

Taxic Revisions

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Parsimony analysis provides a straightforward way of assessing homology on a tree: a state shared by two terminals comprises homologous similarity if optimization attributes that state to all the stem species lying between those terminals. Three-taxon statements (3ts), although seemingly “exact” in that each either fits a tree or does not, do not provide a satisfactory assessment of homology, because that assessment can be internally contradictory and because 3ts systematically exclude homologous resemblance in reversed states. Modified 3ts analysis (m3ta), a method in which both plesiomorphic and apomorphic states of “paired homologue” (PH) characters (those other than presence/absence data) are regarded as “informative” (able to distinguish groups), can (obviously) group by symplesiomorphy and so form paraphyletic groups unless data are clocklike enough. Patterson’s pattern analysis (ppa) has the same shortcoming, to which it adds the drawback that only characters fitting the tree perfectly are used, a restriction that can easily lead to discarding most of the structure in the data. Revised m3ta (rm3ta), a method in which plesiomorphic states are not taken as informative, can also form paraphyletic groups, because it cannot apply reversals as apomorphies. The idea that knowledge of phylogeny has been derived from classifications does not imply that nonevolutionary methods should be

employed for classification, but instead means that systematic methods must be logically capable of phylogenetic interpretation. Neither m3ta nor rm3ta satisfies that requirement because of their contradictory assessments of homology. © 2001 The Willi Hennig Society

OVERVIEW

Carine and Scotland (1999) followed Patterson’s (1982) taxic approach to homology, and on that basis they proposed a new method, modified three-taxon statement analysis (m3ta). The modification did not affect the treatment of presence/absence data, called “complement relation” (CR), but only that of other characters, called “paired homologue” (PH).¹ Whereas Nelson and Platnick’s (1991) original 3ta (N/P 3ta) treated only putatively apomorphic similarities as grounds for grouping, m3ta treated both apomorphic

¹“Paired” because it originally referred to two-state characters. Scotland (2000a) now calls multistate characters “shared homologies,” apparently in order to rhyme.

and plesiomorphic states of PH characters as informative,² that is, able to support groups. But Kluge and Farris (1999) pointed out that this treatment of PH characters makes m3ta—like phenetic clustering—sensitive to autapomorphy, so that unless data are clocklike enough, m3ta can group by symplesiomorphy and so form paraphyletic groups.

Scotland and Carine (2000) now object to that observation. At first they claim to refute it—by arguing that autapomorphy does not affect their method for analyzing CR characters! Later they stress that m3ta gets the right tree for a real PH (nucleotide) matrix for apes. But then those data happen to be clocklike, and other real cases show the autapomorphy effect quite dramatically. Scotland and Carine seem to realize this, for while they never acknowledge such cases, they do finally try to address the problem, by discarding the taxic idea that plesiomorphic PH states must be treated as informative. When they change their clustering method accordingly, the revised version (rm3ta) is like the old N/P 3ta.

Yet despite abandoning their old taxic principles, Scotland and Carine (2000) still wish to connect their views to Patterson's (1982) taxic homology, and for that purpose they maintain that their method can test homology, whereas parsimony cannot. But their criticism of parsimony consists only of not mentioning how parsimony is actually used in evaluating homology, while their own approach gives internally contradictory assessments and systematically excludes homologous similarities in reversed states. The latter difficulty arises because their revised clustering method suffers from the reappearance of a weakness found in N/P 3ta, that reversals are not applied as synapomorphies. Their attempt to relate their approach to Patterson's views, moreover, rests only on ignoring the differences between their method and Patterson's own.

These issues are straightforward in themselves, but exposing them turns out to be another matter. While Scotland and Carine (2000) have revised both their method and their taxic principles they go to some lengths to avoid stating that fact directly. Because of that complication, we will begin our discussion by

²This is not the usual meaning of "informative"; we have employed it here only to facilitate discussion of Scotland and Carine's comments.

calling attention to relevant aspects of Carine and Scotland's (1999) earlier treatment.

ROOTS

The crucial premise of Carine and Scotland's (1999, p. 121) position was what may be called their taxic assumption. Note that the bracketed insertion "[to the study of homology]" is theirs; Patterson's original comment had "(the one I am advocating)" in that place

Patterson (1982: 34) distinguished two approaches to the study of homology which he called taxic and transformational homology, terms derived from the taxic and transformational approaches to evolutionary theory described by Eldredge (1979). According to Patterson (1982: 34), "The taxic approach [to the study of homology] is concerned with monophyly of groups. The transformational approach is concerned with change, which need not imply grouping." Thus, for four taxa (ABCD) in which taxa A and B share character state X and taxa C and D share character state X', two groups (AB) and (CD) are hypothesized from a taxic perspective (Fig. 1).

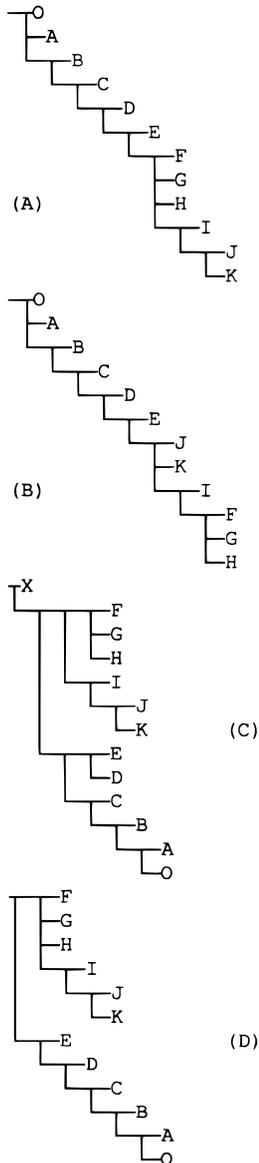
The taxic tree would then be ((A B) (C D)), as they showed in their Fig. 1D. This effectively assumed that neither state could have arisen from the other. If state X' were a modified (or substituted) form of X, for example, the tree could obviously be (A B (C D)) instead.

Readers accustomed to Eldredge's (1979) usage of "taxic" should keep in mind that Patterson (1982) changed the meaning of the term substantially (cf. Farris, 2000a). Eldredge (1979, p. 17) used taxic for evolutionary theories that include transformational theories:

A complete evolutionary theory requires the presence of two distinct components—(a) a theory of mechanics to explain genetic, morphologic, and behavioral change, and (b) a theory pertaining to the origin of species. . . . Many of the classic areas of investigation, especially in paleontology and genetics, emphasize the aspect of evolutionary mechanics (the "transformational" approach) to the point of near exclusion of consideration of the origin of taxa (the "taxic" approach). . . . Integration of the two approaches is best effected by considering the issues of the transformational approach as a subset of those of the taxic approach.

In his taxic approach to homology, in contrast, Patterson (1982, p. 67) admitted no connection with evolutionary change—or with evolution:

O	000000000	O	ccccccccc
A	100000000	A	gcccccccc
B	110000000	B	ggccccccc
C	111000000	C	gggcccccc
D	111100000	D	ggggccccc
E	111110000	E	gggggcccc
F	111111111	F	ggggggggg
G	111111111	G	ggggggggg
H	111111111	H	ggggggggg
I	011111111	I	cgggggggg
J	001111111	J	ccggggggg
K	001111111	K	ccggggggg



The role of homology in phylogenetic reconstruction is limited to the production of cladograms, or classifications. These activities need have no evolutionary connotations. If phylogeny has to be about evolution, homology has nothing to contribute to it.

Unfortunately for the curious, Patterson never explained what phylogeny would be about, if not evolution. Whatever that might be, however, the taxic assumption fits a nonevolutionary view very well, for as Kluge and Farris (1999, p. 207) pointed out:

The taxic choice of ((A B) (C D)) thus rests on a ruling out *a priori* the possibility that either state has replaced (changed into, been substituted for) the other. If applied to nucleotide data, then, the taxic assumption would have the paradoxical implication that substitution could not have occurred at all!

Carine and Scotland (1999, p. 122f) applied the taxic assumption only to PH characters. For CR characters they retained N/P 3ta,³ explaining

Scotland (1999b) [*sic*] has shown that for three-taxon statement analysis the two relations [i.e., complement relation and paired homologue] need to be dealt with differently. This is because in t.t.s. analysis it is only the ones (1's) in a matrix that can provide evidence of group membership. For complement relation characters this is unproblematic because presence coded one (1) is the only part of the relation which provides evidence of grouping. However, for paired homologue data both homologues [states] constitute hypotheses of groups. By designating one of the homologues zero (0), that homologue is rendered uninformative because an all zero "functional outgroup" is an essential part of implementing t.t.s. To overcome this problem Scotland (1999b) [*sic*] proposed a modification of t.t.s. analysis (hereinafter called modified t.t.s.) which treats all homologues [states] as being potentially informative.

³Except that, unlike Nelson and Platnick (1991), Carine and Scotland (1999) used Nelson and Ladiges' (1992) fractional weighting, discussed further below, but this has no connection with their views on outgroups.

FIG. 1. Matrix from Kluge (1994, his Table 2), presented first as 0/1 characters (the original version) and then as nucleotide codes for selected sites. The two versions give the same results. The outgroup O is supposed to have plesiomorphic states for the characters shown. (A) Most parsimonious tree. (B) Consensus of N/P 3ta trees. This is also the consensus of rm3ta trees, with or without fractional weighting. (C) Consensus of m3ta trees (cf. Carine and Scotland, 1999, their Fig. 8), computed with fractional weighting. (D) Most parsimonious tree as rerooted by Carine and Scotland (1999, cf. their Fig. 7).

“Scotland (1999b)” (Scotland, 2000b) does not actually describe modified its analysis, or m3ta, but Carine and Scotland (1999: 123) went on to do so:

To treat all homologues equally, the first step in Scotland’s modified procedure is to recode all homologues [states] in absence/present [sic] format as shown in Table 2 with the presence of a homologue coded one (1) and the absence of a homologue coded zero (0). This modified absence/presence coding provides the basis for three-taxon statement matrices.

Thus a character with states red and blue would be recoded into two separate 0/1 variables, absence/presence of red and absence/presence of blue. This is the same as nonadditive binary coding, an old technique used by pheneticists (see Sokal and Sneath, 1963). This approach has the unfortunate side effect of associating “absence/presence” coding variables with PH characters, whereas Carine and Scotland (1999) meant to distinguish PH characters from CR characters, that is, from real presence/absence characters. In what follows we will stipulate PH or CR as needed to avoid misunderstanding.

While Carine and Scotland’s (1999) recoding might seem just a more verbose way of writing a PH data matrix, their application of this method has an important consequence. The zeros of m3ta’s “all zero outgroup” are those of the coding variables, and each of those zeros indicates absence of one of the original states. Because of this, that “outgroup”—labeled X in the figures—is not (even conceptually) a taxon with plesiomorphic states, but instead a lack-all node, an artificial node constructed so that it has *no state whatever*: “Outgroup” X thus differs fundamentally from the outgroups employed in parsimony analysis, for those are real taxa with real character states.

One of the effects of “outgroup” X is illustrated by a matrix of Kluge’s (1994, his Table 2), shown in Fig. 1. Both the most parsimonious tree (Fig. 1A) and the N/P 3ta tree (Fig. 1B) are rooted according to Kluge’s original outgroup, O (as throughout, outgroup O is supposed to have plesiomorphic states for the characters shown). Treating both states of these PH characters as informative, in contrast, leads to the X-rooted m3ta tree of Fig. 1C. In this tree, the original outgroup O is placed apically. It will be seen later that similar effects occur with real data matrices as well.

While they also used this matrix as an example, Carine and Scotland (1999; see their Fig. 8) did not mention the placement of O. They removed O from the analysis and

rerooted the parsimony result so that, with their new rooting (Fig. 1D; cf. their Fig. 7), the basal split would correspond as closely as possible to that of the X-rooted m3ta tree (Fig. 1C). Removing O was necessary, they insisted, because (Carine and Scotland, 1999, p. 127)

[f]or [parsimony] analysis, which produces unrooted trees, use of an all zero outgroup is unjustifiable as both homologues [states] are potentially informative. Therefore, in the [parsimony] analysis of these data treated as paired homologues an all zero outgroup is not included.

That wording tends to obscure the actual point of their argument. That the outgroup O is “all zero” is irrelevant, since it does not matter whether the states of a *real* outgroup are called zero or something else.⁴ This is easily seen on observing that the 0/1 and c/g versions of Kluge’s example (Fig. 1) give the same results. No more would one omit the outgroup because parsimony “produces unrooted trees.” That would be the height of nonsense, inasmuch as the purpose of the outgroup is precisely to root the tree. The relevant part of Carine and Scotland’s (1999) comment was just their contention that

... use of an ... outgroup is unjustifiable as both [states] are potentially informative.

The idea that both PH states are informative is of course the taxic assumption. Carine and Scotland wished to dispose of parsimony’s real outgroups because such outgroups serve to distinguish plesiomorphy from apomorphy. The point of the taxic assumption—and the effect of lack-all “outgroup” X—is just that sympleiomorphy is *not* distinguished from synapomorphy as grounds for grouping.

Failing to make that distinction leads to a difficulty, as is readily discovered from one of Carine and Scotland’s (1999, p. 128) comments on this example (emphasis added):

The two results differ only in that [m3ta; see our Fig. 1C] resolves a clade (FGH) which is not found in the [parsimony; our Fig. 1D] analysis. . . . *From a taxic perspective*, both characters 1 and 2 support the groups (FGH) and (JK).

As Kluge and Farris (1999, p. 210) pointed out,

⁴Carine and Scotland (1999) apparently confused Kluge’s “all zero outgroup” O, which is a terminal with real states, with the “all zero outgroup” used in m3ta, which is lack-all X. That was a particularly unfortunate mistake, as Kluge and Farris (1999, p. 209f) have discussed in detail.

On inspecting the matrix (Fig. 1) and the most parsimonious tree (Fig. 1A), however, it is easily seen that the states common to (FGH) are simply those of the stem species of (FGHIJK). “Clade” (FGH) is merely a paraphyletic group, based only on symplesiomorphies. The “support” for that group, then, comes only from the taxic assumption—the same assumption that would imply that substitution does not occur and that grouping should be based on all similarities.

If apomorphy is not distinguished from plesiomorphy, grouping is based on all similarities,⁵ rather than on shared apomorphies. Grouping by all similarities, which is the approach used in phenetic clustering, has the well-known shortcoming that it is sensitive to autapomorphy. That is, it can yield a correct phylogeny only if the data are close enough to clocklike; otherwise it may group by symplesiomorphy and so produce paraphyletic groups. In this respect, m3ta has a marked disadvantage compared to the original N/P 3ta. While N/P 3ta certainly has its drawbacks (Kluge, 1993, 1994; Farris *et al.*, 1995; Deleporte, 1996; De Laet, 1997; Farris, 1997, 2000b, De Laet and Smets, 1998; Farris and Kluge, 1998; Kluge and Farris, 1999), at least it makes an effort to distinguish apomorphy from plesiomorphy.

Kluge and Farris (1999, their Fig. 2; see our Fig. 2) illustrated the effect of m3ta's treatment of PH characters by modeling the debate between pheneticists and phylogeneticists on the classification of amniotes (for a review see Farris, 1979). In that example (Kluge and Farris, 1999, 206),

[t]he characters have been made congruent so that the [phylogenetic] grouping is clear. Two lines, A and H, have been supplied with several autapomorphies, reflecting the divergence of birds and mammals, and to make this apparent, the most parsimonious tree (Fig. 2A) is drawn with branch lengths. In the debate, phylogeneticists (for example, Hennig, 1975) pointed out that grouping should be based on synapomorphy. This gives the most parsimonious tree (Fig. 2A) (for the relationship between synapomorphy and parsimony, see Farris, 1983, 1986; Farris and Kluge, 1985, 1986). Pheneticists (Mayr, 1974; Sokal, 1975; Michener, 1978) insisted that grouping should instead be based on all similarities. That would cause highly divergent groups to be removed from their genealogical positions, leaving residual groups based only on symplesiomorphy. This is seen in groups (BCD) and (EFG) of Fig. 2B, which is the consensus of UPGMA phenograms. But those paraphyletic groups, and the same displacement of A and H, also occur in Fig. 2C, which is the

consensus of m3ta trees. The new method is sensitive to autapomorphies and can group by symplesiomorphy. Carine and Scotland have reinvented phenetics.

Similar effects of autapomorphy on X-rooted m3ta are also found in real cases, as will be seen shortly. In contrast, N/P 3ta in this case groups by synapomorphy, yielding the same tree as parsimony (Fig. 2A).

OMISSIONS

In summary, when Carine and Scotland (1999) modified N/P 3ta by treating plesiomorphic PH states as able to distinguish groups, the natural result was a method that can group by symplesiomorphy. The striking feature of Scotland and Carine's (2000) objections is that they involve almost every conceivable topic except that connection.

One of those other topics is the treatment of CR data. As a background for discussing this, it will be useful to recall Kluge and Farris' (1999, their Figs. 3 and 4) illustration of the effect of autapomorphy on m3ta in a real case, using Wheeler *et al.*'s (1993) data on arthropod relationships. It will be of interest that these are *not* CR data, but instead PH, comprising nucleotide sequences and multistate morphological characters. The X-rooted m3ta tree is shown in Fig. 3. To indicate degrees of divergence, the most parsimonious tree (Fig. 4) is drawn with branch lengths. Membership of these terminals in well-established higher taxa is indicated in Fig. 7B. Kluge and Farris (1999, p. 207) reported

Nephila, placed apically in the most parsimonious tree (Fig. 4), is highly divergent, so that it is separated from its closest relatives and placed more basally in the m3ta tree (Fig. 3), thereby creating a series of paraphyletic groups (beginning with *Anoplo-dactylus*). This is much like the cases of A and H in Fig. 2. The same is seen again with divergent *Drosophila*, except that it drags its sistergroup *Papilio* with it to its new position. Further, the basal split of the tree is misplaced. In the most parsimonious tree (Fig. 4) it lies between the outgroup, mollusks (*Lepidochiton*, *Loligo*), and the remaining taxa. In the m3ta tree (Fig. 3) onychophorans (*Peripatus*, *Peripatoides*) are placed with annelids (*Glycera*, *Haemopsis*, *Lumbricus*) and mollusks rather than with arthropods (*Callinectes*, etc.)! The new method simply places the basal split between the phenetically most divergent groups, regardless of the actual relationships, and again this is as seen in Fig. 2.

Scotland and Carine (2000) dispute neither those calculations nor the relationships of those taxa—they do

⁵All similarities in PH characters; that is, Carine and Scotland (1999) treated CR characters differently. The examples presented here involve only PH characters.

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O cc c c c c c c ccccccccc c c c c c c ccccccccc
A gg g g g c c c ggggggggg c c c c c c ccccccccc
B gg g g g c c c ccccccccc g c c c c c ccccccccc
C gg g g c c c c ccccccccc c g c c c c ccccccccc
D gg g c c c c c ccccccccc c c g c c c ccccccccc
E gg c c c g c c ccccccccc c c c g c c ccccccccc
F gg c c c g g c ccccccccc c c c c g c ccccccccc
G gg c c c g g g ccccccccc c c c c c c ccccccccc
H gg c c c g g g ccccccccc c c c c c c ggggggggggg

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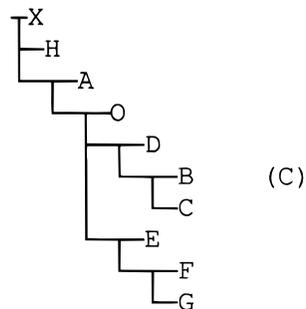
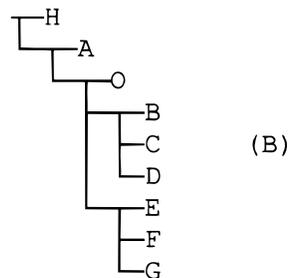
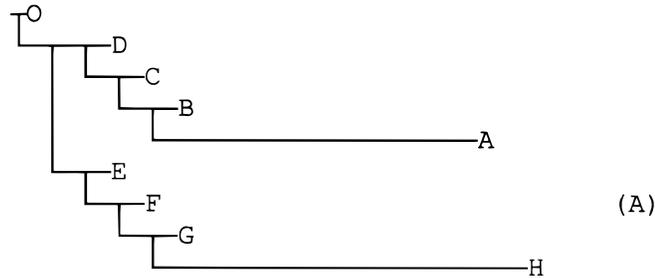


FIG. 2. Matrix illustrating extensive autapomorphy. The entries are nucleotide codes for selected sites. The outgroup O is supposed to have plesiomorphic states for the characters shown. (A) Most parsimonious tree, shown with branch lengths. (B) Consensus of UPGMA phenograms. (C) Consensus of X-rooted m3ta trees, computed with fractional weighting.

not mention the taxa or the data at all—but they nonetheless object to that conclusion. Note that the “[3ta]” here is their insertion, not ours.

Kluge and Farris (1999: 207) claim that “the new method [3ta] simply places the basal split of the tree between the phenetically

most divergent groups.” Figure 2, shows for five taxa, one paired homologue (column 1) and six complement relation homologues (columns 2–7). The [parsimony] matrix for these data is shown in Table 2a. Analysis of these data with UPGMA and [parsimony] results in Figs. 3a–b respectively. If “phenetically most divergent groups” is defined as the longest branch on a

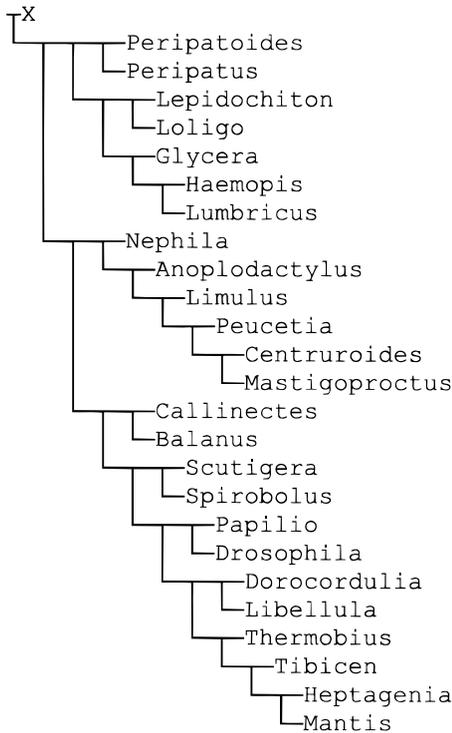


FIG. 3. X-rooted m3ta tree for the data of Wheeler *et al.* (1993) with *Trilobita* omitted, computed with fractional weighting. Compare to Fig. 4.

tree, then for these data groups (CDE) and (AB) are the phenetically most divergent taxa (Table 2b). The m3ta view of these data, treating all homologues as potentially informative, yields 33 three-taxon statements (Table 2c) and one minimal rooted tree Fig. 3c. The basal dichotomy is not placed between the phenetically most divergent groups (AB)(CDE) as Kluge and Farris (1999) claim. Kluge and Farris's (1999) assertion that m3ta simply places the basal split between phenetically most divergent groups is simply false.

Or else Scotland and Carine's comment is simply camouflage. Carine and Scotland's (1999) way of analyzing CR data was like the old N/P 3ta. By "the new method" Kluge and Farris (1999) meant Carine and Scotland's *new* way of treating PH data. That is why the matrices in Kluge and Farris' examples (Figs. 2–4) consisted of PH characters. Scotland and Carine (2000), however, have arranged the example of their Table 2 so that the location of the root in their "m3ta" tree is determined by CR characters. Far from providing evidence against Kluge and Farris' observation, Scotland and Carine's example is not even on the same subject.

Another of Scotland and Carine's (2000) arguments shows a similar pattern:

Kluge and Farris (1999: 207) claim that Carine and Scotland (1999) have reinvented phenetics. However, there are fundamental differences between phenetics and m3ta. Firstly, in contrast to most phenetic clustering algorithms, m3ta does not group on the absence of a homologue.

Carine and Scotland's (1999) views on the treatment of absences certainly did have weaknesses, as will be mentioned later. Kluge and Farris' (1999, p. 207) comment on reinventing phenetics, however, did not concern absences—CR data—but was part of their discussion, quoted above, of the PH example of Fig. 2. For those PH data, as already seen, the X-rooted m3ta tree (Fig. 2C) does indeed closely resemble the phenogram (Fig. 2B), while both differ drastically from the tree obtained by grouping according to synapomorphy (Fig. 2A).

Scotland and Carine (2000) dispute neither the X-rooted m3ta tree nor the phenogram for that example; they just never mention that phenogram or its resemblance to the m3ta result. Their only apparent justification for ignoring such cases is the supposition that their way of treating PH data must not resemble phenetics because their way of treating CR data does not do so. But that supposed analogy is entirely misleading with respect to their PH method and would be so even if Scotland and Carine were correct in insisting that their view of absences distinguishes them from pheneticists. A systematist who accepted their reassurances and used X-rooted m3ta to analyze nucleotide sequence data might well be rewarded with results influenced by autapomorphy. It would be little consolation to such a victim that the problem might not have arisen if he had instead collected CR data and used a different method of analysis.

BRANCHES

Scotland and Carine (2000) do eventually mention parts of Fig. 2, when they wish to object that the example involves long branches.⁶

⁶Scotland and Carine (2000) give an incorrect impression of Siddall's (1998) paper, which called attention to cases in which long branches do *not* mislead parsimony.

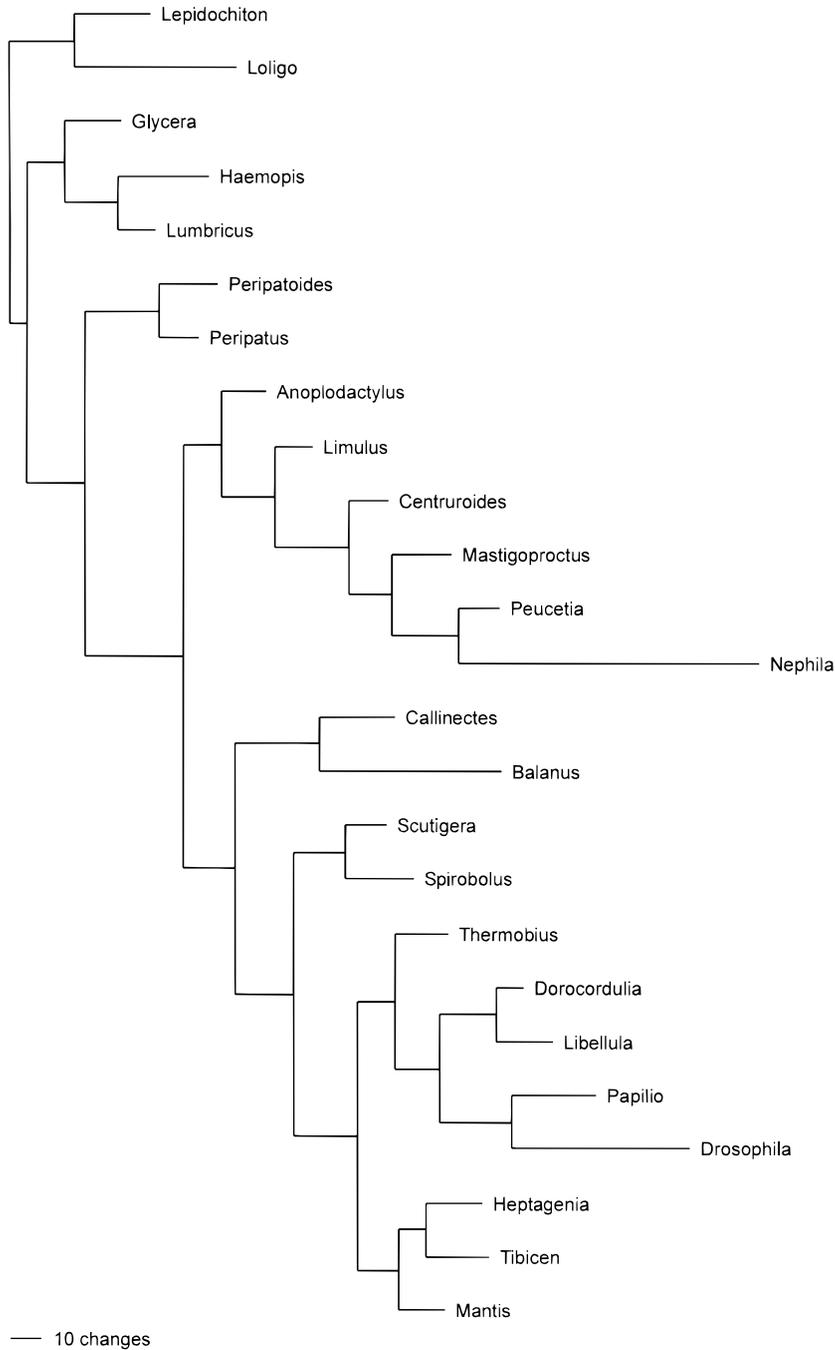


FIG. 4. Most parsimonious tree for the data of Wheeler *et al.* (1993). *Trilobita* is omitted, since it lacks nucleotide sequence data. *Loligo* and *Lepidochiton* comprise the outgroup.

Kluge and Farris take a tree (Fig. 4b) [our Fig. 2A], invent a matrix (Table 3) [our Fig. 2], and demonstrate that m3ta fails to recover the tree given this matrix. This example is used to demonstrate that m3ta gets the wrong tree because it groups

on symplesiomorphies. However, the expediency of their argument is made clear relative to [sic!] Table 5 which is similar to Table 3 in that the data imply two long branches pertaining to taxa A and H. The strict consensus tree from [parsimony] of

Table 5 is shown in Fig. 7. If we assume that the ‘true tree’ is that shown in Fig. 4b, then comparison of Fig. 4b and Fig. 7 shows that [parsimony] gets the wrong tree. Table 5 demonstrates that [parsimony] is sensitive to long branches and unequal rates of change, a phenomenon which is widely known (Felsenstein, 1978; Hillis *et al.*, 1994; Siddall, 1998).

Again they rely on changing the subject. They do not even try to show that m3ta is free of sensitivity to autapomorphy, but instead suggest that parsimony has that sensitivity. And in fact they do not show the latter either, for the long branch effect to which Scotland and Carine (2000) appeal is a result of homoplasy rather than autapomorphy. Combined with his stochastic model, Felsenstein’s (1978) long branches provided a device for generating a misleading pattern of homoplasy; it is the homoplasy that causes parsimony to give the wrong tree in such cases. But any method can be misled by a suitable pattern of homoplasy. While they are careful not to mention it, with the data of Scotland and Carine’s (2000) Table 5, m3ta also puts A and H together. What the example of Fig. 2 illustrates, in contrast, is that autapomorphy *by itself* can cause X-rooted m3ta to produce misleading results, *even when homoplasy is entirely absent*. That is a drawback which parsimony does not share and one that Scotland and Carine do not address at all.

With that in mind, consider Scotland and Carine’s (2000) complaint that Kluge and Farris (1999) “take a tree” and “invent a matrix.” That, of course, is precisely what Scotland and Carine do in their own argument. Their example depends on introducing homoplasy, and homoplastic characters as such have no unique relationship to a tree, so that some relationship must literally be invented in order to produce an example. There is no such occasion for invention in examples such as that of Fig. 2, for there the synapomorphies in the data correspond directly to the groups of the tree (Fig. 2A). Parsimony recognizes that correspondence, but as the example illustrates, methods sensitive to autapomorphy cannot be relied on to do so.

APES

If Scotland and Carine (2000) disapprove of invented matrices, one might wonder, why do they try to argue, as already discussed, from the hypothetical example

of their Table 2? For that matter, why do they never consider Wheeler *et al.*’s (1993) real matrix? That question seems even more pertinent when they object to the example of Fig. 2 on the grounds that simulations or real examples should be used instead:

However, both the examples of Kluge and Farris (1999) [our Fig. 2] and that presented in Table 5 are trivial and provide no insight into the performance of methods in the context of phylogenetic accuracy. In contrast, simulated data matrices or either known or well corroborated phylogenies may be used to assess the performance of methods (e.g., Hillis, 1996) and as an example of this approach, we compare [parsimony] and 3ta relative to the emerging consensus that man is more closely related to chimp than to gorilla. . .

It develops that not just any real example will do.

Scotland and Carine (2000) select a particular real data matrix, Brown *et al.*’s (1982) 896-site mitochondrial DNA sequence data, reporting the m3ta trees of their Figs. 8B and 8C. Although (as is discussed later) they omit the lack-all node X from their diagrams, these are X-rooted m3ta trees, as shown in our Figs. 5B and 5C. Those m3ta trees place *Pan* (chimpanzees) with *Homo* (humans), but the most parsimonious tree, which Scotland and Carine report as in Fig. 5A (cf. their Fig. 8A), groups *Pan* with *Gorilla* (gorillas). Parsimony, they conclude, has given the wrong tree.

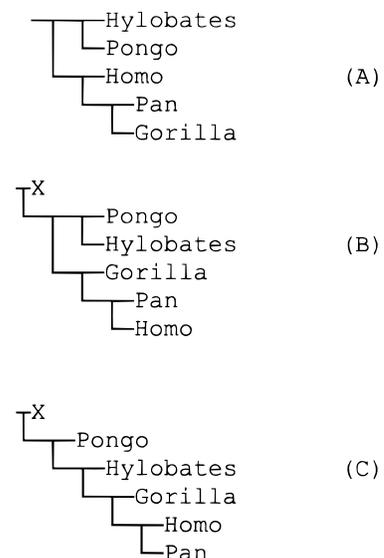


FIG. 5. Trees for the data of Brown *et al.* (1982). (A) Most parsimonious tree, rooted as in Scotland and Carine’s (2000) Fig. 8A. (B) X-rooted m3ta tree calculated with fractional weighting; compare to their Fig. 8B. (C) X-rooted m3ta tree calculated without fractional weighting; compare to their Fig. 8C.

In attributing importance to that result, Scotland and Carine (2000) neglect the fact that the grouping to which they object is not well supported by Brown *et al.*'s data. That was Brown *et al.*'s (1982) own assessment, and Wilson *et al.* (1985), after performing a statistical test to compare alternative trees, concluded that placing *Pan* with *Gorilla* was not significantly better than placing *Pan* with *Homo*. With those data, the difference in tree length is no greater than sampling error. This seems, then, to be merely a case of ambiguous data. Strangely, although Scotland and Carine also mention that "the signal in these data is weak," they make no effort to obtain more decisive information.

To remedy that omission, we have analyzed all the whole-mitochondrial sequences for apes available in GenBank, including baboons (*Papio*) to serve as an outgroup. We included all parts of the mitochondrial sequence except the control region (which is difficult to align), so that the data comprised 15,561 sites. To assess strength of support, we used parsimony jackknifing (Farris *et al.*, 1996) with 1000 replicates, branch swapping, and 20 random addition sequences per replicate. As is seen from the jackknife tree (Fig. 6A), parsimony places *Pan* with *Homo*, and that conclusion is very strongly supported.

The other apes turn out to be even more interesting, not least because Scotland and Carine (2000) present the matter as if one should consider only the grouping of *Homo*, *Gorilla*, and *Pan*:

These data are used here to compare the results for [m3ta] and [parsimony] relative to the three-taxon problem in relation to man, chimp and gorilla. For the purposes of outgroup comparison for [parsimony] and assessing the generality of homologues for [m3ta], gibbon and orang-utan are included in the analysis.

That is not the real reason for their designation of outgroups, for Scotland and Carine (2000) report no assessment of "generality of homologues" (plesiomorphy, as is discussed later) for these data. Instead, as Carine and Scotland (1999) did for the example of Fig. 1, Scotland and Carine (2000) wish to arrange the rooting of the most parsimonious tree (Fig. 5A; cf. their Fig. 8A) so that the basal split agrees as well as possible with that of the X-rooted m3ta tree of Fig. 5B (cf. their Fig. 8B). Their selection of outgroups provides the desired effect:

It [the parsimony tree] is shown here rooted on the branch between the ingroup and outgroup. . .

That contrived agreement makes the basal split of the m3ta tree seem uncontroversial and so conceals a problem. The m3ta tree does not depend on which real taxa are called outgroups. M3ta trees are always rooted according to lack-all X, and the X-rooted m3ta tree of Fig. 5B groups *Pongo* (orangutans) with *Hylobates* (gibbons) instead of with the other great apes, which can hardly be genealogically correct. This error cannot reasonably be attributed to paucity of data. The X-rooted m3ta tree for the whole-mitochondrial data (Fig. 6B) still places *Pongo* with *Hylobates*, and now it even places *Pongo* and *Hylobates* with baboon *Papio* rather than with *Gorilla*, *Homo*, and *Pan*! This is much like the displacement of the root seen in the m3ta analysis of Wheeler *et al.*'s (1993) data (Fig. 3).

While Scotland and Carine (2000) do not explicitly address this problem, they do seem to have considered it. In their Fig. 8C (cf. our Fig. 5C) they present a second X-rooted m3ta tree, one with a more satisfactory placement of *Pongo*. Whereas the first tree (Fig. 5B; cf. their Fig. 8B) was computed using the fractional weighting method of Nelson and Ladiges (1992), the second tree was obtained from unweighted calculations. Since Carine and Scotland (1999) used fractional weighting, discarding that method would mean a shift of position⁷—perhaps that is why Scotland and Carine (2000) do not present the idea more directly—but at least it would solve the *Pongo* problem for these data.

It would create other problems, however, as can be seen by applying unweighted m3ta to Wheeler *et al.*'s (1993) data (Fig. 7A). Recall that Fig. 4 shows the degrees of divergence among these taxa, while well-established higher groups are indicated in Fig. 7B. The X-rooted m3ta tree (Fig. 7A) breaks up the Mollusca (*Loligo*, *Lepidochiton*), placing Onychophora (*Peripatus*, *Peripatoides*) among them and putting both with Annelida (*Glycera*, etc.). It displaces the divergent whipspider *Nephila* (cf. Fig. 4) to the base of the tree, so breaking up Araneae, Chelicerata, and Arthropoda. It

⁷Carine and Scotland (1999) always used fractional weighting, but Scotland (2000b) and Scotland and Carine (2000) include unweighted analyses. Neither of the latter papers provides any explanation for this change of position, but it appears that they were influenced by De Laet's (1997; cf. De Laet and Smets, 1998) demonstration that fractional weighting cannot achieve Nelson and Ladiges' (1992) goal of removing the effects of dependence among three-taxon statements.

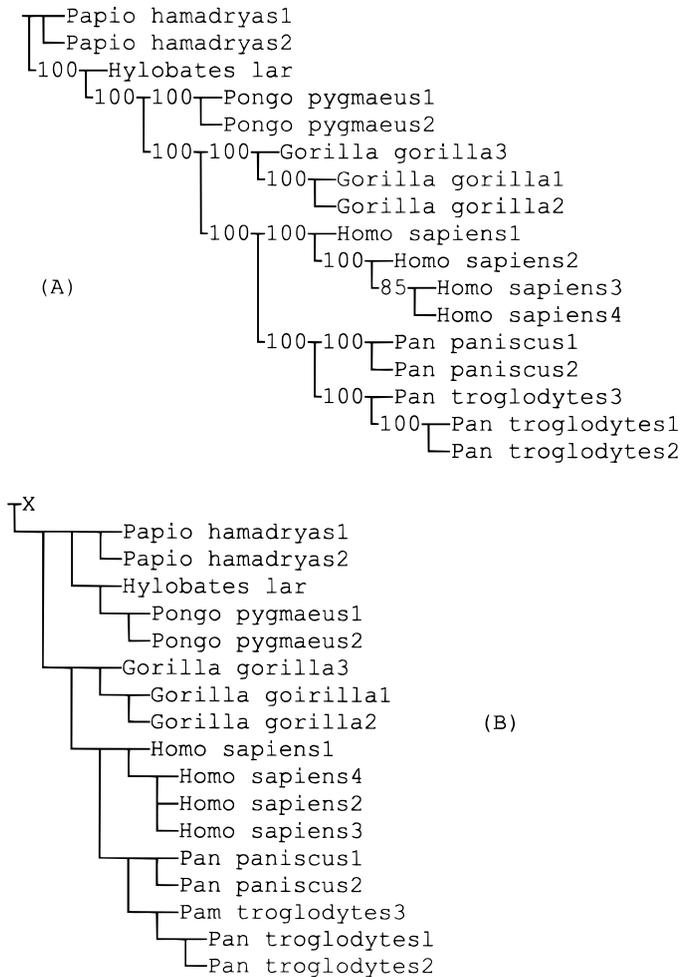


FIG. 6. Trees for whole-mitochondrion sequences for apes. (A) Parsimony jackknife, using baboons (*Papio*) as the outgroup. (B) X-rooted m3ta tree, computed with fractional weighting.

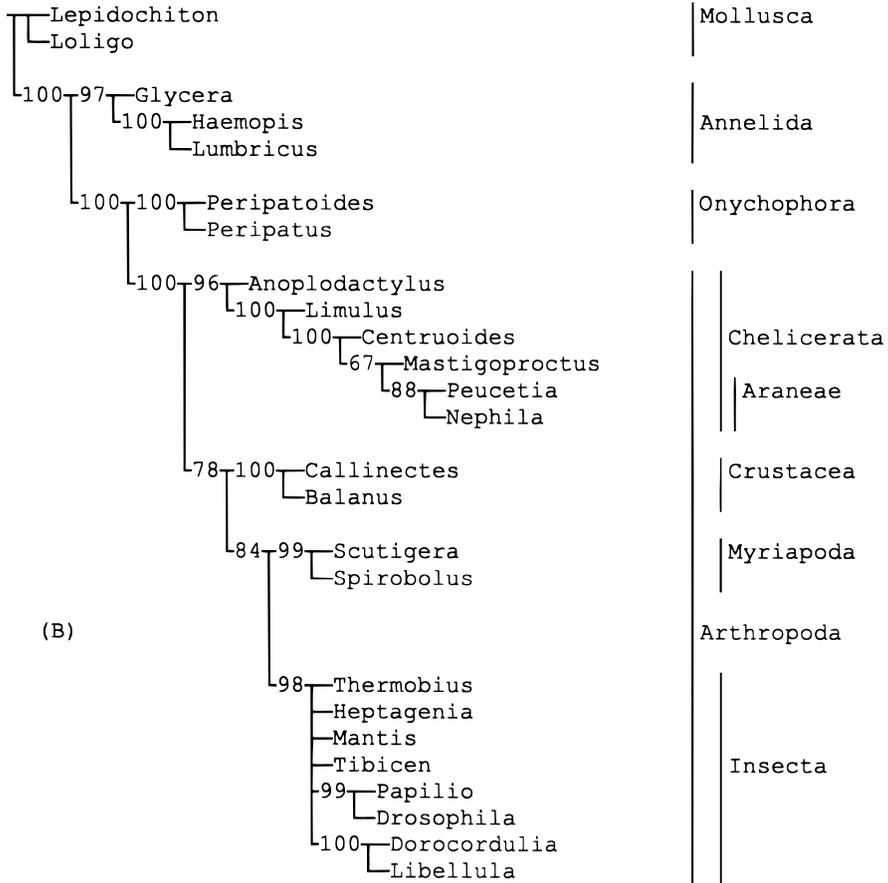
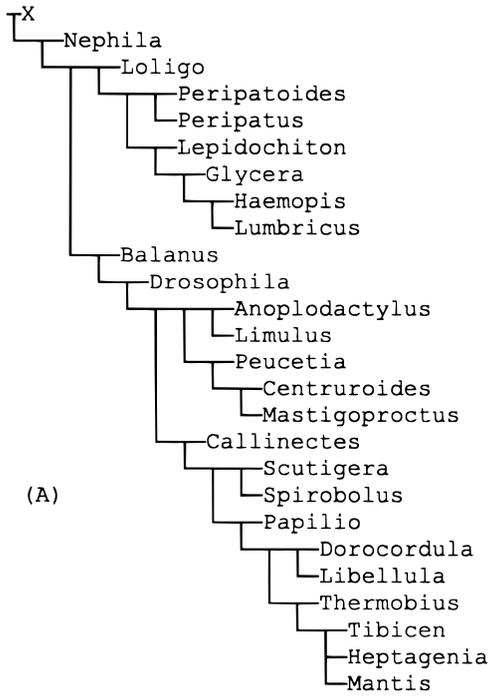
also breaks up both Insecta and Crustacea, managing to place divergent fruit fly *Drosophila* next to barnacle *Balanus*! In summary, it gives an even more absurd result than fractionally weighted m3ta (Fig. 3) gives with the same data. Again this cannot reasonably be attributed to paucity of data, for parsimony jackknifing (Fig. 7B) gives a strongly supported—and much less bizarre—arrangement.

EXAMPLES

If Scotland and Carine (2000) had simply wished to use a real example, they could have reanalyzed

Wheeler *et al.*'s (1993) data, but they never mention that matrix. Rather than being motivated by a desire for realism, their choice of mitochondrial DNA, combined with their concentration on *Pan*, *Homo*, and *Gorilla*, seems intended to conceal m3ta's sensitivity to autapomorphy. It is well known that mitochondrial DNA in those taxa happens to have diverged in an almost clocklike fashion; UPGMA gives the same grouping as that seen for parsimony in Fig. 6A. While m3ta is able to group those three genera correctly with these data, this does not mean that m3ta is not sensitive to autapomorphy, only that clocklike data would not reveal such sensitivity in any event.

Indeed, most of Scotland and Carine's (2000) paper consists of finding ways to avoid any test that would



show the effects of autapomorphy on X-rooted m3ta. The autapomorphy effect is important for PH data, so they try to change the subject to CR data. An example of nonclocklike evolution is likely to involve long branches, so they try to dispose of examples with long branches. Their seeming advocacy of simulations is another version of the same strategy:

However, both the examples of Kluge and Farris (1999) [our Fig. 2] and that presented in Table 5 are trivial and provide no insight into the performance of methods in the context of phylogenetic accuracy. In contrast, simulated data matrices or either known or well corroborated phylogenies may be used to assess the performance of methods (e.g. Hillis, 1996). . .

Despite that favorable citation of Hillis (1996), they evince no intention of actually using such an approach, and it is not difficult to see why. Hillis' simulations of nucleotide sequence evolution did not incorporate a molecular clock. This had the natural result—Scotland and Carine do not mention—that parsimony produced much more accurate trees than did grouping by all similarities, the average accuracy for trees calculated from a large number of sites being less than 40% for phenograms, but over 99% for parsimony. Hillis used UPGMA for grouping by all similarities, but much the same conclusion would apply to X-rooted m3ta.

But then Scotland and Carine's (2000) objection that hypothetical examples such as Fig. 2 provide "no insight" is just the same strategy again. Hypothetical examples are limited in that they do not show which effects are important in real cases, but they have the benefit that they can make particular effects more easily understood. That limitation is no serious drawback, moreover, when the effect in question is already well established. Such is precisely the case here, for there is abundant evidence—Wheeler *et al.*'s (1993) data, for example—that evolution cannot be relied on to be clocklike, and thus that autapomorphy effects can be important. Under these circumstances, examples such as Fig. 2 are quite useful in providing insight into

the behavior of m3ta.⁸ Scotland and Carine pretend otherwise only because they do not wish to admit the effect that Fig. 2 illustrates. Their complaint that the example is hypothetical, is merely a pretext, as is clear from the fact that they also avoid any real or simulated case that would show the effects of autapomorphy.

The example of Fig. 2 may profitably be related to another of Scotland and Carine's (2000) arguments:

In this case [their Table 4b] tail colour is *a priori* uninformative of relationships for [parsimony] because the character-state red is autapomorphic, and only one partition (Fig. 5) is supported. In contrast the topology from m3ta is as shown in Fig. 6b. [Parsimony] cannot treat tail colour as containing unambiguous evidence because it is primarily concerned with phylogeny and character evolution. In contrast, m3ta recognizes a taxonomic group with blue tails for Table 4a and 4b because the data contain this information, irrespective of the truth of phylogeny, or indeed plesiomorphy and autapomorphy.

It is noteworthy that otherwise Scotland and Carine (2000) do not show such an interest in information on grouping. When parsimony (Fig. 2A) recognizes more groups than does m3ta (Fig. 2C) in the example of Fig. 2, they do not take this to mean that m3ta has missed such information. Nor is this a matter of whether the groups have distinguishing states, for all seven of the groups on the most parsimonious tree (Fig. 2A) have such states, while only one of the six groups on the m3ta tree (Fig. 2C) has any. In Scotland and Carine's view, evidently, groups with distinguishing states are desirable only when m3ta happens to form them. What their comment actually reflects, then, is just that they

⁸Similarly, Scotland and Carine's (2000, their Table 5) example shows that parsimony can be affected by homoplasy, but since it shows the same about m3ta, it contributes nothing to choosing between methods. It may be added that the type of long-branch attraction that Scotland and Carine meant to model has proved difficult to demonstrate in real cases (see Siddall and Whiting, 1999). While this does not matter here, it is relevant to some arguments for likelihood methods (see Siddall and Whiting, 1999; Farris, 1999).

FIG. 7. Trees for the data of Wheeler *et al.* (1993) with *Trilobita* omitted. (A) Consensus of X-rooted m3ta trees. Unlike the tree of Fig. 4, this tree is calculated without fractional weighting. (B) Parsimony jackknife tree, using mollusks (*Loligo*, *Lepidochiton*) as the outgroup.

have already decided on some other, unspecified grounds that the m3ta result must always be accepted.

That argument is also noteworthy in a further respect. Like the example of their Table 2, discussed earlier, Scotland and Carine's (2000) examples of their Table 4 are hypothetical. Such examples, it seems, are perfectly acceptable when used to argue for m3ta. This being the case, we see no difficulty in continuing to use hypothetical examples of our own.

REVERSIONS

While Scotland and Carine (2000) devote considerable effort to denying X-rooted m3ta's sensitivity to autapomorphy, they evidently realize that this will not work in the long run, for in another comment they adopt an entirely different approach to addressing the example of Fig. 2:

A related criticism of m3ta by Kluge and Farris (1999) and the purpose of their Fig. 2 (our Table 3 and Fig. 4) is to show that m3ta, as implemented in Carine and Scotland (1999), is sensitive to plesiomorphy and autapomorphy (Fig. 4a). Although the example is taken as given here, in relation to Table 3, if taxon O is a priori taken to be a functional outgroup for assessing character generality as in Kluge and Farris (1999), m3ta results in Fig. 4b which is the same result as [parsimony; our Fig. 2A].

This "m3ta" is *not* the X-rooted m3ta discussed above. The "functional outgroup" here is not a lack-all node X, but one with actual states, just the kind used in N/P 3ta and just what Carine and Scotland (1999) insisted on doing away with before. The same shift of position is seen when Scotland and Carine (2000) (re)describe "m3ta." The shifted part is between the braces, which are added here

3ta *sensu* Nelson and Platnick (1991) codes data relative to functional outgroups or a *priori* estimates of putative synapomorphy (Williams, 1996). 3ta as implemented in Carine and Scotland (1999, hereafter m3ta) and proposed by Scotland ([2000a]), only differs from 3ta of Nelson and Platnick (1991) in that all observations from all terminal taxa are available as evidence of sister group relationships, {although prior inferences with regard to character generality may result in the exclusion of certain homologues from the analysis (Scotland, [2000a]; Fig. 1).}

In Scotland and Carine's (2000) present treatment of the matrix of Fig. 2, for example, "exclusion of certain

homologues" means excluding all plesiomorphic states. In Carine and Scotland's (1999) view, quoted earlier, excluding plesiomorphic PH states—treating them as uninformative—was precisely the problem with N/P 3ta, and the modified method, m3ta, was introduced specifically to avoid that problem. Yet now exclusion of "general" states—the same thing under a different name—is supposed to be part of m3ta. In this argument, Scotland and Carine have tried to save "m3ta" from sensitivity to autapomorphy just by turning "m3ta" back into N/P 3ta.

RENDITIONS

But then what of the taxic assumption, which was supposed to justify lack-all X as an "outgroup" and to forbid excluding states? Scotland and Carine (2000) now do not mention that idea. While Carine and Scotland's (1999) Fig. 1D, discussed above, specifically showed that two PH states pick out two groups, Scotland and Carine's (2000) Fig. 1 now shows that only one of two PH states sets off a group if the other state is considered more general (plesiomorphic). Now both states are supposed to be informative only if generality is unknown.⁹ The taxic assumption has been abandoned.

Or rather, it has been eradicated, for Scotland and Carine (2000) go to great lengths to wipe out every trace of the taxic assumption. Whereas Carine and Scotland (1999, their Fig. 8) included lack-all node X in their tree diagrams, Scotland and Carine (2000, their Figs. 3C, 8B, and 8C; cf. our Figs. 5B and 5C) now omit X from diagrams of trees that are in fact X-rooted. Scotland and Carine even devise edited versions of Kluge and Farris' (1999) comments on the taxic assumption, using these to create the impression that those comments concerned some other subject. According to Scotland and Carine (2000)

The argument adopted by Kluge and Farris (1999: 208) rests on their claim that m3ta "directly contradicts evolution." In the case of hominoid evolution it would appear that it is the result of [parsimony] that conflict with the phylogeny of this group.

⁹Even this is illogical. Either of the groups might turn out to be supported, but this does not mean that they both are. But this problem does not affect our examples (below) of applying the revised method.

“Appear” would seem to be just the right word, but in any case, Kluge and Farris’ (1999, p. 208) observation pertaining to a contradiction did not concern m3ta, but rather the taxic assumption (*italics added*):

Writing of “clades” and “monophyly,” Carine and Scotland [(1999)] create the impression that theirs is a phylogenetic approach, but this is entirely misleading. Their approach is phenetic, and *their taxic assumption* directly contradicts evolution.

Nor was that contradiction a matter of accuracy in some example. Instead it arose directly from the taxic assumption (Kluge and Farris, 1999: 207; *italics added*):

The taxic choice of ((A B) (C D)) thus rests on a ruling out *a priori* [*italics in the original*] the possibility that either state has replaced (changed into, been substituted for) the other. If applied to nucleotide data, then, *the taxic assumption* would have the paradoxical implication that substitution could not have occurred at all!

Scotland and Carine (2000) also use editing to deal with Kluge and Farris’ (1999, p. 207f; braces and *italics added*) further discussion of that contradiction: they quote only the part within the braces:

Carine and Scotland might consider this reasoning inadmissible: it involves possible substitutions, whereas substitutions do not belong in their taxic view, but instead pertain to the transformational view. This does no good, however, for then *the taxic view simply amounts to ruling out substitution directly*, and phylogenetic interpretation of a taxic-based tree would still rest on a contradiction. Nor should this be surprising. {No one but a creationist could think it realistic to exclude transformational considerations from the process of grouping. Character patterns are the product of changes. It would be astonishing if trying to analyze those patterns, while ignoring this fact, did not lead to paradox.}

Carine and Scotland (1999) did not just ignore evolutionary change; their taxic view implied that evolutionary change is impossible. Now unwilling to acknowledge this, Scotland and Carine (2000) simply omit the part of the passage that identifies the problem. Or not quite *simply*, for they take this opportunity to change the subject again. Much as in the case of long branches, their comments do not address the taxic assumption, but instead suggest that parsimony is not suitable for phylogenetic analysis:

However, these criticisms [the braced part, just quoted] are at odds with Kluge’s recent pronouncement that “. . . if we discover tomorrow that all life is the product only of special creation, we can still do cladistics, operationally, in terms of summarizing the observed character generalities” (Siddall and

Kluge, 1997: 320). It seems therefore that in the context of disagreement with proponents of maximum likelihood, [parsimony] is about character generalities (Siddall and Kluge, 1997) but in the context of m3ta, it is “astonishing” to ignore the process of change (Kluge and Farris, 1999). If systematics is about change, then surely the rate of change is an important variable and the estimation of that rate, a model of character evolution, is necessary.

Considering their other views, it seems ironic that Scotland and Carine’s (2000) reasoning concerning rates rests on an evolutionary assumption and an ill-founded one at that. The use of rate estimates in likelihood methods is invariably based on homogeneity assumptions, that is, on the premises that the relative rates of any two characters are the same in all parts of the tree and that all characters’ rates are drawn from the same distribution (see Farris, 1999). Such assumptions are plainly unrealistic; likelihoodists have adopted them only for computational convenience. If the likelihood principle is applied without making homogeneity assumptions, likelihood turns out to be equivalent to parsimony, as Tuffley and Steel (1997) have demonstrated.

That result, it may be added, corresponds closely in effect—though not in method of proof—to Farris’ (1983, 1986; cf. Farris and Kluge, 1985, 1986; Farris, 2000c) demonstration that most parsimonious trees have greatest explanatory power, that is, they are best able to explain observed similarities among organisms as the result of inheritance. As this advantage of parsimony has often been pointed out in discussion of 3ta (Kluge, 1993; Farris *et al.*, 1995; Farris, 1997; Farris and Kluge, 1998), it seems remarkable that Scotland and Carine (2000) have remained unaware of it.

No better founded is Scotland and Carine’s (2000) interpretation of Siddall and Kluge’s (1997) comment. Of course it is true, as Siddall and Kluge noted, that parsimony can be used descriptively, and indeed it has great advantages in that application, a fact that has been useful in refuting pheneticists’ attempts to attack phylogenetic systematics (see Farris, 1979, 1980, 2000b). That a descriptive application is possible, however, certainly does not mean that parsimony does not have a phylogenetic interpretation, as has just been seen. This is in strong contrast to the taxic assumption, which would make phylogenetic interpretation contradictory. As Scotland and Carine (2000) do not wish to address that contrast, they create a diversion by suggesting

that phylogeneticists (or at least Kluge) do not actually want to study phylogeny. A few lines later, they produce more “evidence” to that effect (the italics are theirs):

The extent to which accuracy is a goal of [parsimony] however, remains unclear. Siddall and Kluge (1997: 319) stated that “[i]n phylogenetics, however we are not interested in some abstract generality regarding the group of taxa we are working with. We are concerned with uncovering the actual spatio-temporally *real history of divergence, the species genealogy*” [our italics]. Whilst this is in contrast to Kluge (1995: 77) who argued “. . . accuracy as it pertains to knowing the truth is not an obsession of cladists,” it is evident from Kluge and Farris (1999) that in the context of the debate surrounding 3ta, issues relating to phylogenetic accuracy are paramount.

That “truth is not an obsession of cladists” represents another of Scotland and Carine’s (2000) exercises in editing, as is seen from Kluge’s (1995, p. 77) discussion:

Generally in science explanatory power is understood to be a function of theory conforming to observation, and in phylogenetic systematics the theory is inheritance and the observation is a novel trait shared by two or more groups of organisms. Thus, it is the most parsimonious cladogram that maximally explains shared-derived similarity as due to inheritance, i.e., synapomorphy as homology. Of course, providing such an explanation is no guarantee of accuracy, but then accuracy as it pertains to knowing the truth is not an obsession of cladists. Cladists focus on discovering the most rigorously tested and highly corroborated phylogenetic hypothesis, and that is why they seek the most parsimonious cladogram.

If further clarification is needed (Kluge, 1997, p. 92):

Scientists do not actually seek the truth, because truth is unknowable. Scientists do, however, attempt to approach some unattainable objective truth, and do so by critically evaluating different explanations. Hypotheses can never be proven true, as inductivists seek to do, nor be proven false, as deductivists claim to be able to do; however, they can be found to be more or less corroborated.

But Scotland and Carine (2000) do not seem interested in having this point clarified. That would conflict with using their rendition of “Kluge’s” views as one of their closing arguments:

We agree with Kluge (1995) in that accuracy as it pertains to knowing the truth is not a concern of cladists. Phylogenetic accuracy is not the goal or aim of m3ta.

Given their method of argument, one can only wonder why they do not declare Darwin and Hennig creationists as well.

REVERSALS

Diversions aside, the taxic assumption has vanished, and by employing an outgroup with real states, Scotland and Carine’s (2000) revised “m3ta” (rm3ta) avoids some of X-rooted m3ta’s tendency to group by sympleiomorphy. Their revised approach does not entirely avoid the problem of sympleiomorphy, however, as can be seen by recalling Kluge’s (1994) example of Fig. 1. The original point of that example was that, unlike parsimony (Fig. 1A), N/P 3ta fails to recover groups whose synapomorphies are reversals. The N/P 3ta tree (Fig. 1B) lacks groups (I(J K)), which are distinguished by the 0 or c states of I–K in the matrix. The taxa sharing the reversals are displaced down the tree, so that they form a paraphyletic group—one based only on sympleiomorphy.

Carine and Scotland (1999) used that example to argue for m3ta. The consensus of X-rooted m3ta trees (Fig. 1C; cf. their Fig. 8) did have (I(J K)), and Carine and Scotland (1999, p. 128) considered the reversal problem solved:

Kluge (1994: 408) asserts that t.t.s. analysis [N/P 3ta] distorts the “. . . phylogenetic informativeness of evolutionary reversals. . .” However, both the modified t.t.s. analysis [m3ta] and the standard cladistic analysis [parsimony] recover the clades (IJK) and (JK).

But with the latest revision, the reversal problem resurfaces. Using Kluge’s outgroup O “for assessing character generality,” the consensus of rm3ta trees is Fig. 1B, the same result obtained from N/P 3ta (fractional weighting makes no difference in this case). Like N/P 3ta, rm3ta does not recover the groups in question, but instead groups by sympleiomorphy.

This difficulty arises from a well-known (Kluge, 1993, 1994; Deleporte, 1996; De Laet, 1997; Farris, 1997; De Laet and Smets, 1998; Farris and Kluge, 1998) characteristic of N/P 3ta, that the three-taxon statements (3ts) used in that method reflect only similarities in the state initially taken as apomorphic. Reversals are apomorphies (Hennig, 1966, p. 95):

For example, the absence of the wings in fleas is undoubtedly an apomorphous character in comparison with the presence of wings in other holometabolic insects. On the other hand, the possession of wings is an apomorphous character in comparison to their absence in the so-called ‘Apterygota.’

They are not known as such initially, however, but

must be discovered by phylogenetic analysis. When a reversal has occurred, a method such as N/P 3ta or rm3ta will continue to group by the state initially assumed apomorphic, and this is actually grouping by symplesiomorphy, for in these circumstances that state is plesiomorphic relative to the reversal.

That example of Hennig's involves an absence, or loss, and Carine and Scotland (1999, p. 125) argued against applying losses as synapomorphies:

'The absence of a character is not a character' (Nelson, 1978: 340); absence can never provide evidence of systematic relationship.

Their position had two weaknesses. First, it depended on their taxic view, that is, on denying evolutionary change, for they explained (same page):

From a transformational perspective these data support clades (JK) and (JK). The result of the [parsimony] analysis (Fig. 4) [see our Fig. 1A] which recovers these clades is consistent with a transformational view of homology, whereas the [N/P 3ta] result (Fig. 5) [see our Fig. 1B] is not consistent with this view because it does not recover these clades.

Second, their argument applied specifically to presence/absence (CR) data; in that passage they took (as Kluge did not) the 0 states of Fig. 1 to be absences. Even if their nonevolutionary reasoning were accepted, consequently, it would provide no excuse for treating reversed PH characters incorrectly. But that is just the mistake that rm3ta (Fig. 1B) makes with the PH c/g version of Kluge's matrix (Fig. 1).

Siebert and Williams (1998, p. 343) found another way to object to that example. In their view, the example did not illustrate the effects of reversal on N/P 3ta, because the N/P 3ta tree (Fig. 1B) was *really* the same as the most parsimonious tree (Fig. 1A):

The analysis of Table 2 in Kluge (1994) is also incomplete: Interpretation 2 (Nelson and Platnick, 1980) of multiple branching allows the [parsimony] solution.

The most parsimonious tree, they meant, could be obtained by applying interpretation 2 to the N/P 3ta tree, but in fact (Farris and Kluge, 1998, p. 351):

Interpretation 2, again, is a rule concerning ways of resolving multifurcations. Obtaining the most parsimonious tree (Fig. 1A) from the 3ta tree (Fig. 1B) would require *inter alia* moving terminal I inside the FGH group. Interpretation 2 does not cover such a move, since terminal I is not involved in a multifurcation.

Nor was there any basis for Siebert and Williams' (1998)

supposition that interpretation 2 is related to 3ta (Farris and Kluge, 1998, p. 350):

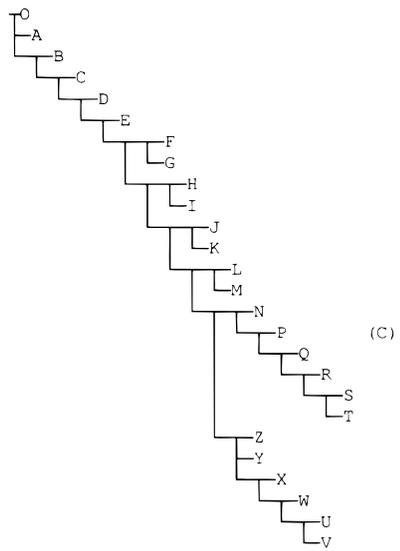
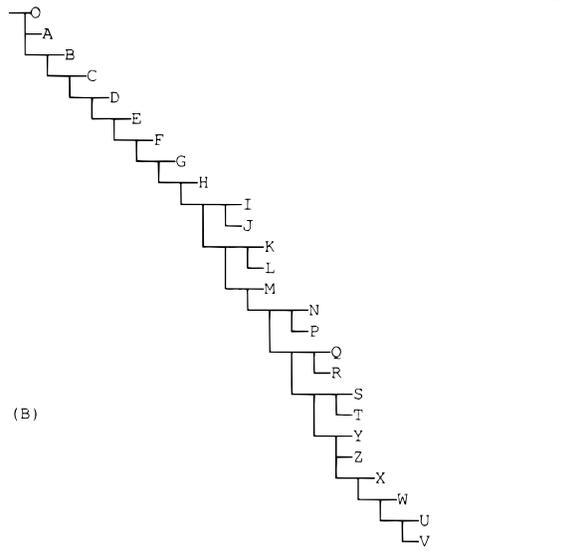
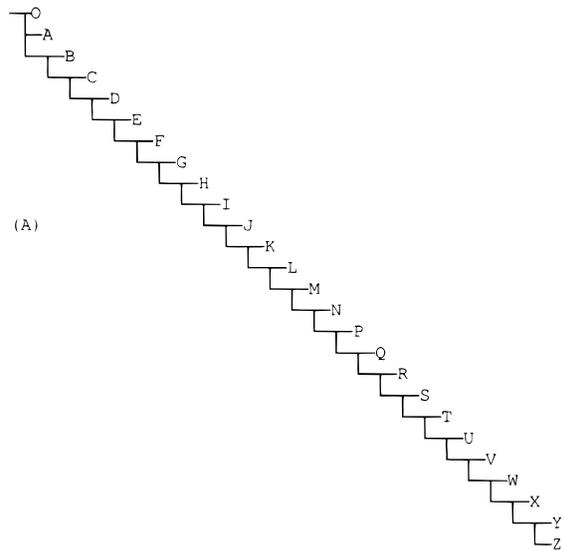
The distinction between interpretations 1 and 2 not only does not align with that between parsimony and 3ta, it is not even the same kind of distinction. Parsimony and 3ta are different ways of choosing among trees on the basis of character data. Nelson and Platnick's (1980) interpretations are rules for resolving multifurcations on given trees. They concern trees only as abstract diagrams, not the connection of trees to characters.

Farris and Kluge (1998; cf. Farris, 1997) explained these points in detail, but there seems to be no need to expand on this subject here, for in their more recent advocacy of 3ta, Williams and Siebert (2000) no longer mention interpretation 2. Neither do Williams and Siebert (2000) mention this example, and the omission seems noteworthy, inasmuch as they devote a section of their paper ("Three-item examples revisited," pp. 200–204) to what gives the impression of being a reexamination of examples published between 1991 and 1997.¹⁰

A still more revealing example of the effects of reversal in PH characters is seen in Fig. 8, which is adapted from Farris and Kluge's (1998) Fig. 5. In this case, deeply nested apomorphies make it obvious that the cs of V–Z are reversals, and it is then easily seen that these provide synapomorphies for a nested series of monophyletic groups (V(W(X(Y Z)))), as in the most parsimonious tree (Fig. 8A). The fractionally weighted rm3ta tree (Fig. 8B), in contrast, turns that series upside down and moves the whole assemblage below terminal U, so that all those groups become paraphyletic:

¹⁰Williams has subsequently discussed Kluge's (1994) example of Fig. 1, however, in a presentation at the 1999 meeting of the Willi Hennig Society (subsequently, because Williams and Siebert's [2000] paper was presented at an earlier meeting of the Systematics Association). For the matrix of Fig. 1 and several similar matrices, Williams emphasized, the taxa showing the reversals are moved down the tree with N/P 3ta but not with parsimony, a fact that he took to reflect 3ta's superior precision and sensitivity. This makes an interesting contrast with Siebert and Williams' (1998) insistence that 3ta really gives the parsimony result, which (if true) would mean that 3ta does *not* move the reversed taxa down the tree in this example. This history is much like that of 3ta's incompatibility with evolution, a flaw that Platnick (1993) would not admit, but a feature on whose benefits Carine and Scotland (1999) insisted. When a drawback of 3ta is first pointed out, advocates of 3ta always deny it, then avoid any mention of the matter when the denial cannot be maintained. If they ever do mention the subject again, it will be only after the drawback has been reinterpreted as an advantage.

O cccccccccccccccccccccccc
 A cccccccccccccccccccccccc
 B gccccccccccccccccccccccc
 C gggcccccccccccccccccccc
 D ggggcccccccccccccccccccc
 E gggggcccccccccccccccccccc
 F ggggggccccccccccccccccccc
 G gggggggcccccccccccccccccc
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 J ggggggggggccccccccccccccc
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 Q gggggggggggggggcccccccccc
 R ggggggggggggggggcccccccccc
 S gggggggggggggggggcccccccccc
 T ggggggggggggggggggcccccccc
 U gggggggggggggggggggggggggg
 V cccggggggggggggggggggggggg
 W cccggggggggggggggggggggggg
 X cccggggggggggggggggggggggg
 Y cccggggggggggggggggggggggg
 Z cccggggggggggggggggggggggg



(Y Z(X(W(V U))))). The unweighted rm3ta tree (Fig. 8C) shows the same problems, but compounds them further by displacing all those taxa below terminal N, thus creating even more paraphyletic groups.

Those paraphyletic groups illustrate how rm3ta can group by symplesiomorphy instead of synapomorphy, but the same trees also show another, even more peculiar effect. In these examples rm3ta manufactures whole series of groups—IJ, KL, NP, QR, and ST in Fig. 8B, and FG, HI, JK, and LM in Fig. 8C—that do not seem to correspond to anything in the data. These terminals are not involved in the reversals; evidently with rm3ta reversals can have side effects. It is not just that rm3ta does not recognize groups whose synapomorphies are reversals, the grouping of other taxa can be distorted as well.¹¹

HOMOLOGY

While they have abandoned the taxic assumption, Scotland and Carine (2000) still wish to identify their views with Patterson's (1982) taxic approach, and so now they need new grounds for making a connection. They decide on Patterson's tests of homology:

Thus, Table 1 illustrates an important distinction between [parsimony] and 3ta: the latter is consistent with Patterson's tests whereas the former is not.

That does not prove a very good choice. Despite that plural "tests," Scotland and Carine's Table 1 shows no difference between 3ta and parsimony with respect to the similarity test. The tabulated difference concerns only the congruence test—and "Patterson's" congruence test is not actually Patterson's (1982, p. 74)

¹¹This peculiar effect also arises with four-taxon analysis (for which see De Laet, 1997). It seems to be a general feature of methods that work by breaking the data into tuples of taxa.

Since the manuscript of this chapter was submitted in May 1980, I have realized that E. O. Wilson's [(1965)] "Consistency test for phylogenies" is a more rigorous formulation of my congruence testing of homologies, described on p. 38. I failed to appreciate this earlier because Wilson's paper ostensibly concerns phylogeny, whereas I was investigating homology.

The idea of "Patterson's" test is just that characters are incongruent when they distinguish conflicting (overlapping, yet not nested) groups. In addition to Wilson (1965), that concept was described by Hennig (1966, pp. 123–127), and again by Le Quesne (1969). It had long been common knowledge by the time that Patterson started using it.¹²

Nor is Scotland and Carine's (2000) method based on Patterson's (1982) use of that that idea. In Patterson's approach (discussed further below), the distribution of a state among taxa defined a group directly, so that incongruence between characters was the same thing as logical incompatibility between groups. Three-taxon statements are not used to define groups in that way, and while one *could* assess incongruence between 3ts, Scotland and Carine do not do so. Instead they are concerned with fit of 3ts to trees:

The table demonstrates that in 3ta a given three-taxon statement derived from a homology proposition that passes the similarity test either fits a tree as evidence of relationship or fails to fit the tree. The test of homology implemented in 3ta is therefore consistent with Patterson's (1982) tests of homology. 3ta thus provides a test for discriminating homology from non-homology.

Scotland and Carine's claim of a connection with "Patterson's" congruence test is merely gratuitous.¹³ Their

¹²Scotland and Carine's (2000) attribution of this idea to Patterson is reminiscent of Kitching *et al.*'s (1998) attempt to call outgroup rooting "taxic" (see Farris, 2000a). So redesignating procedures already in wide use seems to be the primary means of developing "taxic" methods.

¹³It would appear that Scotland and Carine (2000) are not actually acquainted with this test. Although both Scotland (2000a) and Scotland and Carine (2000) appeal to the congruence test, neither paper discusses the operation of the test, and Scotland (2000b, p. 498) thinks that the test "remains to be accurately described!"

FIG. 8. Matrix illustrating reversal in PH characters. The entries are nucleotide codes for selected sites. The outgroup O is supposed to have plesiomorphic states for the characters shown. Note that here X is a terminal with states, not a lack-all node. (A) Most parsimonious tree. (B) Fractionally weighted rm3ta tree. (C) Unweighted rm3ta tree.

position actually consists of no more than their contention that 3ta discriminates homology from nonhomology on a tree, whereas—they say—parsimony does not.

Yet even so simplified, Scotland and Carine's (2000) position claims more than their Table 1 establishes, for that table merely represents what might be called a play on levels of specificity. A given 3ts either fits a given tree or does not, so that 3ts fit is "exact." In contrast, a normal character that admits of more than one extra step need not show either perfect fit or complete lack of fit, but may show intermediate amounts of homoplasy, called "not exact" in the table. But 3ta's exactness in this sense is maintained only by mentioning just one 3ts at a time. A normal character typically represents a much larger amount of information than a single 3ts. If one were to assess 3ta fit for a comparable amount of information, for example, by counting how many of the 3ts obtained from a normal character conform to a tree, 3ta could also show various levels of imperfect fit, and then 3ta would be "not exact." For example, both A(FG) and K(BC) are 3ts obtained from the second character of the matrix of Fig. 1. A(FG) fits the rm3ta (or N/P 3ta) tree of Fig. 1B, but K(BC) does not.

On the other hand, more specific statements of homology can easily be addressed in parsimony analyses. In a parsimony analysis, a point of similarity between two terminals is taken as homologous just when it can be attributed to inheritance from a common ancestor, and the latter in turn is easily established by inspecting the reconstructed states of stem species, as provided by character optimization (Farris, 1970). Continuing with the second character of Fig. 1, on the most parsimonious tree (Fig. 1A) the similarity between J and K is definitely homologous, as the c state which they share would also be found in their common ancestor. The similarity between D and E is likewise homologous, as the g state is found in all the stems lying between them, and there are many more such pairs. In contrast, the similarity between A and K in state c is definitely not homologous, because several of the stems lying between those terminals have state g instead. Scotland and Carine's (2000) contention that parsimony does not assess homology is thus entirely vacuous, being based on nothing but ignoring this well-known procedure.

Their claim that 3ta does assess homology is little

better, for in fact 3ta systematically excludes some homologies. In the example of Fig. 8, the c states shared by V–Z obviously comprise homologous similarities on the most parsimonious tree (Fig. 8A). Yet even if that tree is used, rm3ta (or N/P 3ta) cannot count those similarities as homologous: no 3ts that fits that tree corresponds to any of those similarities. This happens because those similarities, while in fact apomorphic, are in the state initially taken as plesiomorphic. Nor is this omission of homologies the only difficulty with 3ta's assessment. Scotland and Carine's interpretation of fit of a 3ts to a tree as meaning homology can itself lead to contradictory conclusions.

Such contradictions are easily found for the plesiomorphy-free 3ts used in Carine and Scotland's (1999) m3ta. An example is seen in Fig. 9A, which is based on Tree 1 of Farris *et al.* (1995, their Fig. 2).¹⁴ (The tree is supposed to be established by other characters, not figured.) 3ts A(UZ) fits the tree, so that the c state

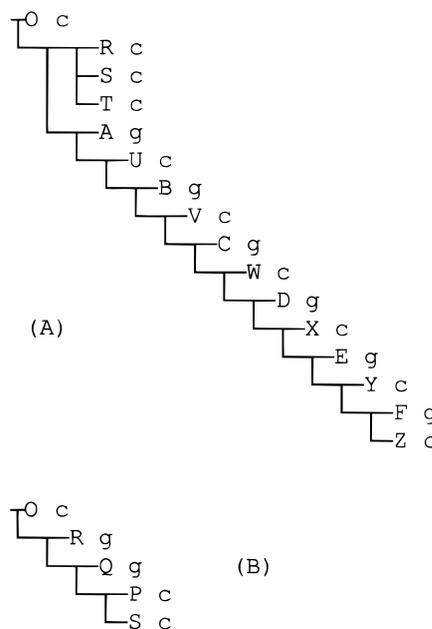


FIG. 9. Two trees illustrating contradictory conclusions of homology in 3ta, as explained in the text. Uppercase letters are terminal names, while lowercase letters are nucleotide codes, all for the same site. The outgroup O is supposed to have the plesiomorphic state. Note that in tree (A) X is a terminal with state c, not a lack-all node.

¹⁴Farris *et al.* (1995) took this example from Platnick (1993, his Cladogram 1)—who thought that it favored 3ta!—but it was originally devised by Dr. P. Goloboff.

shared by Z and U would be taken as homologous resemblance, and this would mean that all the stem species between Z and U must have possessed state c as well. But 3ts U(BF) also fits the tree, implying homology for the g states shared by F and B and thus that all the stems between F and B had state g. Yet according to A(UZ), all those same stems had state c instead.

A similar type of contradiction can arise in N/P 3ta and rm3ta because of 3ts P(QR) as used in those methods implies both that the apomorphic resemblance between Q and R is homologous and that the plesiomorphic resemblance between P and the outgroup is homologous. In Fig. 9A, 3ts R(AF) fits the tree, so that the g state found in A and F would be taken as homologous resemblance, in which case all 11 of the stem species between A and F must have had state g. But X(EF) also fits the tree, and if the plesiomorphic state c of X is homologous with that of O, then all the ancestors of X must have had state c. That, however, includes 8 of the 11 stem species that—according to R(AF)—must have had state g instead.

Although Farris *et al.* (1995; cf. De Laet, 1997; Farris, 1997) presented a similar example, Scotland and Carine (2000) make no attempt to address this difficulty. But Williams and Siebert (2000, p. 200) offer an objection:

In other words, three-item statements do not conform to the usual kind of optimization. . . . The attempts by Farris *et al.* [(1995)] to consider ambiguous optimizations of three-item statements in the same fashion as standard characters misses the point (as does Kluge, 1993: 250; Kluge, 1994: 405; Deleporte, 1996). In short, optimization is irrelevant to the result, notwithstanding De Laet's (1997: 58–63) efforts to 'correct' the problem.

It is a curious objection, for optimization—Farris' (1970) method for reconstructing the states of stem species—has no connection with the example. While the example does involve states of stem species, those states are not calculated by optimization, but are instead deduced from Scotland and Carine's premise that fit of a 3ts to a tree indicates homology. The point of the example is that accepting that premise can lead to contradictions.

Williams and Siebert's (2000) belief that optimization is used in that example seems particularly curious on recalling that Farris *et al.* (1995, p. 216f) were careful to make this point clear:

It is important to note that the present discussion does not rely on standard optimization. The conditions attributed here to

stem species are just those that follow logically from the premise that a three-taxon statement is explained by inheritance and common ancestry. The point of making those deductions is simply to show that explanations of accommodated statements may be mutually exclusive, which is to say that what 3ta counts does not measure explanation.

Explanation of similarity by inheritance, that is, which is to say homology. It would appear that Williams and Siebert's (2000) view arises only from lack of familiarity with Farris *et al.*'s (1995) paper.

Platnick *et al.* (1996, p. 249) proposed to rescue 3ta from that example in another way, by maintaining that fit of P(QR) to a tree corresponds just to homologous resemblance between Q and R, regardless of whether the plesiomorphic resemblance between P and the outgroup is homologous. That must be true, they declared, because

. . . the notion that plesiomorphies require explanation is simply not a cladistic idea. . . . the fact that both lice and ticks lack spinnerets is no more in need of explanation than the fact that they lack mammary glands, or the fact that they lack Cadillac engines in their stomachs.

If it could be justified, however, their position would undermine 3ta, for it is not compatible with 3ta's assessment of fit. This is illustrated by the case of 3ts P(QR) on the tree of Fig. 9B. If the putatively plesiomorphic c state shared by O and P is allowed to be homoplastic, this tree is consistent with a single origin of—homologous resemblance in—the assumed apomorphic state g shared by Q and R,¹⁵ so that this case would conform to Platnick *et al.*'s concept. But according to 3ta, 3ts P(QR) does *not* fit this tree. If correct, consequently, Platnick *et al.*'s (1996) view would mean that 3ta counts homologies incorrectly.

UNITS

Since the purpose of Scotland and Carine's (2000) discussion of homology was to create the impression that three-taxon approaches follow from Patterson's views, it seems relevant to point out that Patterson (1980, 1982, 1988, 1994) expressed no such opinion. On

¹⁵Attribute state g to the stems of (RQPS) and of (QPS). This requires that the c state of (PS) originate separately from that of O, but according to Platnick *et al.*'s (1996) view this does not matter.

the contrary, 3ta conflicts with Patterson's own method.

That is not how Scotland and Carine (2000) present the matter:

Analysis of the m3ta matrix for these data [Brown *et al.*'s (1982)] yields a single minimal tree (Fig. 8b) (Scotland, [2000a])... The same tree was found by Patterson (1988) using an electric form of compatibility analysis.

That was what Patterson (1988, his Fig. 4A) called his pattern analysis, but in fact the best tree according to that method was like that of Scotland and Carine's (2000) Fig. 8C (see our Fig. 5C), not their Fig. 8B (see our Fig. 5B). To see how such discrepancies can arise, consider (as Scotland and Carine do not) how Patterson's pattern analysis (ppa) operates.

In ppa the tree is selected to maximize the number of states that fit it, a state being considered to fit a tree when the terminals showing the state comprise one of the groups of the tree (cf. Patterson, 1980, 1988). For PH data, plesiomorphic as well as apomorphic states are counted; that is, the two are not distinguished, for in Patterson's (1988, p. 76) view

... it is not necessary to polarize characters, or to sort them into primitive and derived, to find a cladogram that is unambiguously rooted.

Technically, after all, phenograms are rooted trees. Much as with X-rooted m3ta, ppa can produce groups based on symplesiomorphy when data are non-clocklike enough (cf. Nayenizgani, 1990). This is seen with the data of Fig. 2, for which ppa (Fig. 10A) displaces divergent H to the base of the tree, creating a whole series of paraphyletic groups. For Wheeler *et al.*'s (1993) data, ppa (Fig. 10B) similarly displaces divergent whip-spider *Nephila*, so breaking up Araneae, Chelicerata, and Arthropoda (cf. Figs. 4 and 7B). In this respect, that result resembles the unweighted m3ta tree (Fig. 7A).

Yet while ppa shares some of the drawbacks of m3ta, it is not the same method, for the two procedures work with different units, one counting 3ts while the other counts whole states. That difference can and does lead to disparities in results, as is immediately seen by comparing the m3ta tree (Fig. 2C) with the ppa tree (Fig. 10A) for the data of Fig. 2. There are even greater discrepancies between the unweighted m3ta tree (Fig. 7A) and the ppa tree (Fig. 10B) for Wheeler *et al.*'s

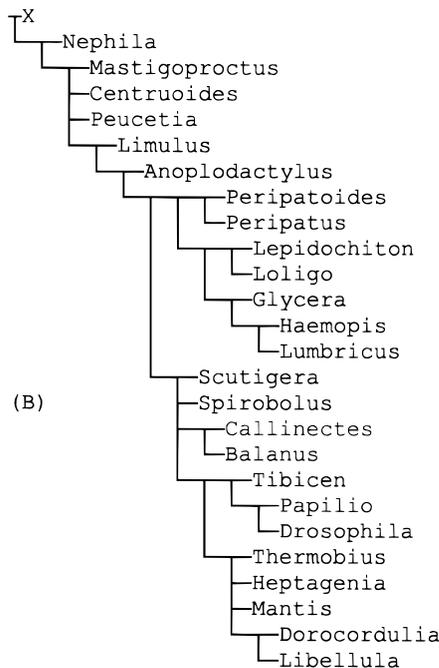
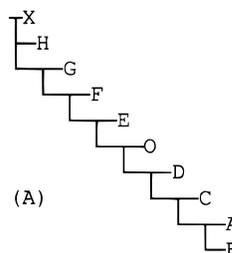


FIG. 10. Trees calculated by Patterson's (1980, 1988) method. (A) For the data of Fig. 2. (B) For the data of Wheeler *et al.* (1993) with *Trilobita* omitted (consensus of multiple trees).

(1993) data. Unsatisfactory as its placement of *Nephila* is, ppa at least avoids removing *Drosophila* from Insecta.

Three-taxon statements, then, cannot be blamed on Patterson.¹⁶ Nor is that the only respect in which

¹⁶This, however, is the only useful feature of Patterson's views. Not only does ppa require a clock assumption, it counts only characters that fit the tree perfectly. In the latter respect it resembles clique methods (concerning the faults of which see Farris, 1983, 1986, 2000; Farris and Kluge, 1979, 1985, 1986, 1997). That strategy discards most of the information in the data in all but the simplest cases. It would be particularly unsuitable for large molecular data sets such as those studied by Källersjö *et al.* (1999), in which it is precisely the more homoplastic characters (sites) that contribute most of the phylogenetic structure.

Scotland and Carine (2000) depart from Patterson's position. Patterson (1988, p. 76), again, did not wish to exclude plesiomorphic similarities:

... it is not necessary to polarize characters, or to sort them into primitive and derived, to find a cladogram that is unambiguously rooted.

In order to rationalize rejecting it, accordingly, Patterson (1982, p. 52) misrepresented outgroup comparison:

Further, this method does not seem to differ from in-group comparison: a homology is recognized, and unless it is secondarily missing, it will define a monophyletic group. In-group and out-group comparison turn out to be the same thing. . .

And (Patterson, 1988, p. 74)

Outgroup analysis is still subject to the charge of circularity (Colless, 1984).

Yet Scotland and Carine (2000) now exclude plesiomorphic ("general") states in rm3ta, and they use outgroups to do so, resolving that discrepancy with Patterson's views by simply not mentioning it. While Patterson's phenetic version of "cladistics" no doubt provided the inspiration for Carine and Scotland's (1999) use of the taxic assumption, Scotland and Carine's (2000) present contention that their approach is like Patterson's means only that they are unwilling to admit that they have abandoned their old position.

REASONS

Although both characteristics are well known as drawbacks of N/P 3ta, Scotland and Carine (2000) never mention that rm3ta can fail to apply reversals as apomorphies or that any kind of 3ta can yield contradictory conclusions on homology. It is a crucial omission, for those problems directly undercut Scotland and Carine's primary justification for their method:

Classifications have been described as a hierarchy of homology (Rieppel, 1988) and 3ta (three-taxon statement analysis) is a method of data analysis which seeks to maximize the information content of taxic homology propositions for the purpose of constructing classifications. For the purposes of analysis, 3ta maximizes propositions of homology, in the form of accommodated three-taxon statements such that the minimal (optimal) tree contains the maximum amount of homology.

What rm3ta (or N/P 3ta, or m3ta) counts cannot be taken as an amount of homology, as it can include mutually contradictory propositions. Nor could it represent a complete assessment of homology, since rm3ta (like N/P 3ta) systematically fails to recognize homologous resemblance among reversed states.

The rest of Scotland and Carine's (2000) position is no better. They say that their ideas are based on Patterson's (1982), but there is actually no connection beyond a shared dislike of evolution, and in any case they never even attempt to explain why one should accept Patterson's views (or their own) in preference to scientific ones like Hennig's (1966). Nor do they ever explain why one should count three-taxon statements, instead of something else, when calculating a tree. Their reasoning seems to consist mainly of the hope that, if only classification could be separated from phylogeny, then suddenly it would be acceptable to place fruit flies next to barnacles.

But Scotland and Carine (2000) have one last argument:

We agree with Platnick (1979) who argued that our knowledge of phylogeny largely stems from what we know about classification.

They think that this supports their approach, but in that they are mistaken.¹⁷ If knowledge of phylogeny has been gained in that way, this can only have been accomplished by interpreting systematic results phylogenetically, in which case those results must have been logically capable of such interpretation. Most parsimonious trees can be so interpreted, and in view of parsimony's connection with explanatory power and corroboration (Farris, 1983, 2000c; Kluge, 1995, 1997), they are ideally suited to that purpose. The same can hardly be said for methods that would imply contradictory assessments of "homology."

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¹⁷Sneath (1988, p. 262) tried the same argument: "Evolution was inferred from the classification, not *vice versa*." He thought that it would justify phenetics (cf. Nayanizgani, 1990).

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