

## COMMENT AND REPLY

### Character distributions are phylogenetic evidence

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In his criticism of phylogenetic analyses based on character distributions in taxa, Vermeij (1999) cites a number of commonly recognized impediments to such analyses (noise, instability of nodes, homoplasy, ambiguity of polarity, etc.) as if they were the basis for such repudiation in the general case. Of course, the impact of these factors will vary from case to case and the notion that phylogenetic analysis can be difficult if data are spotty, complex, or ambiguous does not obviate the method. In addition, Vermeij notes, as have others (Hecht 1976; Kirsch and Archer 1982), that application of the parsimony principle to the analysis of character-taxon matrices may be misguided because evolution is not necessarily parsimonious. But parsimony is a means of selecting among alternative explanations by using the most efficient summary of the data, an application that does not presuppose any a priori knowledge of the complexity of evolution. (Farris 1983; Sober 1983).

Rather than dwelling on these more familiar criticisms, I here address what Vermeij considers an especially “serious matter” (p. 431) for character-taxon analysis. He argues that the basic assumption that eukaryotic evolution involves branching of clades that become genetically independent of one another is violated by phylogenetic analysis of a character-taxon matrix. This assertion is based on the observation that, in such an analysis, the pattern of branching within any given clade is influenced by the distribution of characters in all the taxa of the matrix, whether those taxa belong to the given clade or not. Vermeij notes that this “lack of independence” (p. 431) among taxa is highly demonstrable when taxa are added to or removed from the matrix, and

I agree that topologies often do change when such alterations and additions are made. The problem with Vermeij’s argument is that he seems to regard the recognition of genetically independent clades at some level as sacrosanct and immune to changes in topology based on new information on characters and taxa. Of course the true phylogeny cannot be ascertained, and the hypotheses for various clades are potentially fallible, no matter how compelling they seem with the data at hand. New character-taxon data could affect any estimate of phylogeny. Indeed, the phylogenetic analysis yields patterns that comprise both independent and shared events. For example, character-taxon data might be consistent with the hypothesis that the acquisition of homeothermy in birds is an event genetically independent from the genetically nonindependent (shared-derived) acquisition of homeothermy in clades grouped together as mammals (Gauthier et al. 1988). As unlikely as it may seem given the current state of the evidence, a revised matrix with new information on characters and taxa could be more consistent with the genetic interdependence of homeothermy as one of the characters uniting birds and mammals (Gardiner 1993).

A second difficulty with Vermeij’s argument concerns his proposal that the alleged violation of evolutionary rules by phylogenetic analysis can be mitigated by drawing on developmental, stratigraphic, and ecological evidence as a way of constraining the character-taxon analysis. The problem here is whether such evidence is independent from information on character distributions in taxa. For example, Vermeij offers the case of progenesis—namely early onset of reproduction in a de-