that cladograms match: A method of biogeographical inference. Syst. Zool. 36:175-195.

- SMITH, A. G., A. M. HURLEY, AND J. C. BRIDEN. 1981. Phanerozoic paleocontinental world maps. Cambridge Univ. Press, Cambridge, England.
- STRANEY, D. O. 1982. Review of Advances in Cladistics: Proceedings of the First Meeting of the Willi Hennig Society, edited by V. A. Funk and D. R. Brooks. Syst. Zool. 31:337–341.
- SWOFFORD, D. L. 1993. PAUP: Phylogenetic analysis using parsimony, version 3.1. Illinois Natural History Survey, Champaign.
- THORSON, T. B., D. R. BROOKS, AND M. A. MAYES. 1983. The evolution of freshwater adaptation in stingrays. Natl. Geogr. Soc. Res. Rep. 15:663–694.

- THORSON, T. B., R. M. WOTTON, AND T. A. GEORGI. 1978. Rectal gland of freshwater stingrays, *Potamotrygon* spp. (Chondrichthyes: Potamotrygonidae). Biol. Bull. 154:508–516.
- WHITE, B. N. 1986. The isthmian link, antitropicality and American biogeography: Distributional history of the Atherinopsinae (Pisces: Atherinidae). Syst. Zool. 35:176–194.
- WILEY, E. O. 1988. Parsimony analysis and vicariance biogeography. Syst. Zool. 37:271–290.

Received 3 August 1995; accepted 2 September 1996 Associate Editor: David Cannatella

Syst. Biol. 46(1):230-231, 1997

Limitations on the Use of Compatibility Methods for Polarizing and Ordering Characters

MARK WILKINSON

School of Biological Sciences, University of Bristol, Bristol BS8 1UG, England; E-mail: mark.wilkinson@bris.ac.uk

Sharkey (1994) recently introduced a suite of new compatibility measures and a new method of tree construction, the reduction routine, that uses his character discriminate compatibility measure as a basis for differential weighting of characters. These new measures and the reduction routine require that characters be polarized and that they be binary or, if multistate, that they be ordered so that they can be represented by an analytically equivalent set of binary factors. Because much systematic data comprises unordered multistate characters (e.g., DNA or protein sequences) and polarity is often uncertain, the applicability of these new methods would seem to be severely limited. However, Sharkey (1994) also proposed that his discriminate character compatibility measures be used to polarize characters of uncertain polarity and to order unordered multistate characters.

Sharkey's techniques for ordering and polarizing characters are conceptually the same. In each case, all possible data sets comprising alternative polarizations or orderings are compared, and his data set discriminate compatibility measure or average data set discriminate compatibility measure are determined for each. The polarity and/or ordering implied by the data sets that achieve the highest values for these indices are adopted, and the ordered, polarized data are input into the reduction routine. Sharkey (1994) provided examples of this approach, but his examples are very simple. In assessing polarity, he considered the case of a data set of three binary characters, one of which is nonpolar. Alternative polarities produce just two data sets to be evaluated using the discriminate compatibility measure. For ordering multistate characters, he considered a data set of four binary characters and a single three-state character, requiring nine alternative data sets to be evaluated.

Unfortunately, computational problems will arise as increased demands are made of these methods. When used to polarize binary characters, the number of alternative data sets to be compared is 2^n , where *n* is the number of such characters. Thus,

for example, with 10 characters there will be a little over a 1,000 alternative data sets, with 20 there will be over one million, with 30 over one billion, and with 100, a moderate number by modern standards, the number is in excess of 10³⁰. Even with powerful computers, the time required for such comparisons will render the approach impractical in many cases.

Similarly, increases in the number of states of unordered multistate characters produce exponential increases in the number of possible character state trees, just as increases in the number of taxa increase the number of possible trees. Thus, for four-state characters (e.g., nucleotide sequence data) there are 64 (polar) character state trees, and for five-state characters (e.g., nucleotide data with indels coded as an additional state) there are 565 (polar) character state trees. A modest data set including 100 unordered and unpolarized five-state characters would require that some 10275 alternative polarized and ordered data sets be compared to select one for input into the reduction routine. An additional problem not discussed by Sharkey (1994) concerns the possibility that his approach might yield multiple equally optimal solutions rather than a single optimal solution.

Wilkinson (1992) suggested that compatibility methods might be applied to the problem of ordering multistate characters but did not discuss the practicalities. Sharkey's (1994) methods provide a step towards exploiting compatibility methods for ordering and polarizing characters and may be applicable to small data sets, but the practical problems will make their application to many data sets, including most molecular data, infeasible. As in parsimony analysis, heuristic methods might be developed to extend these approaches to cases where exact methods cannot be applied, but what form such heuristic methods might take is unclear.

ACKNOWLEDGMENT

I am grateful to Michael Sharkey for providing a preprint of his paper and for his comments on the manuscript.

References

- SHARKEY, M. J. 1994. Discriminate compatibility measures and the reduction routine. Syst. Biol. 43:526– 542.
- WILKINSON, M. 1992. Ordered versus unordered characters. Cladistics 8:375–385.

Received 16 February 1996; accepted 2 June 1996 Associate Editor: David Cannatella