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Measuring Topological Congruence by Extending Character Techniques

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A measure of topological congruence which is an extension of the Mickevich–Farris character incongruence metric (*i.e.*, ILD; Mickevich and Farris, 1981) is proposed. Group inclusion characters (1 = member of a clade; 0 = not a member) are constructed for each topology to be considered. The sets of characters derived from the topologies are then compared for character incongruence due to data set combination. Each homoplasy signifies a disagreement among topological statements. The value is normalized for potential maximum incongruence to adjust values for unresolved topologies. This measure is compared to other topological and character congruence techniques and explored in test data.

INTRODUCTION

Many phylogenetic studies employ measures of topological congruence. Most frequently this is done to gauge the consistency of systematic results in the face of multiple data sets or multiple analysis conditions. The most frequently used measure of topological congruence is the resolution level of a consensus cladogram created from the input topologies (Mickevich, 1978). This consensus cladogram is usually a strict or semistrict or combinable component consensus, using the nomenclature of Bremer (1990), depending on the treatment of unresolved groups. The meaning of these consensus indices (*e.g.*, Consensus Information of Mickevich, 1978; Consensus Fork Index of Nelson, 1979; Colles, 1980, 1981) is clear. Either groups are present in all input cladograms (strict) or are uncontravened (semistrict)—that is, unresolved groups do not disagree with their resolutions. This number of consensus clades is then divided by the maximum possible number of consistent clades or some other related number.

The advantage of this consensus-based measure of congruence is that their meaning is clear. Some fraction of clades are present in (or consistent with) all the compared topologies. The drawback of this type of measure is that small changes in topology can destroy all consensus structure (Fig. 1; Farris's Octodent; pers. anec). Other measures (*e.g.*, Common Pruned Trees of Gordon, 1980; Finden and Gordon, 1985) have been developed to deal with this particular problem but have other shortcomings (such as nonuniquness, Page,

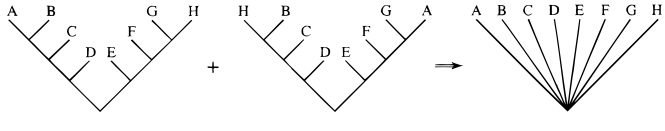

FIG. 1. Farris' Octodents and consensus cladogram.

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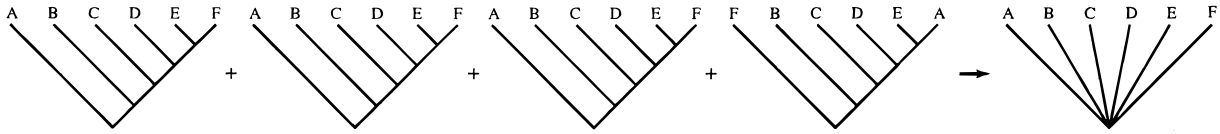

FIG. 2. Consensus of three identical and a single mildly different cladogram.

1993). Furthermore, when multiple cladograms are compared, unless the topologies are nearly identical, little resolution will remain. Even a single discordant taxon in one topology combined with a large number of ***identical*** topologies can cause complete collapse of the consensus (Fig. 2).

THE METHOD

Here, I propose a measure of topological congruence based on character congruence measures. This measure is, in essence, an extensions of the distortion coefficent of Farris (1973) and the character incongruence metric of Mickevich and Farris (1981). The measure, topological Mickevich–Farris or TILD, is calculated through the use of group inclusion characters (Farris, 1973).

Group inclusion characters are derived from topologies. Each resolved clade in the cladogram generates a character with the derived state (1) assigned to the members of the group, and the primitive state (0) assigned to the rest (Fig. 3). The maximum number of characters for a toplogy of n taxa would be the number of nontrivial clades in a completely bifurcating tree $(n - 2)$.

IILD is calculated using the group inclusion characters as if they were standard characters and determining the Mickevich–Farris character incongruence measure (Mickevich and Farris, 1981) for the clade-based characters.

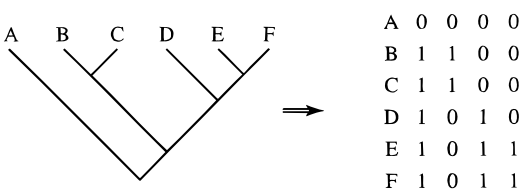

FIG. 3. Derivation of group inclusion characters.

$$\text{TILD} = (L_{\text{combined data}} - \Sigma\, L_{\text{individual data}})/L_{\text{combined data}},$$

where $L_{\text{combined data}}$ is the minimum length cladogram derived from the combination of the group inclusions characters from all the input topologies and $L_{\text{individual data}}$ is that length for the individual sets of clade characters. Each extra step or homoplasy required when the topological data sets are combined signifies disagreement among the input cladograms. This TMF can be modified (IILD_N)for the maximum incongruence possible among the data to correct for the effect of unresolved input topologies.

$$\text{IILD}_N = (L_{\text{combined data}} - \Sigma\, L_{\text{individual data}})/ (\text{Max}L_{\text{combined data}} - \Sigma\, L_{\text{individual data}}),$$

where $\text{Max}L_{\text{combined data}}$ signifies the maximum length of the combined clade characters (*i.e.*, on a bush). In other words, the index measures the ratio of how much topological "homoplasy" there is versus how much there could be in the worst case. The octodent example (Fig. 1) of Farris yields a TILD value of 0.4 and a TILD_N value of 0.44, whereas the CFI (Consensus Fork Index, Colles, 1980) would be 0.0 so its incongruence value would be at maximum (1.0).

DEMONSTRATION

The arthropod data of Wheeler *et al.* (1993) as augmented in Wheeler (in press) were used to demonstrate this measure. These data consist of morphological, small ribosomal subunit (18S rDNA), large ribosomal subunit (28S rDNA), and Ubiquitin data. These data generate individual and combined phylogenetic hypotheses. Additionally, these data sets differ in the number of taxa coded. The morphological data were scored for 25 extant taxa and a single extinct lineage

(Table 1). The 18S rDNA and Ubiquitin data sets contain data for the 25 extant taxa and the Ubiquitin 15 of these. Three methods of parsimony analysis were performed. The first of these were the multiple-sequence-alignment approach, where sequences are first aligned and then subjected to systematic analysis. Here, the sequences were aligned with a gap cost of 2 and transitions and transversions equal in their cost of 1 (MALIGN, Wheeler and Gladstein, 1992, 1994). Phylogenetic reconstruction was performed using PHAST (Goloboff, 1996) using gaps as character states and weighted as in alignment. The second was the optimization-alignment method of Wheeler (1996). In this method, the multiple alignment is avoided and the cladogram lengths are determined directly through generalized optimization. The third method was the fixed-states optimization regime (Wheeler, submitted for publication). In this procedure, entire strings of nucleotide bases are treated as complex multistate characters. The later two analyses were performed using the program POY (Gladstein and Wheeler, 1997). Group inclusion character data sets were constructed from topologies using the utility program jack2hen (freely available via anonymous ftp *ftp.amnh.org* / pub / molecular). The individual results are shown in Fig. 4 and the TILD, $TILD_N$, and comparative character incongruence values in Table 2. When compared with the consensus fork indices (which are zero in each case), the TILD values are higher and jibe more with our desire for finer scale discrimination than consensus-based measures. If we were to use the TILD values

TABLE 1
Taxon List

Mollusca		
Cephalopoda	*Loligo pealei*	
Polyplacophora	*Lepidochiton cavernae*	
Annelida		
Polycheata	*Glycera* sp.	
Oligocheata	*Lumbricus terrestris*	
Hirudinea	*Haemopis marmorata*	
Onychophora		
Peripatoidae	*Peripatus trinitatis*	
Peripatopsidae	*Peripatoides novozealandia*	
Trilobita	Groundplan of Ramskold and Edgecombe (1991) (morphological analysis only)	
Chelicerata		
Pycnogonida	*Anoplodactylus portus*	*
Xiphosura	*Limulus polyphemus*	*
Scorpiones	*Centruroides hentzii*	*
Uropygi	*Mastogoproctus giganteus*	*
Araneae	*Nephila clavipes*	*
Araneae	*Peucetia viridans*	*
Crustacea		
Cirrepedia	*Balanus* sp.	*
Malacostraca	*Callinectes* sp.	*
Myriapoda		
Chilopoda	*Scutigera coleoptrata*	*
Diplopoda	*Spirobolus* sp.	*
Hexapoda		
Zygentoma	*Thermobius* sp.	
Ephemerida	*Heptagenia* sp.	
Odonata	*Libellula pulchella*	*
Odonata	*Dorocordulia lepida*	
Dictyoptera	*Mantis religiosa*	*
Auchenorrhyncha	*Tibicen* sp.	*
Lepidoptera	*Papilio* sp.	*
Diptera	*Drosophila melanogaster*	*

Note. *Denotes 28S rDNA sequence available for this taxon.

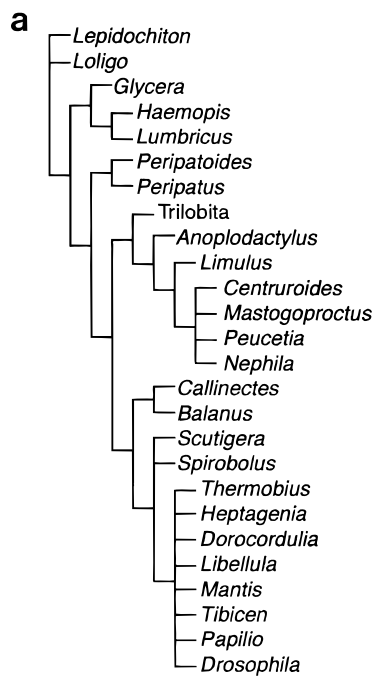

FIG. 4. Arthropod cladograms. (5a)-Morphology. (5b)-Cladograms of individual data partitions when subjected to different analytical techniques. (A) 18S rDNA and multiple sequence alignment. (B) 18S rDNA and optimization alignment. (C) 18S rDNA and fixed-state optimization. (D) 28S rDNA and multiple sequence alignment. (E) 28S rDNA and optimization alignment. (F) 28S rDNA and fixed-state optimization. (G) Ubiquitin and multiple sequence alignment. (H) Ubiquitin and optimization alignment. (I) Ubiquitin and fixed-state optimization.

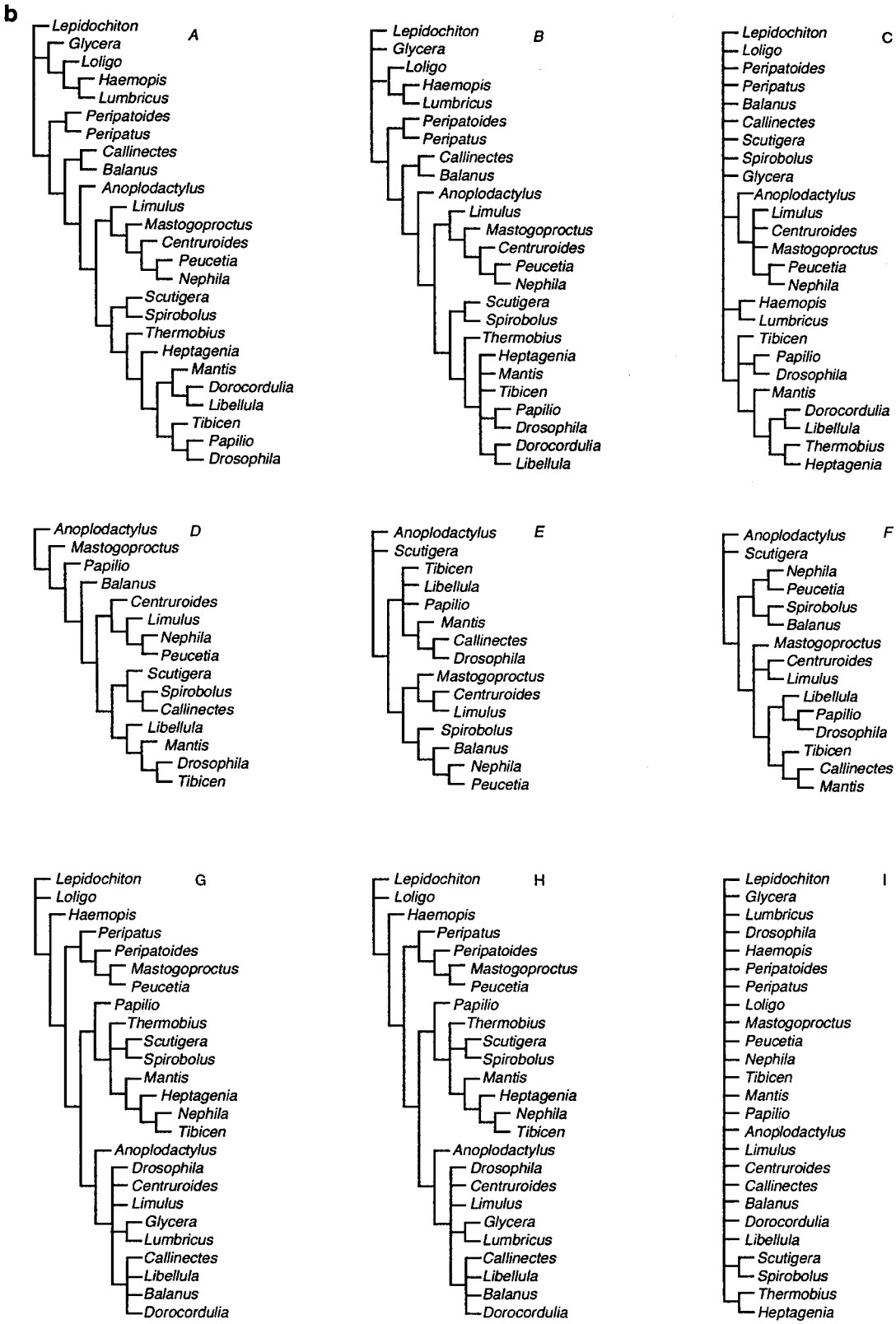

FIG. 4.—*Continued*

TABLE 2
Comparisons of Topological Congruence for Arthropod Data

Method	Combined length	Morphology	18S	28S	Ubiquitin	Maximum length	TMF	TMF_N	1-CF	CMF
Multiple alignment	85	14	19	12	8	227	0.38	0.18	1.0	0.0292
Optimization alignment	75	14	19	10	8	224	0.32	0.14	1.0	0.00698
Fixed-state	48	14	10	12	1	151	0.23	0.096	1.0	0.00352

as an optimality criterion, the fixed-states method would be the most favored.

CONCLUSION

Like all metrics, this topological congruence measure is to some extent arbitrary. It measures group level disagreements among cladograms as homoplasy-like events. The TILD measure is applicable in situations with unequal numbers of taxa and does not collapse to trivial complete incongruence in the face of seemingly small single taxon shifts. These aspects are superior to those measures based only on the resolution of consensus cladograms. Although there is no real epistemological reason to favor this metric over any other (such as the CFI or minimally pruned trees), the utility, simplicity, and correspondence with character incongruence measures commend its use.

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