it is helpful to attach qualifying adjectives to the term to designate each particular usage. I went on to recognize five (not six) types of species: taxonomic species, biosystematic species, biological species, successional species, and microspecies. Each type of species was characterized.
   Wagner claims (p. 646) that Grant favors biological species, but "clearly does *not* favor the taxonomic species . . . ." My stated position was that each type of species "is valid in its own sphere" (1981, p. 78). And, "The taxonomic species is the basic unit of formal classification" (p. 79). However the taxonmic species has its weaknesses as well as strengths, and the former should be recognized.
   Taxonomic species and biological species are members of different hierarchies, the first a hierarchy of taxa, the second a hierarchy of population systems. Taxa and population systems are not the same thing. I lined up the two hierarchies in tabular form (1981, pp. 81–82). In some groups the taxonomic and population hierarchies coincide; in such cases a single system of units is sufficient. But in many other groups the actual populational system can not be expressed adequately within the taxonomic set of categories, which is essentially pre-evolutionary, and here it is useful to have the hierarchy of population systems with its greater information content.
   In the light of the above one wonders why Wagner thought it necessary to state that "It is not likely