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HENNIG86 and PAUP are reliable

A reply to Lorenzen and Sieg

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Abstract

Recently LORENZEN and SIEG (1991) criticized cladistic computer programs as unreliable because they fail to find “all most parsimonious trees of relationships” and they find “wrong” ones. These authors suggest criteria which a “perfect parsimony program” should meet. Their analysis is flawed because of their: 1. peculiar definition of parsimony and relationship, 2. use of an outdated version of PAUP, and 3. misinterpretation of the programs’ output. It is shown that PAUP and HENNIG86 by and large meet their criteria and find all most parsimonious cladograms for the hypothetical data set used by LORENZEN and SIEG.

Key words: PAUP – HENNIG86 – Cladistics – Computer analysis

Introduction

In a recent paper LORENZEN and SIEG (1991) criticized the current parsimony programs used in cladistics as unreliable for finding all most parsimonious cladograms. This criticism is based upon the programs’ inability to produce the types of “trees of relationships” these authors desired for a hypothetical data set. They further list criteria that an efficient computer program should meet: 1. use of “logical” parsimony over Wagner parsimony, 2. acceptance of polytomies, 3. graphical representation of all cladograms with all possible mappings of characters (optimizations), and 4. elimination of all “wrong” cladograms. We will show that the current versions of PAUP (vers. 3.0) and HENNIG86 (vers. 1.5) by and large meet all appropriate criteria and that LORENZEN and SIEG’s criticism of the program’s reliability is entirely unjustified. Because PAUP and HENNIG86 are the most commonly used programs for parsimony analysis, we will restrict our comments to these programs. For the sake of clarity, we refer to a *topology* as an unrooted set of relationships and to a *cladogram* as a rooted topology with or without characters mapped onto it. We will not use “phylogenetic tree” because this term is best restricted to a particular hypothesis of relationship (PLATNICK 1977) and is inappropriate when applied to a hypothetical example.

1. LORENZEN and SIEG neither define “logical” parsimony nor their particular usage of Wagner parsimony. Because the usage of logical parsimony varies within the literature (e. g. FARRIS 1970 vs. FELSENSTEIN 1982) it remains unclear what it is and why it is preferable to what LORENZEN and SIEG consider Wagner parsimony. Despite these authors’ concerns, however, the theoretical basis of parsimony in cladistic analysis has already been well established (FARRIS 1983; AX 1984). We agree with FARRIS that most parsimonious cladogram(s) are preferable because they minimize the number of ad hoc hypotheses required to explain the distribution of characters among taxa. Because both PAUP and HENNIG86 found all most parsimonious cladogram(s) for LORENZEN and SIEG’s data

set by minimizing ad hoc hypotheses (i. e. number of character state changes), we fail to understand LORENZEN and SIEG's criticism of these programs on the basis of parsimony.

Apparently LORENZEN and SIEG's "logical parsimony" refers to something in addition to the minimization of steps on a cladogram. For example, in their Figure 2, they criticize PAUP and PHYLIP for transforming any polytomy into dichotomies with unsupported nodes. This they consider a violation of "logical parsimony". While these unsupported dichotomies may be nuisance, they do not violate the principle of parsimony *sensu* FARRIS since the polytomous and dichotomous cladograms require the same number of steps. This property of the programs (outdated in the case of PAUP 3.0) does not violate the principle of parsimony as is used in cladistics.

Another point concerning parsimony which LORENZEN and SIEG likewise confuse is their belief that parsimony algorithms must first designate a root prior to finding the most parsimonious topology. They specifically criticize PHYLIP for initially constructing an unrooted topology and apparently overlook the fact that both PAUP and HENNIG86 proceed in a similar fashion. According to these authors, this method of construction will make the cladograms less parsimonious once rerooted. What these authors overlooked is that for any data matrix, the number of steps required to explain the distribution of characters on a topology is independent of the root designated. All computer parsimony programs initially find unrooted topologies that are subsequently rooted to the outgroup (e. g. KLUGE and FARRIS 1969). This approach does not violate the "theory of evolution" *sensu* LORENZEN and SIEG, it is simply a search strategy for finding parsimonious cladograms. Similarly, this rooting strategy does not violate the principle of parsimony as commonly held in cladistics.

2. LORENZEN and SIEG correctly state that HENNIG86 produces trees with polytomies. While it is true that their version of PAUP (version 2.4.1) does not, the current version of PAUP (version 3.0, 1989) does produce trees with polytomies. As mentioned above, in the older version of PAUP all polytomies were arbitrarily broken up into dichotomies that were not supported by any character. Systematists collapsed by hand the unsupported dichotomies and all polytomies were restored. This feature of the output, while unfortunate, did not perpetuate confusion in the literature. The criterion of displaying polytomies has been met by PAUP since 1989.

As LORENZEN and SIEG have correctly pointed out, under certain circumstances unsupported branches can occasionally be found in cladograms in the output of HENNIG86 and PAUP (Fig. 1). In our example based on LORENZEN and SIEG's data matrix, there are two different initial cladograms (Ia and IIa) with characters mapped favoring parallelisms over reversals. In each of these cladograms, one node is unsupported and these nodes are collapsed (Ib and IIb) to produce polytomies. If reversals are favored, a different node is unsupported and collapses (Ic and IIc). Note that all of these cladograms are equally parsimonious. All relationships indicated by the cladograms are in the set of most parsimonious trees. Once again these unsupported branches will hardly cause any confusion because, as already mentioned, systematists will collapse them as soon as the characters are mapped onto the cladograms; all polytomies are restored.

3. LORENZEN and SIEG have a rather unconventional definition of "relationships". Apparently, they consider "hypotheses of relationships" to consist of both branching order and mapped characters (usually referred to as optimizations). In the discussion, two cladograms (Ia and IIc in their Fig. 1) are treated as two different "equally most parsimonious trees of relationships". Yet relationships are identical for the two cladograms (all sister groups are the same) and only optimizations (character mapping) differ. In the literature there is a clear distinction between cladogram structure and the optimization of characters onto a cladogram (FARRIS 1970; FITCH 1971). Relationships are defined by branching order and not by character optimization. All current phylogenetic programs are designed to find all most parsimonious branching orders, initially without regard to a particular

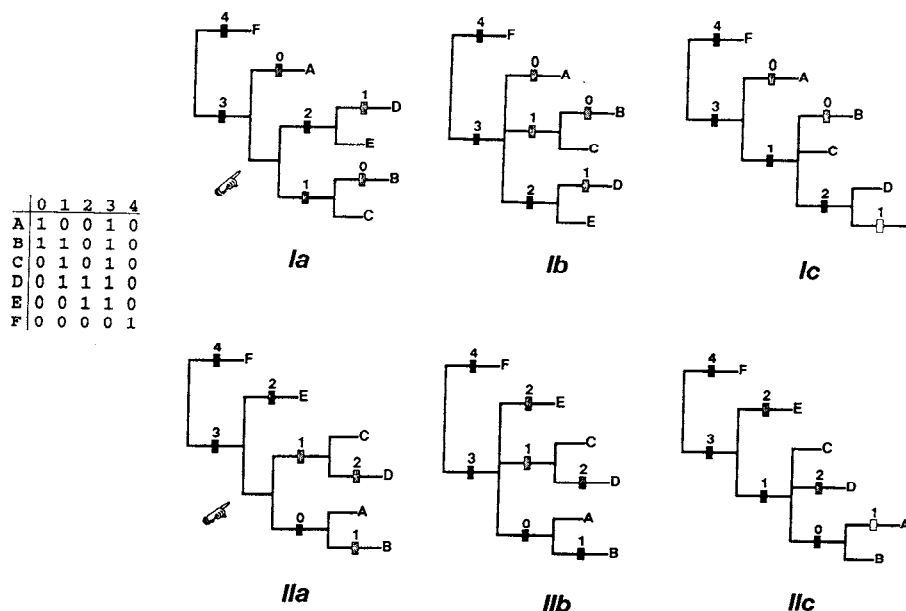


Fig. 1. Unsupported cladograms found by PAUP and HENNIG86 (Ia and IIa, hand points to unsupported node, optimized favoring parallelisms). Dark bars represent forward changes, gray bars parallel changes, and white bars reversals. Cladogram after collapsing unsupported nodes (Ib and IIb). Cladogram after collapsing unsupported nodes with optimization favoring reversals (Ic and IIc). Illustration made with CLADOS (NIXON 1992)

optimization. Later the characters are mapped onto the cladogram after it has been rooted (FARRIS 1970). Thus, if a conventional definition of “relationships” is used all most parsimonious hypotheses of relationship are found by both computer programs.

This terminological issue having been clarified, we return to LORENZEN and SIEG’s criticism that HENNIG86 and PAUP do not display alternative optimizations for particular cladograms (their Fig. 1: Ia and IIc). The initial output of HENNIG86 consists only of the topologies with *no* characters mapped onto them. Optimizations are obtained through additional files which list the character states at particular nodes (HENNIG86: “Dos equis; xsteps h”). If there are several different optimizations, this is indicated by 0.1 assignment to the node. Thus the information desired by LORENZEN and SIEG can be found in the output. PAUP has similar output files (Describe Trees Command).

LORENZEN and SIEG would like the “perfect parsimony program” to present all possible optimizations. This may cause practical problems. Often there are many more optimizations than there are most parsimonious cladograms. If all optimizations were to be displayed, the output would become cumbersome, and it would become increasingly difficult to find all the different cladograms. However, if one is interested in finding all possible optimizations, SWOFFORD and MADDISON (1987) provide a method for doing so.

4. As already mentioned, we agree with LORENZEN and SIEG that only cladograms with supported branches should be generated by computer programs. Nevertheless, this minor inconvenience does not render the programs unreliable because, after all, all most parsimonious cladograms are found and any unsupported node can be collapsed by hand.

There remain a few additional points to be made. LORENZEN and SIEG criticize HENNIG86 for always assuming the first taxon in the character table to be the outgroup. It is clearly specified in the manual of HENNIG86 that this is the default procedure, and that it can be overridden by the specification of an alternative outgroup (outgroup =

taxon Y). Moreover, LORENZEN and SIEG state: "As phylogenetic systematics deals with both branching modes and holophyly of taxa, the program should deal adequately with *both* aspects, instead of overemphasizing one of them" (p. 471). Since the holophyly of taxa is based exclusively on cladogram structure (= branching order), we fail to see any distinction that could be made.

Conclusions

The criteria that LORENZEN and SIEG list for the "perfect parsimony program" are by and large currently met by PAUP and HENNIG86. These authors should not fault the programs for not conforming to their version of "logical parsimony", which is clearly at odds with the type of parsimony commonly used in cladistics. They further overemphasize the problem of occasional unsupported nodes in the output since: 1. this can be easily remedied by inspection of the proper output files which were designed for this purpose, and 2. this does not affect whether the solutions are the most parsimonious.

We agree that graphical representation of cladogram and characters is important. Both HENNIG86 and PAUP currently have companion programs that combine cladogram and optimization in a graphical representation. CLADOS (NIXON 1992) is interactive with HENNIG86, and McClade (MADDISON and MADDISON 1991) is interactive with PAUP. When the current parsimony programs are properly used and the output properly interpreted, they become powerful and reliable tools for finding the most parsimonious cladograms.

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Zusammenfassung

HENNIG86 und PAUP sind doch zuverlässig – Eine Antwort auf Lorenzen und Sieg

In einer kürzlich publizierten Arbeit charakterisieren LORENZEN und SIEG kladistische Computer-Programme als nicht zuverlässig, weil sie nicht nur nicht alle sparsamsten Stammbäume finden, sondern zudem auch falsche Stammbäume produzieren. LORENZEN und SIEG schlagen Kriterien vor, die von „perfekten kladistischen Programmen“ erfüllt werden sollen. Ihre Kritik ist verfehlt, weil sie letztlich das Resultat einer 1. ungebräuchlichen Definition vom Sparsamkeitsprinzip und Verwandtschaftsdiagramm ist, 2. in ihrer Studie eine veraltete Version von PAUP benutzt haben und 3. die Ergebnisdateien der Programme falsch ausgewertet haben. Es wird gezeigt, daß PAUP und HENNIG86 die von LORENZEN und SIEG aufgestellten Kriterien weitestgehend erfüllen und alle sparsamsten Stammbäume für den hypothetischen Datensatz finden, den LORENZEN und SIEG in ihrer Arbeit verwendeten.

Literature

- AX, P., 1984: Das Phylogenetische System. Stuttgart: Gustav Fischer Verlag.
 FARRIS, J. S., 1970: Methods for computing Wagner trees. *Syst. Zool.* **19**, 83–92.
 – 1983: The logical basis of phylogenetic systematics. In: *Advances in Cladistics*. Ed. by N. I. PLATNICK and V. A. FUNK. New York: Columbia University Press. pp. 7–36.
 – 1989: HENNIG86. Port Jefferson Station, New York.
 FEISENSTEIN, J., 1982: Numerical methods for inferring evolutionary trees. *Quart. Rev. Biol.* **57**: 379–404.
 FITCH, W. M., 1971: Towards defining the course of evolution: Minimal change for a specific tree topology. *Syst. Zool.* **20**, 406–416.
 KLUGE, A. G.; FARRIS, J. S., 1969: Quantitative phyletics and the evolution of anurans. *Syst. Zool.* **18**, 1–32.
 LORENZEN, S.; SIEG, J., 1991: PHYLIP, PAUP, and HENNIG86 – how reliable are computer parsimony programs used in systematics? *Z. zool. Syst. Evolut.-forsch.* **29**, 466–472.

- MADDISON, W. P.; MADDISON, D. R., 1991: MacClade: Interactive analysis of phylogeny and character evolution. Sunderland: Sinauer Ass.
- NIXON, K., 1992: CLADOS, PC compatible character analysis program. Ithaca, N. Y.: Bailey Hortorium, Cornell University.
- PLATNICK, N. I., 1977: Cladograms, phylogenetic trees, and hypothesis testing. *Syst. Zool.* **26**, 438–442.
- SWOFFORD, D. L., 1990: PAUP: Phylogenetic Analysis Using Parsimony, Version 3.0. Illinois Natl. Hist. Surv., Champaign, IL.
- SWOFFORD, D. L.; MADDISON, W. P., 1987: Reconstructing ancestral character states under Wagner parsimony. *Math. Biosci.* **87**, 199–229.
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