

FORUM

Cladistics 1(2):186-189

CONSENSUS CLADOGRAMS AND GENERAL CLASSIFICATIONS

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Phylogenetic synthesis refers to the construction of general or consensus cladograms from fundamental cladograms, each based on logically different character sets (sensu Mücke, 1978). These consensus cladograms form the basis for generating general classifications of particular groups (Nelson, 1979; Nelson and Platnick, 1981). Such classifications constitute our best estimates of relationship, given the available knowledge.

A variety of techniques for constructing consensus cladograms from fundamental cladograms (sensu Nelson, 1979; Nelson and Platnick, 1981) is available in the literature (Adams, 1972; Nelson, 1979; Margush and McMorris, 1981; Nelson and Platnick, 1981; Penny et al., 1982). One possible approach for constructing general cladograms (and ultimately classifications) might therefore involve comparing fundamental cladograms for overall patterns of congruence. Stable patterns summarized by consensus cladograms form the basis for generating general classifications. Such classifications are considered stable (sensu Mücke, 1978), because they possess only concordant clades.

However, stability alone is of little systematic value, unless it is coupled with explanatory and descriptive power (Mücke and Farris, 1981; Schuh and Farris, 1981). A stable classification unable to efficiently explain available information is of limited utility, because it is far removed from the data it attempts to summarize (Farris, 1979). Cladistic methods for phylogenetic synthesis should consistently lead to both efficient and stable solutions.

Consensus techniques search for overall stability among individual cladograms by comparing their topologies. Unfortunately, these comparisons do not take into account the relative strength of character evidence among data sets, and therefore, fail to maximize parsimony as well as stability. As such, consensus techniques should not be used to construct general classifications.

An example of two fundamental cladograms and six hypothetical taxa (A-F) is employed to illustrate these points (Fig. 1). Adams (1972) and Nelson (1979) consensus cladograms are used in the illustration because of their general popularity (e.g., Larson et al., 1981; Lindenfelser, 1984). However, the following results apply as well to other consensus techniques.

The two fundamental cladograms (I and II) support two stable (A-C and A-E, excluding the universal set A-F), two unstable (A-D vs. A-E excluding D), and one ambiguous (A-B) components (Fig. 1). Stable and unstable subsets are combined in the Adams and Nelson trees as replicates (A-C and A-E) and trichotomies (A-C, D, and E), respectively (Fig. 2). The ambiguous component (A-B) is replicated in the Nelson cladogram, because it is combinable with the other subsets. In contrast, this component is reduced in the Adams tree to a trichotomy of A, B, and C, because it is not directly supported by fundamental cladogram II. As expected, the consensus cladograms summarize overall patterns of congruence (Fig. 2).

Neither the Adams nor Nelson cladogram represents a parsimonious solution of the original data (characters #1-12; Figs. 1 and 2). These cladograms require five and four extra steps, overall lengths of 17 and 16, and consistencies of 0.71 (12/17) and 0.75 (12/16), respectively, to explain the information (Kluge and Farris, 1969). However,

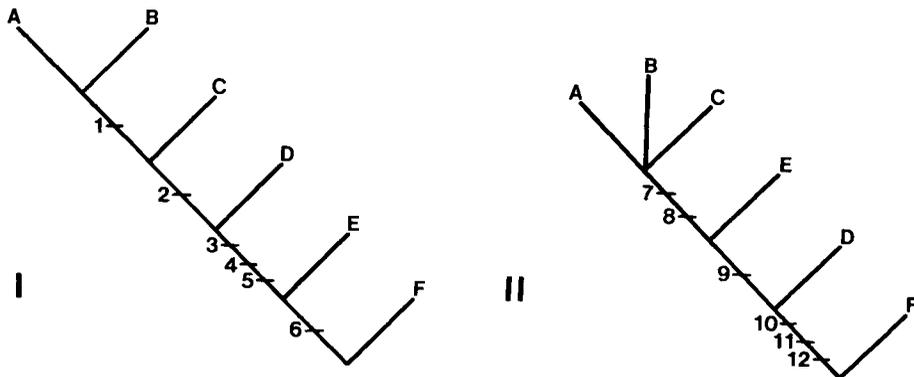


Fig. 1. Fundamental cladograms I and II generated from two different data sets (characters 1-6 and 7-12, respectively) of six hypothetical taxa (A-F). Character data for A-F are summarized by synapomorphies (cross-marks) reflecting the distribution of derived and primitive features.

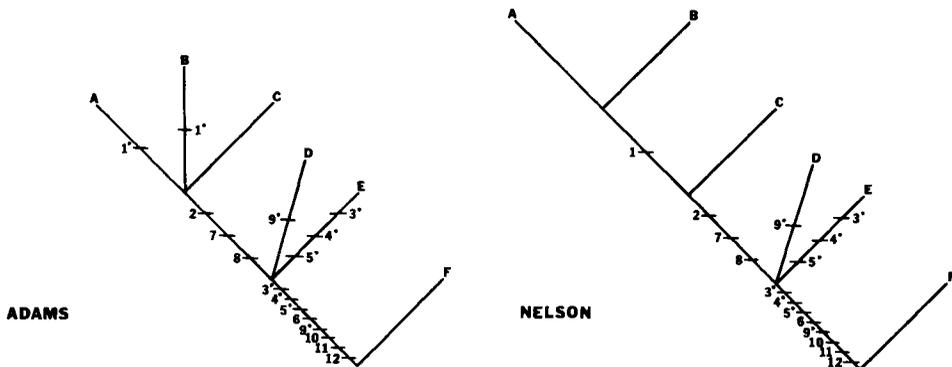


Fig. 2. Consensus cladograms for hypothetical taxa (A-F) constructed from fundamental cladograms I and II. The combined data (characters 1-12) are optimized to these trees as character state changes (cross-marks) by the DIAGNOSE procedure available in the PHYSYS computer package written by J. S. Farris and M. F. Mickevich (Farris, 1982). Homoplasies (convergences, parallelisms, and reversals) are designated by asterisks.

a Wagner tree based on parsimony analysis (Farris, 1970) needs only one extra step, an overall length of 13, and a consistency of 0.92 (12/13) to describe the same data (Fig. 3). Stable subsets (A-C and A-E) are corroborated in the Wagner tree by evidence from both data sets (putative synapomorphies 2, 7, and 8, and 6, 9, 10, 11, and 12, respectively). Support for the resolution of the ambiguous A-B component is provided by a single synapomorphy (no. 1) in the absence of conflicting evidence. The A-D versus A-CE conflict is resolved against the overall strength of evidence in favor of the former.

These results using Adams and Nelson cladograms illustrate a limitation which generally applies to all consensus techniques. Consensus procedures cannot faithfully produce parsimonious solutions from multiple character sets, because they cannot resolve conflict and ambiguity according to evidence. Consensus cladograms are generated from fundamental cladograms instead of original information. This problem with loss of parsimony becomes important whenever consensus cladograms lose resolution unnecessarily. In contrast, parsimony (Wagner) procedures that work from combined data sets ensure efficient results, because they operate directly on available information. Stability is upheld by corroborating evidence, whereas incongruence and ambiguity are resolved against the relative strength of support. Unlike consensus techniques, parsimony approaches

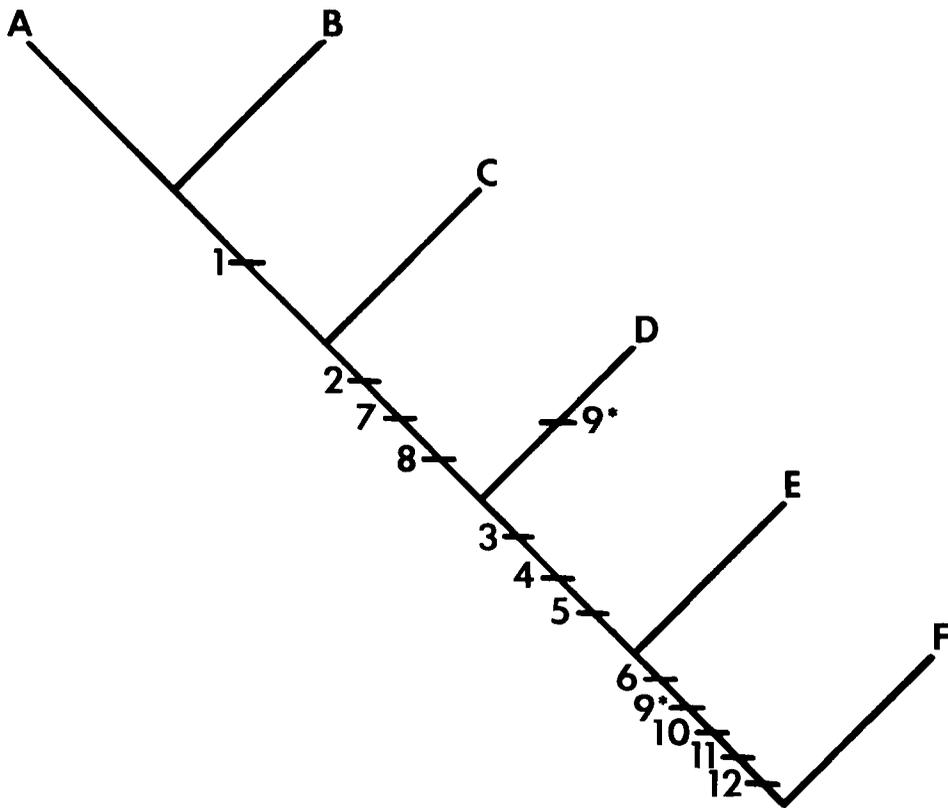


Fig. 3. Wagner tree based on the combined data (characters 1-12) of hypothetical taxa A-F. Asterisks refer to homoplasies.

maximize efficiency as well as stability.

Systematists and specialists of particular groups should base their phylogenetic syntheses and general classifications on cladograms constructed from combined data sets of available information (Mickevich and Johnson, 1976; Miyamoto, 1983, 1984). In this way, efficient and stable classifications can be synthesized and treated as best estimates. Under certain circumstances, systematists may weight the different subsets of combined matrices according to the number of binary character state transitions in the sets. In this fashion, data sets with many character states (e.g., DNA nucleotides) will not overwhelm smaller ones (e.g., morphology) by their sheer numbers (Kluge, 1983).

The homoplasies of general cladograms supported by combined data represent character conflicts both between- as well as within-character sets (Mickevich and Farris, 1981). Fundamental cladograms based on different data matrices collectively estimate the within-character set component of general cladograms, and as such, indirectly measure the between-character set contribution (i.e., taxonomic incongruence) to total homoplasy as the difference. Furthermore, fundamental cladograms may be compared by consensus techniques to reveal which clades of general cladograms are stable, unstable, and ambiguous (see above). Fundamental cladograms supplement general cladograms, and therefore, are useful to phylogenetic synthesis.

Consensus techniques may be useful for comparing the relative stabilities of cladistic and phenetic approaches (e.g., Mickevich, 1978; Nelson, 1979; Schuh and Polhemus, 1980; Rohlf et al., 1983). However, these methods should not be extended to the construction of general cladograms and classifications.

Acknowledgments

This contribution was presented at the "Congruence and Information" symposium (M. F. Mickevich and J. S. Farris, organizers) held in London, England, at the 1984 joint meetings of the Willi Hennig Society, the Linnean Society, and the Systematics Association. Thanks are extended to these societies for the meetings; to M. F. Mickevich and J. S. Farris for their invitation to the symposium; to D. G. Buth, M. P. Hayes, A. G. Kluge, J. M. Savage, D. L. Swofford, and M. R. Tennant for their comments on the manuscript; and to the Department of Biology, University of Miami, for financial assistance.

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