



# On the TTSC–FTSC Formulation of Standard Parsimony

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Standard parsimony analysis has recently been described in a “three-taxon-like” way (the three-taxa statements for contiguous series–four-taxa statements for contiguous series, or TTSC–FTSC procedure) in order to clarify the differences between the standard approach and three-taxon analysis. It is shown that the alleged equivalence of standard parsimony analysis and the TTSC–FTSC procedure does not hold. Some minor defects of the procedure can be fixed within the TTSC–FTSC logic, but no solution is available for two basic problems: (1) the elementary three-taxon-like statements of the TTSC–FTSC procedure are highly artificial; and (2) the equivalence with standard parsimony depends on an incomplete correction for nonindependence between these statements. However, these findings do not invalidate the reported superiority of standard parsimony as a method for biological systematics. © 1998 The Willi Hennig Society

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## INTRODUCTION

Deleporte (1996) recently described the TTSC–FTSC procedure (three-taxa statements for contiguous series–four-taxa statements for contiguous series) and claimed that it exactly reproduced, in terms of elementary three-taxon-like statements, the standard parsimony logic for testing cladograms (Deleporte, 1996: 274, 279). Using this three-taxon-like formulation of the standard approach as a means to analyse

the differences between standard parsimony analysis (e.g. Farris, 1983) and three-taxon analysis (Nelson and Platnick, 1991), Deleporte’s main conclusion was that the standard approach is logically superior to three-taxon analysis as a method of biological systematics. However, as shown in this paper, the TTSC–FTSC procedure is not equivalent to standard parsimony analysis, which might invalidate this conclusion.

We will first discuss the underlying logic of the TTSC–FTSC procedure, which will then serve as a framework to explain why standard parsimony and the TTSC–FTSC procedure are not equivalent. At the same time we will investigate whether slight modifications and/or extensions of the TTSC–FTSC logic might suffice to obtain the claimed equivalence, and we conclude that this is not the case. Lastly, we will examine whether the lack of equivalence between the TTSC–FTSC procedure and standard parsimony affects Deleporte’s (1996) additional argumentation in favour of the standard approach.

## THE UNDERLYING LOGIC OF THE TTSC–FTSC PROCEDURE

In standard parsimony analysis, the best trees are those that minimize homoplasy for the data at hand (Farris, 1983). Deleporte (1996) did not explicitly state the logic he followed to develop a three-taxon-like

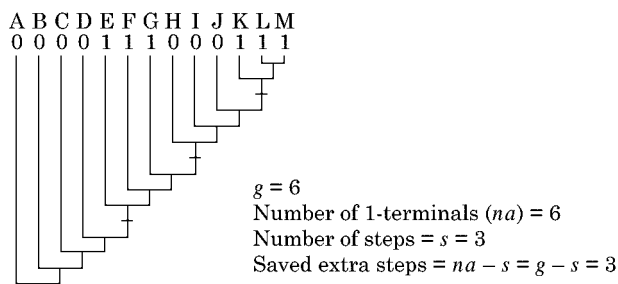


FIG. 1. Paraphyletic group EFG requires two steps, which is one less than the number of 1-terminals it contains; monophyletic group KLM requires a single step, which is two less than the number of 1-terminals it contains. Compared to an independent origin of state 1 in all 1-terminals, this yields a total of three saved extra steps.

formulation of this standard optimality criterion. However, because this underlying logic provides an accurate framework within which to discuss and evaluate the TTSC–FTSC procedure, its examination is worthwhile. For our purpose it can be reconstructed as follows.

First consider the idea of saved extra steps. Assume a polarized binary character without missing entries and with character state 1, the apomorphic state, present in  $na$  terminals (the 1-terminals; the terminals with state 0 are referred to as the 0-terminals). If all  $na$  1-terminals have developed their state independently, the explanation of the character-state distribution requires  $na$  steps on any cladogram. However, when common descent is taken into account, particular configurations of 0-terminals and 1-terminals require less steps than the number of 1-terminals that are present in the configuration. The difference between the number of 1-terminals and the required number of steps when common descent is considered is called “saved extra steps” (Deleporte, 1996: 275).

This is illustrated in the cladogram and the character of Fig. 1. There are two step-saving configurations: the monophyletic group of 1-terminals K, L and M; and the paraphyletic group of 1-terminals E, F and G. The monophyletic group, consisting of three taxa, can be explained by a single step and therefore there are two saved extra steps; the paraphyletic group, consisting of three taxa, can be explained by two steps, yielding a single saved extra step. The number of steps under the standard parsimony criterion ( $s = 3$ ) is then obtained as the difference between

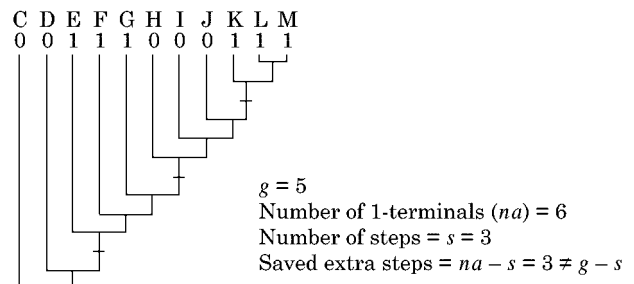


FIG. 2. The number of saved extra steps is not necessarily equal to that part of the maximum possible homoplasy in the character that is not realized on the cladogram.

the total number of 1-terminals and the total number of saved extra steps. Note that in this example the number of 1-terminals is equal to  $g$ , the length of the character on an unresolved tree (Farris, 1989). As a result the total number of saved extra steps is equal to that part of the maximum possible amount of homoplasy in the character ( $g - m$ ; Farris, 1989) that is not realized on the cladogram: the number of saved extra steps equals  $g - s$ . However, this is only true because the number of 1-terminals does not exceed the number of 0-terminals. An example where less than half of the terminals have the plesiomorphic state is presented in Fig. 2.

Deleporte (1996: 275) observes that the best trees under standard parsimony are those trees that maximize the total number of saved extra steps as defined above. Using this observation and the idea of step-saving configurations, the underlying logic of Deleporte’s derivation of the TTSC–FTSC procedure can be reconstructed as follows.

1. Catalogue all possible step-saving configurations into a limited number of types, each with a specific number of saved extra steps.
2. Define for each type of configuration a type of elementary three-taxon-like statement such that the number of saved extra steps in the configuration equals its number of supported three-taxon like statements.

This two-step procedure results in a three-taxon-like formulation of the standard approach only if the classification of step-saving configurations satisfies the two following conditions.

- 1a. Any tree and character can be decomposed

into configurations of these types; this condition ensures general applicability.

1b. The total number of saved extra steps in the character on the tree is obtained as the sum of the saved extra steps in each of the constituent configurations (i.e. there are no step-saving interactions between configurations); this condition ensures that each configuration type can be treated independently in the second step (as is the case in the TTSC–FTSC procedure).

We show below that, according to one’s point of view, the TTSC–FTSC procedure satisfies either the first or the second condition, but not both conditions simultaneously. Deleporte’s (1996) classification of configurations will be extended to satisfy both conditions, but the extension will be of little help because the TTSC–FTSC procedure is also deficient in the second step.

## STEP-SAVING CONFIGURATIONS

### TTSC–FTSC Procedure

In the TTSC–FTSC procedure, only two types of step-saving configurations are considered (Deleporte, 1996: 276, 278–279).

Type A. Monophyletic groups of 1-terminals, such as component KLM in Figs 1 and 2; a type A configuration with  $p$  1-terminals yields  $(p - 1)$  saved extra steps.

Type B. Paraphyletic series of at least three contiguous 1-terminals, such as taxa E, F, and G of Figs 1 and 2; a type B configuration with  $q$  1-terminals yields  $(q - 2)$  saved extra steps.

The term “series” usually implies pectinate grouping and therefore, strictly speaking, the paraphyletic group of 1-terminals C–I in Fig. 3 is not covered by the TTSC–FTSC logic. However, this is only a minor problem which is easily overcome by a slight redefinition of type B configurations as paraphyletic groups (instead of series) of 1-terminals that require two steps.

No such easy solution is available for cases such as

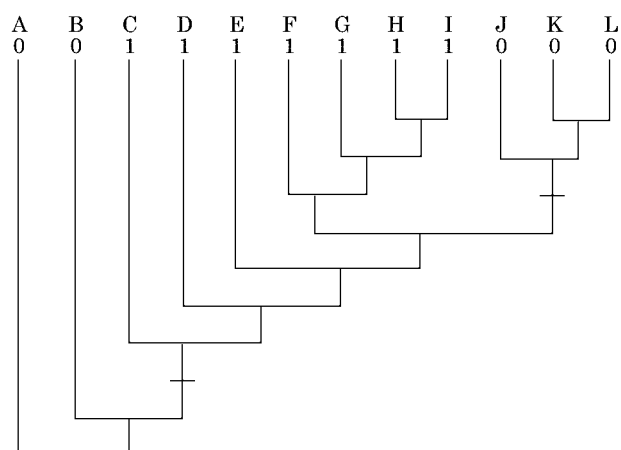


FIG. 3. A nonpectinate paraphyletic group (C–I) which requires two steps.

shown in Fig. 4. The character has six 1-terminals which are grouped in a single non-pectinate paraphyletic group. The character can be explained in three steps, which amounts to three saved extra steps.

Yet, because the 1-terminals are neither in an A nor in a B configuration, the TTSC–FTSC logic cannot account for this configuration (cf. condition 1a). Alternatively, one could argue that the paraphyletic group CDEFGH consists of two subgroups of type B (CDE and FGH), each with three 1-terminals. However, given the character at hand this decomposition is artificial and, more importantly, it does not solve the problem; it only yields two saved extra steps, one for

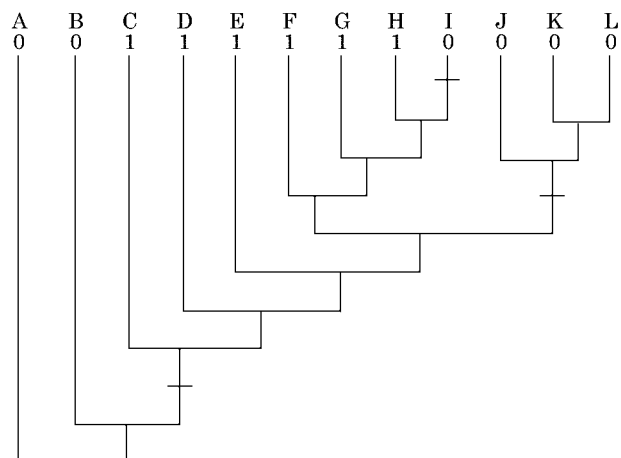


FIG. 4. A nonpectinate paraphyletic group (C–H) which requires more than two steps. Considering CDE and FGH as two type B configurations fails to account for the saved extra step that results from the interaction between both subgroups.

each type B configuration. The third saved extra step, resulting from the interaction between both subgroups, is ignored (cf. condition 1b). Note that a group such as CDEFGH in Fig. 4 is paraphyletic rather than polyphyletic because it can be united by symplesiomorphies (Farris, 1991), but that the reported problem does not depend on this designation. Indeed, it has been argued that such a group is polyphyletic rather than paraphyletic (e.g. Nelson, 1971; Oosterbroek, 1987; see Farris, 1991, for a discussion), but even if this were accepted, it would not change the fact that it requires three steps rather than two.

These problems are not limited to nonpectinate cladograms, as can be seen in Fig. 5. The eight 1-terminals all belong to a single paraphyletic group which requires three steps, amounting to a total of five saved extra steps. Because the 1-terminals of the paraphyletic group are not contiguous in the pectinate series (0-terminal F interrupts the series of 1-terminals), the pattern of 1-terminals is no type B configuration and the TTSC–FTSC logic cannot account for the configuration. As in the above example, one could argue that paraphyletic group CDEGHIJK is composed of two paraphyletic subgroups of type B: CDE and GHIJK. However, as above, this decomposition is both artificial, given the

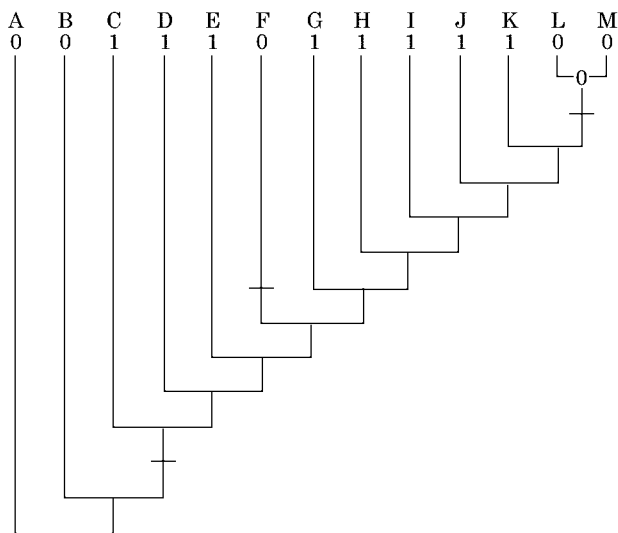


FIG. 5. A pectinate cladogram with a paraphyletic group (CDEGHIJK) which requires more than two steps. Considering CDE and GHIJK as two type B configurations fails to account for the saved extra step that results from the interaction between both subgroups.

character at hand, and of no help; it yields only four saved extra steps. The fifth saved extra step, resulting from the interaction of both configurations, is ignored. Similar interactions may arise between type A and type B configurations.

In summary, two alternative conclusions are possible at this point. (1) The TTSC–FTSC procedure is deficient either because it does not cover all possible step-saving configurations, or (2) if these uncovered configurations are shoehorned into the acknowledged configurations, because it does not cover interactions that may occur between configurations.

## Contiguity

Deleporte's (1996) classification of step-saving configurations can easily be completed such that it allows all cladograms and characters to decompose into configurations that are free from interactions. The concept of contiguity, discussed by Deleporte (1996: 274–275) at the onset of his argumentation, provides a clue for doing so. Deleporte gives the concept a precise meaning by relating it to the well-known concepts of secondary homology and character optimization: for a given character and cladogram, a number of terminals carrying the same character state are contiguous (in contiguity) on the cladogram when that character state is secondarily homologous in these taxa (see de Pinna, 1991, for secondary homology). In this way, contiguity points to hypothesized historical continuity of the character state on the cladogram. From a practical point of view, detection of this hypothesized historical continuity requires optimization of the character on the inner nodes of the cladogram. Note that the “contiguity status” of a group of terminals on a cladogram may be ambiguous with respect to a single character because the character may have multiple optimizations on the cladogram.

Deleporte (1996) apparently did not observe that this concept of contiguity almost directly yields a proper classification of step-saving configurations. One of the reasons may be that after his initial discussion of contiguity he quickly starts using the same term in a more restrictive sense, seemingly without noticing the restriction. An example can be found in

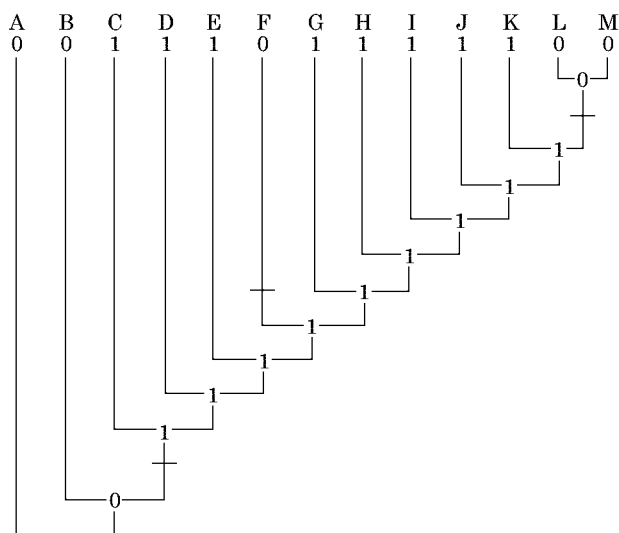


FIG. 6. Character state 1 has historical continuity across all 1-terminals of the pectinate series C–K, but within the pectinate series these 1-terminals are not all adjacent, hence the paraphyletic group consisting of all 1-terminals requires more than two steps.

the following quote:

“In the classical formulation of the standard approach, a paraphyletic series of contiguous taxa carrying state 1 on a cladogram is counted as two steps: one apparition of the derived state, and one extra step which is a reversal at the “distal end” of the series” (Deleporte, 1996: 278).

This is only true if “contiguous” refers to adjacency in the pectinate series, which is more restrictive than referring to historical continuity. This is illustrated in Fig. 6, showing the same pectinate cladogram and character as in Fig. 5 but with the inner nodes optimized. Character state 1 is in complete historical continuity on the cladogram and therefore the 1-terminals are contiguous in the first sense. However, the 1-terminals themselves are not all adjacent in the pectinate series, and therefore they are not contiguous in the second sense; as a result the group requires more than two steps.

For a given cladogram and optimized character, the character state transitions divide the cladogram into a number of “contiguity zones”, zones in which either state 0 or state 1 is secondarily homologous (we will refer to these as 0-contiguity zones and 1-contiguity zones respectively). The number of steps of the character can be obtained by considering, one by one, the 1-contiguity zones, and to count the number of neigh-

bouring 0-contiguity zones for each such zone. If the 1-contiguity zones are seen as step-saving configurations, it follows that there are no step-saving interactions between configurations (condition 1b); general applicability (condition 1a) is met because any character can be optimized on any cladogram. A natural classification of 1-contiguity zones is provided by counting the number of neighbouring 0-contiguity zones, which amounts to counting the number of steps that are associated with the configuration. The TTSC–FTSC procedure treats only 1-contiguity zones which require one (type A configurations<sup>1</sup>) or two (type B configurations) steps; all other cases are ignored.

An example of the decomposition of a cladogram and a character into a number of non-interacting step-saving configurations is presented in Fig. 7. The character has two possible optimizations on the cladogram, both of which are shown. The first optimization has one 1-contiguity zone, in which all eight 1-terminals are present. The zone has four neighbouring 0-contiguity zones, leaving four saved extra steps. The alternative optimization has two 1-contiguity zones. The first one, BCDEFH, has six 1-terminals and three neighbouring 0-contiguity zones, leaving three saved extra steps; the second 1-contiguity zone, LM, has two 1-terminals and one neighbouring 0-contiguity zone, leaving a single saved extra step. The total number of saved extra steps in both configurations is four, which is the same result as obtained with the first optimization.

Note that the decomposition procedure is basically a convoluted way of calculating the steps of a character on a cladogram and not intended nor recommended for regular use; its only purpose is to show why Deleporte’s (1996) TTSC–FTSC procedure does not always work correctly and to examine if a correct TTSC–FTSC-like procedure can be devised.

### THREE-TAXON-LIKE STATEMENTS

The TTSC–FTSC procedure derives its name from the types of three-taxon-like statements that are

<sup>1</sup> It is assumed that the cladogram is rooted by means of a real or hypothetical outgroup that has state 0 (Nixon and Carpenter, 1993).

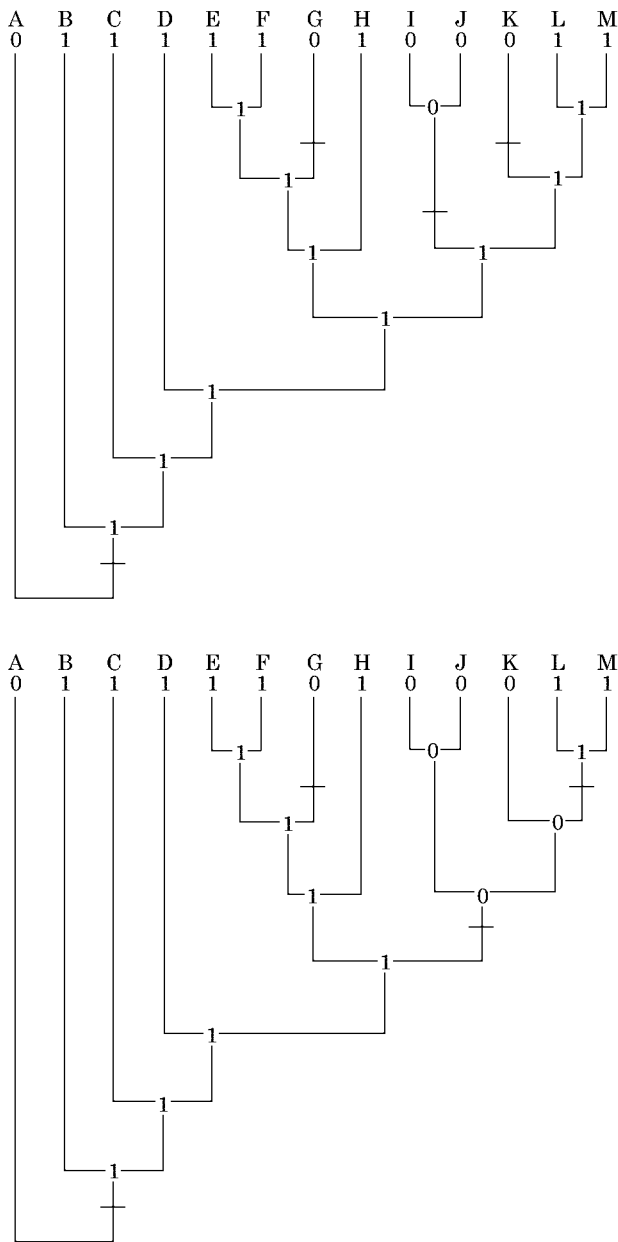


FIG. 7. When a character has multiple optimizations on a cladogram, there are alternative possibilities for decomposing the cladogram into non-interacting configurations. See text for further explanation.

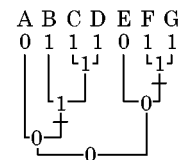
associated with type A and type B configurations (1-contiguity zones requiring respectively one and two steps): TTSCs or three-taxa statements for contiguous series with type A configurations and FTSCs or four-taxa statements for contiguous series with type B configurations (Deleporte, 1996: 276, 279). To obtain a general three-taxon-like formulation of stan-

dard parsimony, similar three-taxon-like statements should also be defined for 1-contiguity zones which require more than two steps. This could be done in analogy with TTSCs and FTSCs and, therefore, we will first examine the logic of associating these three-taxon-like statements with type A and B configurations.

### TTSCs

Consider a polarized binary character (state 1 apomorphic) with  $np$  0-terminals and  $na$  1-terminals, and a cladogram on which the optimized character specifies one or more monophyletic groups that have state 1 (type A configurations). A three-taxon statement for the character is a statement about any two taxa which have the apomorphic state and any third taxon that has the plesiomorphic state (Nelson and Platnick, 1991). If both 1-terminals of a three-taxon statement belong to the same type A configuration, the statement is called a TTSC for that configuration (Deleporte, 1996: 276). An example is shown in Fig. 8. The character has two 0-terminals and five 1-terminals, yielding  $2 * (5 * 4 / 2) = 20$  three-item statements (see, e.g. Nelson and Ladiges, 1992: 490). On the given cladogram, the optimized character specifies two type A configurations: BCD and FG. BCD has six TTSCs: A(BC), A(BD), A(CD), E(BC), E(BD), and E(CD); FG only two: A(FG) and E(FG).

A type A configuration with  $p$  1-terminals has  $(p - 1)$  saved extra steps, but  $np * (p * (p - 1) / 2)$  associated TTSCs. In order to obtain precisely as many associated statements as saved extra steps, two corrections are necessary. The first is a correction for



- A(BC) A(BD) A(BF) A(BG) A(CD) A(CF) A(CG) A(DF) A(DG) **A(FG)**
- E(BC) E(BD) E(BF) E(BG) E(CD) E(CF) E(CG) E(DF) E(DG) E(FG)*

FIG. 8. The character has 20 three-taxon statements. Six of these (in italics) are TTSCs associated with BCD, while two (in bold italics) are TTSCs associated with FG.

nonindependence, which comes down to fractional weighting (Nelson and Ladiges, 1992; see also Nelson and Platnick, 1991: 363) within each type A configuration (Deleporte, 1996: 276). In the example shown in Fig. 8, both TTSCs for FG are logically independent, but in BCD, statements are not logically independent: whichever two of the three statements A(BC), A(BD), and A(CD) are chosen, the third one is implied; the same holds for E(BC), E(BD), and E(CD), leaving a total of four independent TTSC's for BCD<sup>2</sup>. In general, only  $np * (p - 1)$  out of the  $np * (p * (p - 1) / 2)$  TTSCs which are associated with an A-configuration are independent.

Deleporte's correction for nonindependence results in a linear relationship between saved extra steps and independent TTSCs: there are  $np$  times as many independent statements as there are saved extra steps. The proportional constant,  $np$  or the number of 0-terminals, may differ between characters. As a result, standard parsimony logic on the one hand and counting the number of independent TTSCs on the other, may lead to a preference for different cladograms for data sets that have more than one character. The correction for this phenomenon results in reduced TTSCs or rTTSCs (Deleporte, 1996: 278) and hence we will refer to it as "reduction". Reduction itself is straightforward. It consists of dividing the number of independent TTSCs by the number of 0-terminals (Deleporte, 1996: 278; for the example in Fig. 8 this yields two independent rTTSCs for BCD and one for FG). The problem lies in its interpretation. Three-taxon analysis is basically an approach that breaks up character state distributions into the smallest possible statements which are in themselves still informative with respect to cladistic relationships. Reduction actually removes this basic characteristic from the TTSC–FTSC procedure: an rTTSC states that two 1-terminals are more closely related to each other than either is to any 0-terminal, which is no longer an elementary statement in the usual

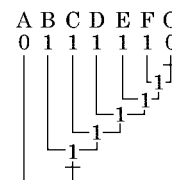
<sup>2</sup>Note that Deleporte's correction depends on the hidden assumption that A(BC), A(BD), and E(BC) do not collectively imply E(BD). The assumption would be true for three-taxon statements in three-taxon analysis (e.g. for character (0(0(1(0(11)))))) on tree (X(A(D(E(BC))))): A(BC), A(BD), and E(BC) are accommodated, but E(BD) is not), but it is false for TTSCs in the standard approach, where inner-node state assignments are taken into account (see De Laet, 1997). Deleporte (1996) does not provide argumentation to the contrary.

three-taxon sense. In this way, still calling the TTSC–FTSC procedure a three-taxon-like procedure appears to be word play which confounds rather than clarifies.

## FTSCs

Deleporte (1996: 279) defined a FTSC for a type B configuration as a statement about four taxa, three of which are 1-terminals belonging to the configuration while the fourth is a 0-terminal. A problem immediately arises. FTSCs, even before reduction, are not elementary statements as usually understood in the three-taxon approach. They can be further decomposed into smaller statements (viz. two independent three-taxon statements) which are still cladistically informative in themselves. Deleporte (1996) does not provide an intrinsic reason why FTSCs should be considered as elementary statements for type B configurations. His only rationale for switching from three-taxon to four-taxon statements seems to be the ad hoc observation (which is erroneous, see below) that this results in the required correspondence between the number of independent reduced FTSCs which are associated with a type B configuration and the associated number of saved extra steps.

From the above discussion of TTSCs, it is clear that the TTSCs which are associated with a particular type A configuration are a subset of the three-taxon statements which are supported by the cladogram in three-taxon analysis (Nelson and Platnick, 1991). This is no longer true for the three-taxon statements which make up the FTSCs associated with a type B configuration. An example is presented in Fig. 9. The optimized character specifies a single type B configuration with which 20 FTSCs are associated. How-



*A(BCD) A(BCE) A(BCF) A(BDE) A(BDF) A(BEF) A(CDE) A(CDF) A(CEF) A(DEF)*  
*G(BCD) G(BCE) G(BCF) G(BDE) G(BDF) G(BEF) G(CDE) G(CDF) G(CEF) G(DEF)*

FIG. 9. Twenty FTSCs are associated with paraphyletic group BCDEF; maximally four of them are fully independent (a possible set of four fully independent FTSCs is in italics). See text for further explanation.

ever, only those that have taxon A as 0-terminal can be decomposed into three-taxon statements supported on the cladogram (e.g. A(BCD) is composed of three-taxon statements A(BC), A(BD), and A(CD), all of which are supported by the tree). Exactly the opposite holds for FTSCs with taxon G as 0-terminal: they are completely composed of three-taxon statements contradicted by the cladogram. This phenomenon further complicates the interpretation of reduction, which for FTSCs also consists of dividing the number of independent FTSCs of a type B configuration by the number of 0-terminals in the character (Deleporte, 1996: 279). In this way, a reduced FTSC or rFTSC simply asserts secondary homology of state 1 in three terminals at a time. Any direct comparison with 0-terminals, as in the three-taxon approach, has disappeared.

Such fundamental differences with three-taxon analysis should come as no surprise. After all, the TTSC–FTSC procedure tries to be an alternative formulation of the standard approach, which clearly differs fundamentally from three-taxon analysis. However, the same observation as above can be made. If, in spite of these differences, the TTSC–FTSC procedure is still called a three-taxon-like formulation of standard parsimony, the differences are concealed rather than highlighted.

The above problems could be argued away as due to interpretation, but the FTSC logic has a more serious defect. The supposed correspondence between independent rFTSCs and saved extra steps is erroneous because it depends on an incomplete correction for non-independence. A type B configuration with  $q$  1-terminals has  $(q - 2)$  saved extra steps and  $np * (q * (q - 1) * (q - 2) / 6)$  associated FTSCs ( $np$  is the number of 0-terminals). Deleporte erroneously considers  $np * (q - 2)$  of these logically independent<sup>3</sup>. The problem is illustrated in Fig. 9. On the cladogram, the optimized character specifies a single type B configuration to which all five 1-terminals belong. Because there are two 0-terminals, the configuration has a total of  $2 * (5 * 4 * 3 / 6) = 20$  FTSCs. According to Deleporte, a maximum of six of these are independent, which is correct as far as it goes. Consider

<sup>3</sup>Note that Deleporte only discusses examples and does not provide general expressions; the expression which is given is extracted from these examples and from his statement that “the TTSC–FTSC logic exactly reproduces the standard character parsimony logic” (Deleporte, 1996: 276).

statements A(BCD), A(BCE) and A(BCF): none of them follows from the two others. The same holds for G(BCD), G(BCE) and G(BCF). If it is assumed that A(BCD), A(BCE) and G(BCD) collectively do not imply G(BCE), then these six FTSCs are truly a set of six independent statements from which all remaining ones can be deduced. However, if the FTSCs are carefully chosen, a smaller set of independent statements is sufficient. Indeed, the FTSCs A(BCD) and A(DEF) together specify that taxon A is outside a type B configuration in which 1-terminals B, C, D, E and F are present. This is sufficient to deduce all other FTSCs which have taxon A as 0-terminal. The same is true for G(BCD) and G(DEF) with respect to the other FTSCs with taxon G as 0-terminal and therefore the set of four independent statements A(BCD), A(DEF), G(BCD) and G(DEF) is sufficient to deduce all remaining FTSCs associated with BCDEF.

The different results follow from the fact that FTSCs can be partially dependent and independent at the same time. This is best explained by considering that FTSCs are composed of two three-taxon statements. As an example, A(BCD) consists of the independent three-taxon statements A(BC) and A(CD) and A(DEF) of the independent statements A(DE) and A(EF). In combination, this yields four independent three-item statements and therefore the two FTSCs are fully independent. Consider, on the other hand, FTSCs A(BCD) and A(CDE). A(CDE) consists of independent three-taxon statements A(CD) and A(DE) and if these are combined with the implied three-taxon statements of A(BCD), only three independent three-taxon statements remain. This is more than the two three-taxon statements which are implied by a single FTSC, but less than four, the possible maximum. Therefore A(BCD) and A(CDE) are partially dependent and independent at the same time. The conclusion is that Deleporte’s proposed correction for logical dependency between FTSCs only partially fulfils this. Note that this conclusion does not depend on the proposed decomposition of an FTSC into two three-taxon statements, as is clear from the example of Fig. 9. Indeed, even if it is argued that FTSCs are elementary statements which cannot be reduced to three-taxon statements, the fact remains that the set of four FTSCs A(BCD), A(DEF), G(BCD) and G(DEF) is sufficient to deduce all remaining FTSCs associated with BCDEF and Deleporte does not provide a reason



why the larger set of six partially redundant FTSCs should be preferred over the smaller one in which no redundancy is present.

In general, only  $np * \lfloor q/2 \rfloor$  independent FTSCs are necessary to deduce all  $np * (q * (q - 1) * (q - 2) / 6)$  associated FTSCs of a type B configuration with  $q$  1-terminals (the square brackets stand for the integer part of the bracketed expression). With  $q$  odd all of these FTSCs will be fully independent, but with  $q$  even two of them will be partially dependent. If more than  $np * \lfloor q/2 \rfloor$  independent FTSCs are considered, unnecessary redundancy is introduced. After reduction this yields  $\lfloor q/2 \rfloor$  independent rFTSCs for  $(q - 2)$  saved extra steps. In this way, the correspondence between saved extra steps and independent rFTSCs only holds for type B configurations which have either three or four 1-terminals. Incidentally, Deleporte does not discuss examples in which larger type B configurations are present.

In summary, FTSCs are problematic for the following reasons. They are not elementary statements in the usual three-taxon sense because they are composed of smaller statements that are still cladistically informative. Moreover, the two three-taxon statements that make up a single FTSC may not be supported by the cladogram. Lastly, the association of FTSCs with type B configurations only establishes an exact correspondence between saved extra steps and supported independent rFTSCs if these configurations have either three or four 1-terminals.

### 1-Contiguity Zones which Require More than Two Steps

According to the TTSC–FTSC logic, an elementary statement for a 1-contiguity zone which requires one step is a statement about two 1-terminals of that zone and one outlying 0-terminal, and an elementary statement for a 1-contiguity zone which requires two steps is a statement about three 1-terminals and one outlying 0-terminal. Generalizing, an elementary statement for a 1-contiguity zone requiring  $s$  steps would be a statement about  $(s + 1)$  1-terminals of that zone and one outlying 0-terminal. This enforces the above conclusion that the switch from three-taxon statements in type A configurations to four-taxon statements in type B configurations is an ad hoc

decision: the number of 1-terminals of an elementary statement is increased such that the required correspondence between saved extra steps and (partially) independent reduced elementary statements is preserved and no intrinsic reason for considering such statements as elementary is provided.

It could be argued that the generalization is not valid because a 1-contiguity zone requiring  $s$  steps may consist of only  $s$  1-terminals, which is less than is required for an elementary statement. However, this is completely analogous to the FTSC case: 1-contiguity zones requiring two steps can have precisely two 1-terminals, which is insufficient for an FTSC. From a technical point of view, this is unproblematic because the group has no saved extra steps anyway (Deleporte, 1996: 279), but at the level of interpretation it is bizarre that a configuration can be smaller than the elementary statements it is supposed to be composed of. This again points to the artificial nature of the TTSC–FTSC approach.

As with FTSCs, the correction for nonindependence that results in the required correspondence with saved extra steps would be only a partial correction: the independent statements must be chosen such that they have maximal partial dependence or minimal partial independence.

## SUMMARY AND DISCUSSION

Deleporte (1996: 279) states that “the TTSC–FTSC procedure exactly reproduces the standard character parsimony logic for testing cladograms”, and he claims that it does so in terms of elementary statements that support those cladograms (Deleporte, 1996: 275). As explained above, this is not true for several reasons. First, the TTSC–FTSC logic gives the same result as standard parsimony logic only for characters and cladograms that can be decomposed into (1) 1-contiguity zones that require precisely one step and/or (2) 1-contiguity zones that require two steps and contain precisely three or four 1-terminals. If the 1-contiguity zones that require two steps (type B configurations) contain more than four 1-terminals, standard parsimony logic is reproduced only if it is accepted that nonindependence between elementary statements must be eliminated only partially. No

reasons are provided for such partial corrections. Moreover, the elementary statements that are proposed for type B configurations, FTSCs, are clearly compound statements, and the TTSC–FTSC logic provides no compelling reasons why they should not be considered so. Lastly, the TTSC–FTSC logic cannot deal with 1-contiguity zones which require more than two steps. It can be extended to deal with such cases, but this extension only highlights the artificial nature of the elementary statements of the approach and, as with FTSCs it depends upon arbitrary partial corrections for nonindependence.

Deleporte (1996: 274) developed the TTSC–FTSC formulation of standard parsimony in order to improve analysis of the differences between standard parsimony and three-taxon analysis. Given the defects of the TTSC–FTSC procedure, it might be expected that Deleporte's main conclusion, of the superiority of standard parsimony as a method for biological systematics, is erroneous. However, strangely enough none of the idiosyncracies of the TTSC–FTSC procedure affect the basis of Deleporte's further argumentation, which hinges upon the importance of contiguity, i.e. hypothesized historical continuity of character states. As this was also the starting point for developing the TTSC–FTSC logic (Deleporte, 1996: 274–275), it can be argued that the concept of contiguity is in itself sufficient for improv-

ing the ability of comparing standard parsimony and three-taxon analysis and that the TTSC–FTSC procedure becomes superfluous.

## REFERENCES

- De Laet, J. (1997). "A reconsideration of three-item analysis, the use of implied weights in cladistics, and a practical application in Gentianaceae". Ph.D. thesis, Katholieke Universiteit Leuven.
- Deleporte, P. (1996). Three-taxon statements and phylogeny reconstruction. *Cladistics* **12**, 273–289.
- de Pinna, M. C. C. (1991). Concepts and tests of homology in the cladistic paradigm. *Cladistics* **7**, 367–394.
- Farris, J. S. (1983). The logical basis of phylogenetic analysis. In "Advances in Cladistics" N. Platnick, and V. A. Funk (Eds) Vol. 2, pp. 7–36. Proceedings of the Second Meeting of the Willi Hennig Society. Columbia University Press, New York.
- Farris, J. S. (1989). The retention index and the rescaled consistency index. *Cladistics* **5**, 417–419.
- Farris, J. S. (1991). Hennig defined paraphyly. *Cladistics* **7**, 297–304.
- Nelson, G. (1971). Paraphyly and polyphyly: Redefinitions. *Syst. Zool.* **20**, 471–472.
- Nixon, K. C., and Carpenter, J. M. (1993). On outgroups. *Cladistics* **9**, 413–426.
- Nelson, G., and Ladiges, P. (1992). Information content and fractional weight of three-item statements. *Syst. Biol.* **41**, 490–494.
- Nelson, G., and Platnick, N. I. (1991). Three-taxon statements: A more precise use of parsimony. *Cladistics* **7**, 351–366.
- Oosterbroek, P. (1987). More appropriate definitions of paraphyly and polyphyly, with a comment on the Farris 1974 model. *Syst. Zool.* **36**, 103–108.