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Total Evidence Versus Relevant Evidence: A Response to O'Leary et al. (2003)

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We commend O'Leary et al. (2003) on their reanalysis of their own data. We could take issue with their list of criticisms of our reanalysis point by point. For example, we disagree with their assertion that a heuristic search yielding 93,578 most-parsimonious trees (MPTs) is necessarily more "rigorous" than a heuristic search that yields 46,209 MPTs. There simply is no way of knowing if their set of 93,578 heuristically derived MPTs represents a better sampling of the landscape of MPTs without conducting an exhaustive search of the tree space, which could potentially yield hundreds of millions of MPTs. Similarly, whether or not one should use a strict or majority rule consensus as a summary of a set of MPTs depends critically on how representative the subsample of heuristically derived MPTs is of the hierarchical patterns contained in the complete set of MPTs. If the subset were truly representative of the complete set, a majority rule consensus would give a better estimate of the overall hierarchical tendency than would a strict consensus. When the subset of heuristically derived MPTs is not representative of the complete set, both strict and majority rule consensus are poor summaries of hierarchical signal. However, what is at stake is much more fundamental than the list of technical issues raised by O'Leary et al. For us, the argument is about how best to estimate phylogeny. The conflicting views expressed by Naylor and Adams (2001) and O'Leary et al. (2003) are a reexpression of the debate between the total evidence versus the what we term herein "relevant evidence" schools of thought.

Both schools are faced with character variation across taxa. One school proposes that any measurable trait has the potential to be phylogenetically informative, whereas the other asserts that some traits are collectively better indicators of phylogeny than others. The first school (total evidence) is skeptical of invoking any reliance on process to differentially weight characters and asserts that the best way to estimate phylogeny is to "let the data speak for themselves." There is an implicit assumption

that the distribution of measurable traits can be relied upon to tell us the truth about phylogeny; that any historical signal present in the data will increase with the number of characters scored, and that this signal will override signals in the data present from other forces. In other words, this approach assumes that character covariance generated from forces other than history will cancel themselves out, allowing the historical signal to be identified. The second school is skeptical of this assumption. Because of this, it asserts that careful choice of characters is of primary importance. In choosing characters, advocates of the second school consider assumptions about developmental processes, morphological integration, and functional morphology and use these factors as a guide in choosing characters that are more likely to contain historical signal (or more commonly to eliminate suites of characters predisposed to contain covarying signals due to forces other than evolutionary history).

In addressing the question "what is a character?", proponents of both schools would agree that a morphological character constitutes a heritable feature that can be reliably identified across taxa. They disagree on the importance ascribed to the idea that *a character should represent a tightly integrated module whose presence or absence is functionally and developmentally dissociated from the presence or absence of other such characters* (the independent and identically distributed assumption). The total evidence school is less concerned about character independence but rightfully wary of the lure of selecting characters that favor one hypothesis over another. The relevant evidence school is rightfully wary of character covariances due to forces other than history but perhaps less concerned about the lure of favoring certain hypotheses over others.

Resolution of these issues will best be addressed through empirical developmental biology and careful functional anatomy. Two key questions remain: (1) Are

the traits that are used as phylogenetic markers truly discrete, tightly integrated, and functionally autonomous modules? (2) At what point is the error associated with relaxing the severity of the criterion for a character significant enough to cause systematic error in phylogenetic reconstruction? Answers to these questions will likely vary from study to study and across systems. The debate is not new and is not one that will likely be settled with a few exchanges in the pages of *Systematic Biology*. Nevertheless, we think it is one that has enduring importance.

We are grateful for the opportunity provided by O'Leary et al. (2003) to voice our perspective. We do not expect the readership to come to a final resolution favoring one view over another. However, for those interested, we simply recommend a rereading of O'Leary and Geisler's (1999) original paper, Naylor and Adams's

(2001) reanalysis, and O'Leary et al.'s (2003) rejoinder herein. We leave it to the readership to come to their own conclusions.

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Matrix Representations with Parsimony or with Distances: Two Sides of the Same Coin?

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Matrix representation with parsimony (MRP) is a method that takes as input a collection of source trees, recodes them as binary matrices, and returns a tree that is closest to the source trees using a parsimony criterion (Baum, 1992; Ragan, 1992). The average consensus method, on the other hand, takes as input a collection of weighted trees (i.e., with branch lengths) and uses a matrix representation with distances (MRD) analysis to seek the weighted tree that is closest to the source trees using a least-squares criterion (Lapointe and Cucumel, 1997). MRP has been mostly used as an alternative to data combination for assembling supertrees from source trees bearing nonidentical but overlapping sets of leaves (for reviews, see Sanderson et al., 1998; Bininda-Emonds et al., 2002). The average procedure has also been employed to produce supertrees while taking into account branch lengths (Lapointe and Kirsch, 2001). However, both of these approaches can be used to combine source trees with identical leaf sets, in the so-called consensus setting (sensu Bininda-Emonds, 2003). In that particular context, MRP and MRD represent two sides of the same coin, and these methods are closely related consensus techniques. Here, we briefly describe the coding and optimization steps of both approaches to identify their resemblances and differences, and we have used an example to illustrate the equivalence among those seemingly different methods, in the consensus setting. Finally, we

note that the close relationship between MRP and MRD may not hold in the supertree context.

CODING TREES FOR MRP

Given a rooted tree t representing the relationships among a set of leaves (taxa) $S = \{1, \dots, n\}$, there exist a variety of possible binary matrix representations m (e.g., Purvis, 1995; Ronquist, 1996; Wilkinson et al., 2001) corresponding to t . Here, we focus on the representation originally introduced by Ragan (1992). We define a binary matrix m , with n rows representing the leaf set S of t and p columns (or matrix elements, sensu Baum and Ragan, 1993) representing the internal nodes of t . For each such element of m , all terminal taxa (leaves) descending from the corresponding node are scored 1, and all others are scored 0. To polarize the elements, an additional line is added to the matrix to represent an outgroup (or root) with all-zero values. A parsimony analysis of this binary matrix representation will recover the corresponding tree it is encoding (Baum, 1992; Ragan, 1992) when zero-length branches, if there are any, are collapsed. As a special case, a fixed number n of additional columns could be added to the matrix to represent the terminal nodes of t , each one scored 1 for the corresponding taxon and 0 otherwise. These elements are noninformative in a cladistic sense (i.e., they represent