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A supertree of early tetrapods

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A genus-level supertree for early tetrapods is built using a matrix representation of 50 source trees. The analysis of all combined trees delivers a long-stemmed topology in which most taxonomic groups are assigned to the tetrapod stem. A second analysis, which excludes source trees superseded by more comprehensive studies, supports a deep phylogenetic split between lissamphibian and amniote total groups. Instances of spurious groups are rare in both analyses. The results of the pruned second analysis are mostly comparable with those of a recent, character-based and large-scale phylogeny of Palaeozoic tetrapods. Outstanding areas of disagreement include the branching sequence of lepospondyls and the content of the amniote crown group, in particular the placement of diadectomorphs as stem diapsids. Supertrees are unsurpassed in their ability to summarize relationship patterns from multiple independent topologies. Therefore, they might be used as a simple test of the degree of corroboration of nodes in the contributory analyses. However, we urge caution in using them as a replacement for character-based cladograms and for inferring macroevolutionary patterns.

Keywords: Palaeozoic; lissamphibians; amniotes; source trees; parsimony

1. INTRODUCTION

This paper sets out to investigate supertree methods as a means of evaluating different tree topologies for Palaeozoic tetrapods, and to provide a summary of the major areas of conflict to be targeted by future character-based analyses. Over the last 15 years, systematists have begun to explore the branching sequences of progressively larger portions of the tree of life in order to infer large-scale evolutionary patterns, from the level of populations to ontogenetic sequences. This has been made possible by a considerable amount of new information for thousands of organisms, both at molecular and at macroscopic levels (Bininda-Emonds *et al.* 2002; Jeffery *et al.* 2002*a*,*b*, and references therein). In parallel with new data acquisition, technological advances have improved data archiving and the effectiveness of phylogenetic methods, including rapid searches for optimal trees in practical time periods. However, total-evidence approaches to phylogeny reconstruction are not always feasible, because retrieval of information for various operational taxonomic units (OTUs) may be impractical for some data sources (e.g. morphology, molecules and behaviour). This is particularly evident when large taxonomic exemplars are included in a single analysis. Increased data collection for ever larger groups of organisms has prompted systematists to explore protocols for combining different phylogenies, especially in the case of trees built from different character sources. The most commonly used of these protocols is supertree construction.

Supertrees (Gordon 1986; reviewed in Bininda-Emonds *et al.* 2002) have gained considerable interest among systematists. Some of their unsurpassed qualities include the abilities to: (i) handle very large numbers of taxa, which is far beyond the practical limits of primary analyses; (ii) combine numerous character-based trees in one tree; (iii) summarize support for nodes that appear in primary analyses; (iv) provide (in some cases) resolution for groups that are poorly resolved in the contributory trees; and (v) minimize and, in many cases, resolve instances of taxon conflict present in such trees. Supertrees force systematists to explore the support (in terms of character distribution) for possible alternative branching patterns, and have been used to investigate evolutionary tempo and mode in groups as diverse as mammals, birds and grasses. However, recent debates have challenged the utility and meaning of supertrees, especially with regard to their use as proxy phylogenetic hypotheses (summaries of debates can be found in Bininda-Emonds *et al.* (1999, 2002), Wilkinson *et al.* (2001), Goloboff & Pol (2002), Pisani & Wilkinson (2002) and Pisani *et al.* (2002)). Goloboff & Pol (2002) argue that the results of supertree analysis can be used as a phylogenetic hypothesis only if their strict or semi-strict topology is well resolved. However, they note that this is likely to be rare when datasets with numerous taxa are used (as is usual for supertree studies). Perhaps of even greater concern is the fact that supertrees can, in certain circumstances, produce spurious groups (i.e. taxon arrangements that are not found in any of the contributory trees; throughout, the term 'spurious' will be used with this meaning), and this has raised questions about their general performance relative to character-based analyses (for alternative supertree methods, with particular reference to the construction of supertrees with which each of the input trees is compatible see Semple & Steel (2000)). We point out that this applies only to some supertree methods, including the matrix representation (MR) encoding of input trees considered in this paper (see § 2). Creation of spurious groups might be a general problem when contributory trees differ considerably in number of taxa, resolution and balance (the last measures the relative

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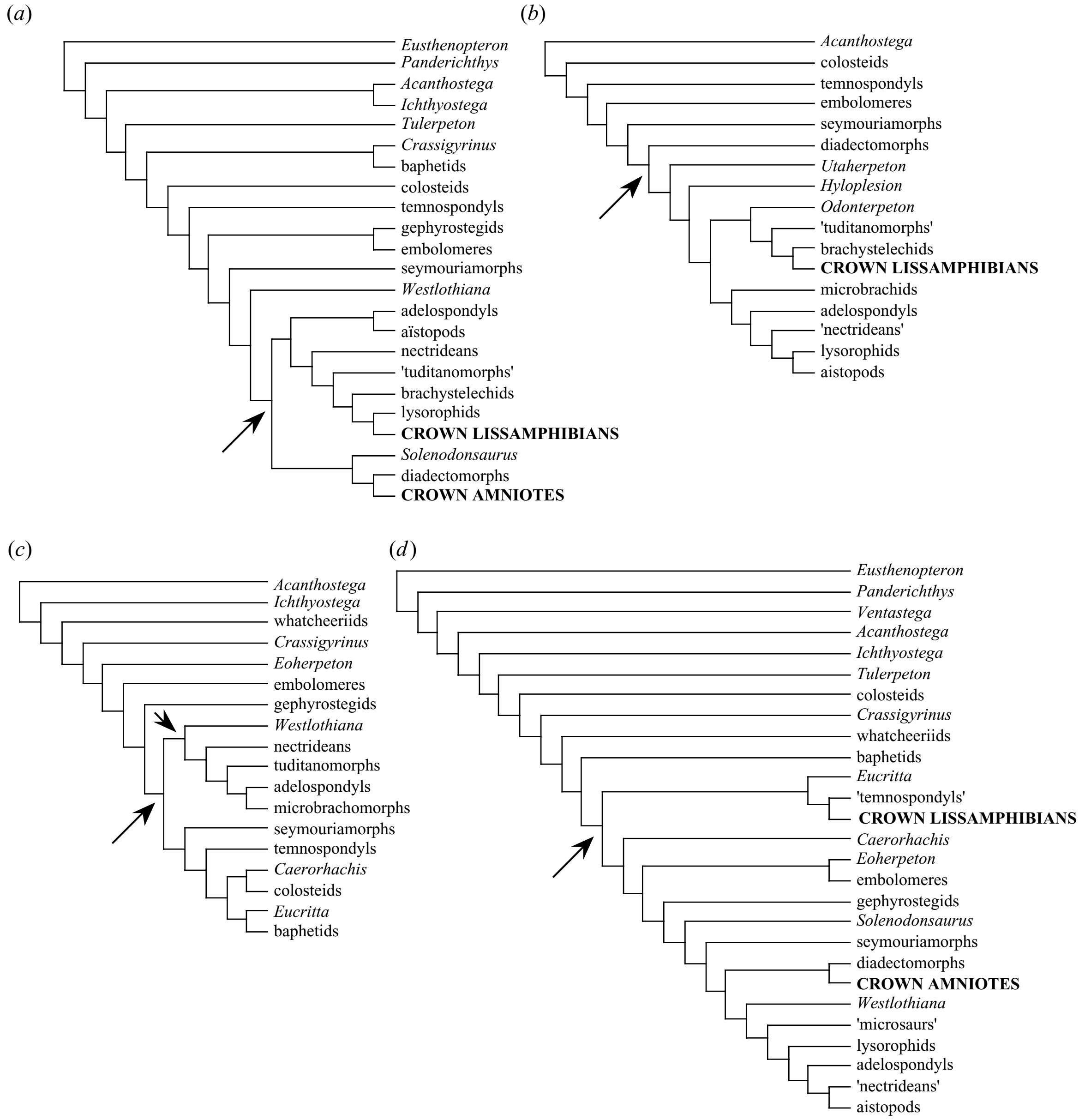

Figure 1. Some cladistic analyses of early tetrapods: (*a*) from Laurin & Reisz (1999); (*b*) from Anderson (2001); (*c*) from Clack (2002); and (*d*) from Ruta *et al.* (2003). Arrows indicate inferred positions of the tetrapod crown-group node. OTUs names in quotes indicate para- or polyphyletic groups.

numbers of terminals from each internal node of a tree to assess how symmetrical or skewed a tree is (Colless 1995)).

Early tetrapods have been the target of several manual and computer-assisted analyses through the last two decades. Such analyses differ in character selection and taxon content, and present incompatible branching sequences (cf. Laurin & Reisz 1999; Anderson 2002; Laurin 2002; Ruta & Coates 2003; Ruta *et al.* 2003). Although the broad affinities of some early groups are retrieved repeatedly, the positions of many others remain controversial. As a result, there is fundamental disagreement about the basal radiation, and about the primitive conditions underpinning the two primary subdivisions of modern tetrapods (figure 1), the lissamphibians and the amniotes. Several analyses predating Laurin's (1998*a*,*b*) and Laurin & Reisz's (1997, 1999) studies assigned the majority of Palaeozoic groups to crown tetrapods, i.e. to the modern tetrapod radiation. As Laurin (2002) pointed out, these analyses did not include members of either crown lissamphibians or crown amniotes. For this reason, they provided less effective tests of the level of phylogenetic splitting among early tetrapods. By contrast, some of the more recent phylogenies that have included crown lissamphibians and amniotes (Laurin & Reisz 1999, and references therein) support a less inclusive crown radiation by reassigning numerous extinct groups to the tetrapod stem. Ruta *et al.* (2003) surveyed existing datasets to assess the implications of different tree topologies, and in particular to assess competing hypotheses of lissamphibian origin (see Anderson 2001, 2002). They employed, so far as possible, taxa and characteristics from all previous studies, and found support for a much deeper split within Palaeozoic groups than that proposed by Laurin & Reisz (1999) (figure 1).

The strength of this paper lies primarily in the exploration of supertree methodology and its applicability to, and comparison with, fossil-based primary analyses. Although specimen-based knowledge of early tetrapods is expanding rapidly, detailed redescriptions of several groups are needed to construct robust phylogenies. However, an all-encompassing character-based analysis is currently unrealistic because of the uneven level of available descriptive data. Supertrees provide the only feasible way to summarize relationship hypotheses for all groups. Although the data source underpinning the contributory trees is uniform (osteology), supertrees remain well suited to identifying areas of conflict and corroboration, to exploring the effects of tree shape and size on a summary tree and to evaluating the 'weight' of multiple versions of analyses undertaken by the same author(s) (the use of multiple trees from successive analyses by the same author, and the problem of non-independence of data in supertree construction have been addressed in detail by Gatesy *et al.* (2002)). Furthermore, the results provide a useful assessment of the emerging shape of basal tetrapod phylogeny.

2. TERMINOLOGY

The contributory trees used to build supertrees are referred to as 'source trees' (Pisani *et al.* 2002), and each is translated into a particular kind of MR, referred to as 'component coding MR'. All taxa subtended by a given node in a source tree are scored as '1'; taxa that are not subtended by that node are scored as '0'; if a taxon is not represented in a source tree, it is scored as '?'. The combined MR for all source trees is processed using an optimality criterion (parsimony, hence 'MR using parsimony' or MRP; Baum 1992; Ragan 1992; Bininda-Emonds *et al.* 1999, 2002). MR 'nodal characters' are called 'matrix elements' (Pisani *et al.* 2002). The most parsimonious tree(s) (MPTs) deriving from MRP analysis are called 'component coding-MRP supertrees' or CC-MRP supertrees (Pisani *et al.* 2002). If terminal branches in a source tree consist of supraspecific OTUs, these are replaced by stars in the MRP. Stars are polytomous groups that include representative taxon samples (Wilkinson *et al.* 2001; Pisani *et al.* 2002). Choice of these samples follows several criteria (see § 4).

3. METHODS

Source trees were input by hand in MacClade v. 3.0.5 (Maddison & Maddison 1992). The MRP topology of each has been checked with Paup* v. 4.0b10 (Swofford 2002). Analyses were run on a Power PC G4 Macintosh dual processor with 1.25 Gb of memory. Inclusion of an all-zero outgroup implies OTUs grouping based on their shared non-zero matrix-element scores (Bininda-Emonds *et al.* 2002). For a summary of major groups of early tetrapods see Ruta *et al.* (2003). Selection of source trees was undertaken through a literature search. We arbitrarily chose only trees produced from 1980 onwards. We excluded several analyses that were not supported by a proper character discussion. We also excluded trees superseded by studies that incorporate a broader taxon and character sample (e.g. stereospondyl analyses predating Schoch (2000); Yates & Warren (2000); Damiani (2001) and Steyer (2002)).

4. SUBSTITUTION OF SUPRASPECIFIC OPERATIONAL TAXONOMIC UNITS

Source trees that include supraspecific OTUs have been modified (see Bininda-Emonds *et al.* (1998) for a discussion of supraspecific OTUs in supertree analysis). In all cases, such OTUs have been replaced by two or more taxa, and a single origin for the group to which they belong has been assumed (Wilkinson *et al.* 2001; Pisani *et al.* 2002). Only taxa described at the time of source-tree publication have been used in OTU replacements (for instance, the edopoid *Adamanterpeton* (Milner & Sequeira 1998) is not included in the MR of Milner's (1990) temnospondyl cladogram). The following examples illustrate star substitution criteria (table 1). The first and simplest type of substitution is called 'minimum substitution'. It is exemplified by the group Temnospondyli, which appears as an OTU in Carroll's (1995) analysis. In the MRP, this group is replaced by *Balanerpeton* and *Dendrerpeton*, as these genera exemplify temnospondyls in subsequent analyses (e.g. Paton *et al.* 1999; Clack 2001). Minimum substitution avoids the extra computation time and computer memory required to decompose and rearrange large all-inclusive stars.

The second type of substitution is called 'all-encompassing star substitution'. Supraspecific OTUs (e.g. nectrideans in Laurin & Reisz (1999)) have been replaced by a diverse species-level exemplar. This substitution is applied when smaller-scale analyses have retrieved nearly congruent branching patterns in largely overlapping exemplars (as in the case of nectrideans; but see Anderson (2001) and Ruta *et al.* (2003)). Unlike minimum substitution, all-encompassing star substitution is therefore unlikely to yield considerable taxon reshuffling.

The third type of substitution, 'partial substitution', has been applied to several OTUs in Milner's (1990) family-level phylogeny of temnospondyls. All taxa included in subsequent analyses are used to replace each family-level star. This substitution avoids the introduction of multiple taxa for which no properly resolved relationships are known. For simplicity, suppose that family F contains species A, B, C, D and E, and that an analysis has included F (but none of its species) as an OTU. Other studies have used species A, B, C and D (separately or in various combinations), but not E. In this case, E does not appear in the F star, which is constructed as (A, B, C, D). If F appears in just one analysis, then only one species (e.g. the type species or the best-known species) is used as a replacement.

Future directions in the study of supertrees include, among others, investigating the effects of different star-substitution methods and the use of topological constraints as a means of eliminating spurious groups. Exploration of these issues is beyond the scope of this work.

5. TAXON PRUNING

In some cases, certain extant taxa (i.e. unambiguous members of the lissamphibian or amniote crown groups) have been deleted from the source trees. The interrelationships of recent members of either crown group are beyond the scope of our analysis, and, from a compu-

Table 1. Rules for the replacement of supraspecific groups. All examples are based on a supraspecific group X used in a source tree. X consists of species A, B, C, D, E and F (all of which were known when the source tree was published).

replacement type	treatment of group X in other analyses	replacement of group X
minimum	species A and B usually included as exemplars	A and B
all-encompassing	most or all species in group X are used	A, B, C, D, E and F
partial	only some species in group X are used	A, B, C and D
partial	only one species in group X is used	B (type species or best-known species)

tational standpoint, these taxon deletions reduced the computing time. For example, several families of Recent caecilians, salamanders and frogs have been excluded from Laurin & Reisz's (1997, 1999) and Laurin's (1998*a*,*b*) matrices, and only the most basal known crown lissamphibians (*Eocaecilia*; *Karaurus*; *Triadobatrachus*) have been considered. Taxon pruning was performed before the construction of a source-tree MRP, because '… pruning a taxon from an MRP matrix will create a matrix that is not representative of the real topology of the pruned tree' (Pisani *et al.* 2002, p. 916). Re-running the datasets after taxon deletion resulted in trees that closely match those obtained from the original component matrices.

6. EVALUATION OF SOURCE TREES

If an original analysis yields more than one MPT, then the strict consensus of all MPTs is used as a source tree. This approach has been questioned, because the strict consensus of several completely overlapping MPTs may not correspond to the tree obtained from their combined MRP, at least when simple examples are used (Goloboff & Pol 2002). However, the use of a strict consensus is justified by the fact that it is '… formed from only those components [that are] common to all members of a set of fundamental cladograms' (Kitching *et al.* 1998, p. 216). In addition, the results of several source analyses of early tetrapods show that the strict consensus topologies, in these cases, are well resolved. The absence of large and widespread polytomies in the component cladograms prevents further loss of resolution in the supertree caused by instability of terminals in the primary trees.

Each primary analysis was re-run with unaltered character coding, weighting and ordering, and no attempts were made to correct character scores. In the case of mismatch between published trees and re-analysed trees, the latter were included. Only the strict consensus from the first parsimony run of Ruta *et al.* (2003), which supersedes Ruta & Coates (2003), was used. Most source trees are from computer-assisted analyses, but some are manual. Only those manual analyses that discuss character distribution have been used (see table 2 in electronic Appendix C, available on The Royal Society's Publications Web site.) One exception is Panchen & Smithson's (1988) tree, in which most taxa are high-level OTUs.

7. TWO-TREE SETS

It can be argued that if an author has produced several versions of an analysis, these may assign excess weight to a particular topology. This is especially problematic in the case of large, highly pectinate and/or fully resolved source trees, because these are likely to affect supertree shape to a much greater extent than small, poorly resolved and/or balanced source trees (Goloboff & Pol 2002; Pisani & Wilkinson 2002). Bininda-Emonds & Bryant (1998) think it reasonable to justify the topology bias introduced by large source trees if these are more accurate and more informative than smaller trees. This may well hold true in some cases, but other problems persist. Effects of source-tree sizes and shapes are still unexplored. Crucially, clades that appear in small analyses can be collapsed or broken in favour of novel topologies in the supertree. The cumulative influence of multiple small trees also remains unknown. The behaviour of MR when source trees exhibit different degrees of taxonomic overlap is similarly unpredictable.

Testing the impact of each source tree on the tetrapod supertree is not practical, especially considering the large amount of computer time required by MR processing. Therefore, we devised two analyses, 'analysis I' (see electronic Appendix A) and 'analysis II' (see electronic Appendix C), to assess the influence of similar source trees. Analysis I is an all-encompassing approach to tetrapod-supertree construction. All source trees are given equal weight. Analysis II uses only some of the source trees. Excluded source trees are those superseded by subsequent analyses of similar datasets (e.g. those that introduce character-score corrections or employ additional taxa and characters). For example, Paton *et al.*'s (1999) analysis is an elaboration of Clack's (1997, 1998) studies. Likewise, Laurin & Reisz's (1999) dataset supersedes Laurin & Reisz's (1997) and Laurin's (1998*a*,*b*) datasets. Analysis II aims to provide a more balanced treatment of competing topologies for early tetrapods and to solve (although not completely) non-independence problems caused by the inclusion of multiple similar trees by the same author(s). If similar matrices show different taxon sets, then they are all included. For example, Clack's (2002) dataset is a version of Paton *et al.*'s (1999), but omits *Casineria*.

8. DATA MATRIX PROCESSING

Searches for the MPTs were performed with PAUP* on a PowerMac G4. The size of the dataset and computer-memory limitations forced us to explore only a relatively small proportion of tree space. We employed 2000 random stepwise additions followed by tree bisection–reconnection branch-swapping searches, holding only one tree in the memory at any one time (MAXTREES = 1). Searching with unlimited MAXTREES recovered the same tree island. Searches were carried out to the limit allowed by computer memory. No shorter trees were recovered by using the iterative reweighting strategy proposed by Quicke *et al.* (2001). The largest numbers of trees from analyses I and II are identical (341 200), and correspond to the maximum number of trees that could be stored at the end of the tree search. However, we are uncertain about the total number of these trees (i.e. the percentage of fundamental trees recovered relative to the absolute size of the island to which they belong). Computer-memory limitations prevented the application of a tree filter to eliminate unsupported nodes, which were consequently retained. The results of the supertree analyses were examined for possible spurious groups, i.e. novel groups that are absent from the source trees. Such groups have not been collapsed in the consensus supertree (cf. Pisani & Wilkinson 2002; Pisani *et al.* 2002) and will be discussed in § 9.

A 50% majority-rule consensus topology has been used to show the frequency of occurrence of all nodes (compatible and incompatible) relative to the set of equally parsimonious CC-MRP solutions. Its use is appropriate, as it provides a direct reading of the number of MPTs that include a given clade (although not necessarily of the proportion of source trees containing that clade (cf. Goloboff & Pol 2002, p. 522)). Statistical methods devised to assess branch support in character-based trees are problematic for supertrees (Goloboff & Pol 2002; Pisani & Wilkinson 2002; Pisani *et al.* 2002), as it is not clear what support indicates, in terms of the position of taxa in the source trees. Reweighting is also of dubious significance, especially when source trees differ considerably in taxon content and overlap. For these reasons, neither bootstrap nor decay values were computed. The MacClade files used to generate analyses I and II are available as electronic Appendices A and B or directly from the authors upon request.

9. RESULTS

(a) *Analysis I*

The MR of all source trees consists of 226 taxa coded for 958 matrix elements. CC-MRP supertrees are 1310 steps long (consistency index = 0.7204 excluding uninformative characters; retention index = 0.9217; rescaled consistency index = 0.674). Tree statistics are of uncertain significance in terms of MRP. Nevertheless, we include them to allow other workers to replicate and assess our results. Major features of the 50% majority-rule consensus tree are illustrated in figures 2 and 3. This consensus largely matches Laurin & Reisz's (1997, 1999) and Laurin's (1998*a*,*b*) trees, but conflicts to some extent with Ruta *et al.*'s (2003) tree.

The sequence of branching events in the lissamphibian stem largely reflects Laurin & Reisz's (1997, 1999), Laurin's (1998*a*,*b*) and Anderson's (2001) conclusions (figures 2 and 3). All these authors hypothesize a close relationship between some or all of the lissamphibians and various lepospondyl groups (figure 1). However, analysis I places lissamphibians as a sister group to a clade of lysorophids and microbrachomorph microsaurs.

The amniote crown group and total group are coextensive: no amniote stem was found.

The tetrapod stem includes a range of Devonian and Carboniferous groups (among the latter, especially, are anthracosaurs and temnospondyls). The sequence of branching events largely matches that of Laurin & Reisz (1999) and references therein.

(b) *Analysis II*

The combined matrix consists of 225 taxa (the nectridean *Peronedon* was excluded because it did not appear in source trees other than Milner (1980)) coded for 710 matrix elements. The CC-MRP supertrees are 982 steps long (CI = 0.7109 excluding uninformative characters; RI = 0.9196; RC = 0.6649).

The 50% majority-rule consensus tree shows a deep split within early tetrapods between stem amniotes and stem lissamphibians (figures 4 and 5), as in Ruta *et al.*'s (2003) study. Unlike analysis I, analysis II includes a stem amniote branch. Anthracosaurs and seymouriamorphs are successive sister groups to a clade of crown amniotes plus diadectomorphs. This larger group is paired with *Solenodonsaurus* plus lepospondyls. *Caerorhachis* is placed at the base of the amniote stem (cf. Ruta *et al.* 2001, 2003). Finally, *Casineria* and *Westlothiana* are successive sister taxa to the crown amniotes.

Post-Devonian stem tetrapods include, as in analysis I, whatcheeriids, *Crassigyrinus*, colosteids and baphetids (cf. Ruta *et al.* 2003). However, temnospondyls now appear as stem lissamphibians (cf. Milner 1990; Bolt 1991; Trueb & Cloutier 1991; Ruta *et al.* 2003).

(c) *Spurious groups*

MRP created very few spurious groups (see § 1 for a definition of such groups). Identification of these is based on comparisons between the topology of the supertree and that of each of the component trees. Spurious groups consist mostly of nodes subtending members of a well-established clade and one or more representatives of other clades. In analysis I (figure 2), the most outstanding example of incompatibility between source trees and MPTs occurs in the amniote branch. Diadectomorphs are polyphyletic in most MPTs, *Diadectes* and *Limnoscelis* being nested within the amniote crown, next to stem diapsids. The synapsid branch is represented by *Ophiacodon* (Paton *et al.* 1999). It is noteworthy that *Solenodonsaurus* (Gauthier *et al.* 1988; Lee & Spencer 1997; Laurin & Reisz 1999) also appears as a crown amniote, as a sister taxon to the diadectomorph *Tseajaia*. This placement conflicts with both Laurin & Reisz's (1999) and Ruta *et al.*'s (2003) hypotheses, which support a more basal position for this taxon.

Further mismatches concern the temnospondyls *Peltobatrachus* and *Lapillopsis*, nested within tuditanomorph microsaurs (see discussions of these genera in Milner (1990) and Yates & Warren (2000)). Another example of incongruence is given by the basal position of *Stegops* among the temnospondyls, in contrast to its usual derived position within the dissorophids (Milner 1990). The branching sequence of stereospondyl temnospondyls (figures 2 and 3) conflicts with those of several recent computer-generated analyses (e.g. Schoch 2000; Yates & Warren 2000; Damiani 2001; Steyer 2002). These are also in conflict with one another. However, our sequence agrees in many respects with Schoch & Milner's (2000) results.

In analysis II, diadectomorphs are, once again, a polyphyletic array within the amniote crown (figures 4 and 5).

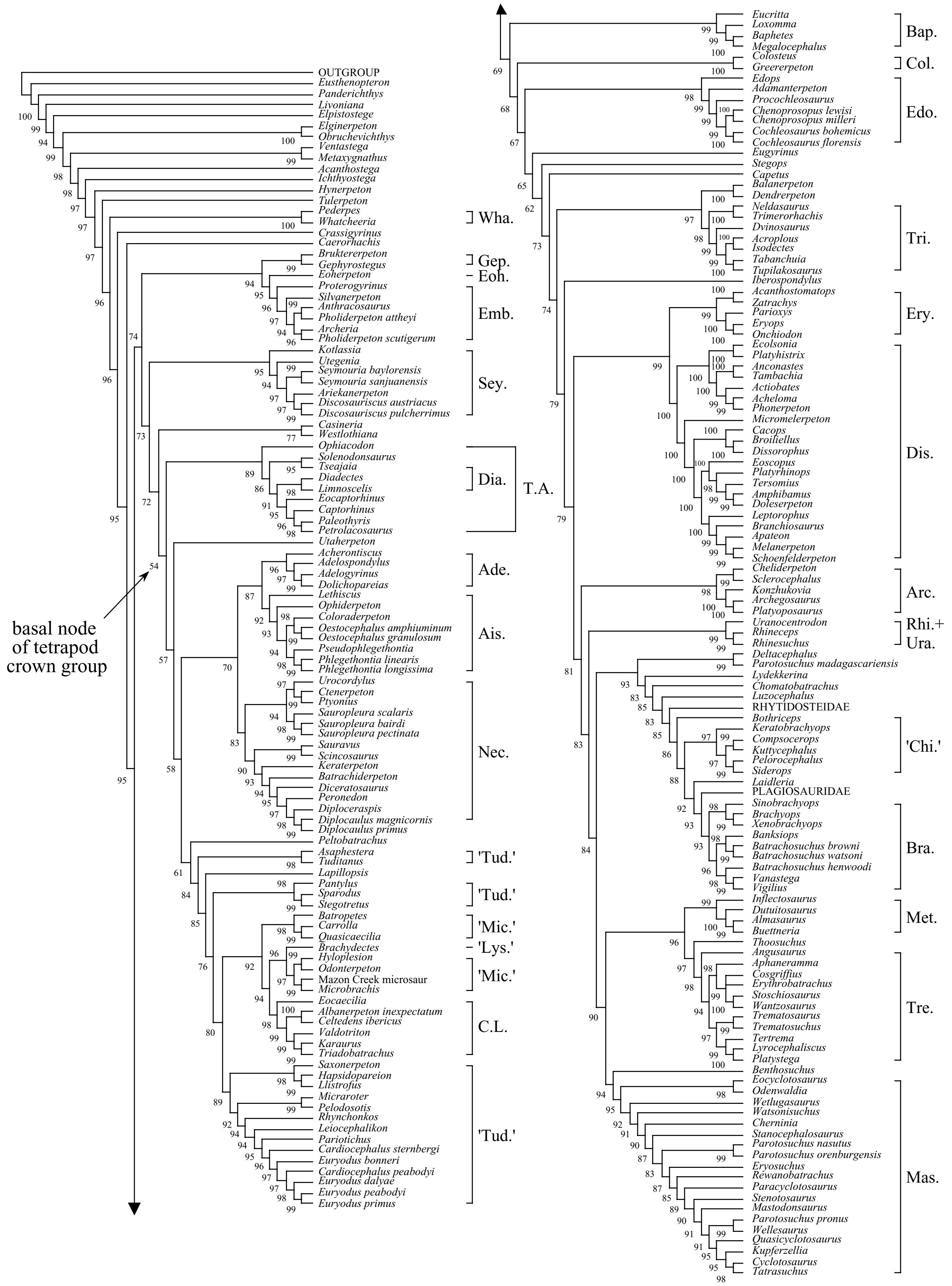

Figure 2. Majority-rule consensus from analysis I (see § 9 for details). Numbers at nodes indicate percentage of CC-MRP trees in which nodes are present. Ade., adelospondyls; Ais., aïstopods; Arc., archegosauroids; Bap., baphetids; Bra., brachyopids; Chi., chigutisaurids; C.L., crown lissamphibians; Col., colosteids; Dia., diadectomorphs; Dis., dissorophoids; Edo., edopoids; Emb., embolomeres; Eoh., eoherpetontids; Ery., eryopoids; Gep., gephyrostegids; Lys., lysorophids; Mas., mastodonsauroids; Met., metoposauroids; Mic., microbrachomorphs; Nec., nectrideans; Rhi., rhinesuchids; Sey., seymouriamorphs; T.A., total group amniotes; Tre., trematosauroids; Tri., trimerorhachoids; Tud., tuditanomorphs; Ura., uranocentrodontids; Wha., whatcheeriids.

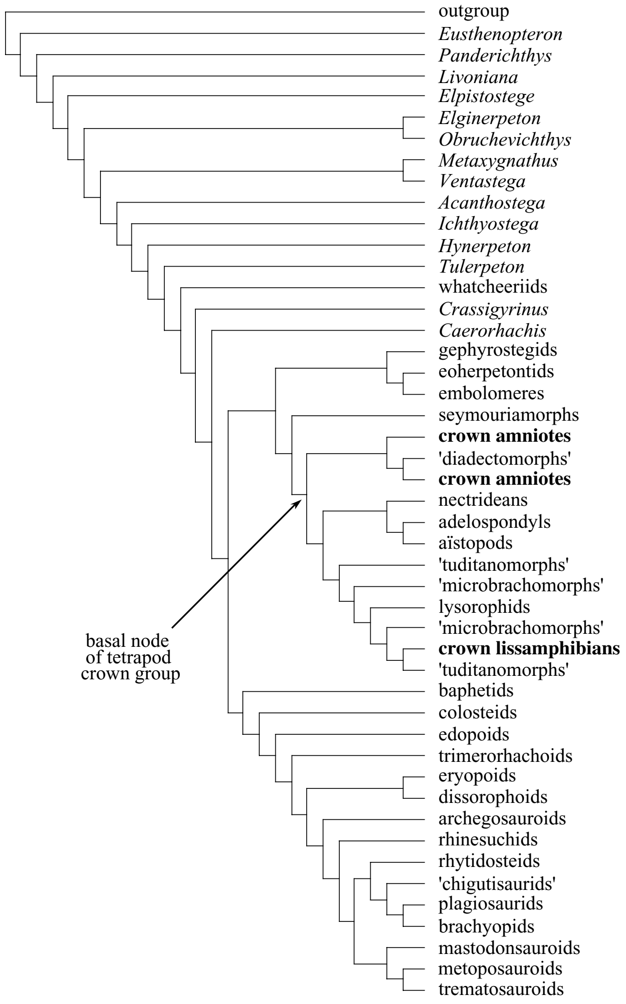

Figure 3. Simplified topology of the majority-rule consensus illustrated in figure 2.

In particular, *Tseajaia* is nested within the stem diapsids, and this result is retrieved in a rather large number of CC-MRP solutions. Even more surprisingly, however, *Solenodonsaurus* now appears as a sister taxon to lepospondyls in almost two-thirds of the MPTs (cf. Gauthier *et al.* 1988; Lee & Spencer 1997; Laurin & Reisz 1999; Ruta *et al.* 2003).

The interrelationships of the dissorophoid temnospondyls are unusual: a non-temnospondyl taxon, the microsaur *Utaherpeton*, is collapsed with an eryopoid–dissorophoid clade. As additional examples of incongruent taxon placements, the dissorophid *Stegops* forms a polytomy with nectrideans in little more than half of the CC-MRP supertrees, whereas *Lapillopsis* and *Peltobatrachus* are paired with the eryopoid–dissorophoid clade (figure 4).

Comparisons between figures 2 and 4 show that the sequence of branching events within each major group of Palaeozoic tetrapods is almost identical in analyses I and II. Major differences are observed in the composition of the tetrapod stem, in the relative positions of the various groups of lepospondyls and, most importantly, in the placement of crown lissamphibians. Out of the 12 input trees that have not been considered in analysis II (not marked by an asterisk in table 2), those of Laurin (1998*a*,*b*) and Laurin & Reisz (1997) are likely to be pivotal for most of these differences, because they are large and highly pectinate, and contribute a large proportion of the total number of matrix elements. Because such trees are very similar to one another and hence contain a large number of nodes in common, their simultaneous presence in analysis I implies that each of these common nodes is given four times as much weight as it would be given by the presence of only one of these trees.

10. DISCUSSION

Comparison of analyses I and II shows key areas of phylogenetic conflict. Part of this revolves around stem taxa close to the base of the tetrapod crown, such as baphetids, colosteids, *Eucritta* and *Caerorhachis*, which are notoriously difficult to place (Clack 2001, 2002; Ruta & Coates 2003; Ruta *et al.* 2003). The analyses also present very different boundaries for the tetrapod crown group. Most of the problems centre on the Temnospondyli and Lepospondyli. One could ask why these groups matter, and the most straightforward answer is that their size, as apparently coherent groups, is bound to affect the way that we model the origin of lissamphibians and amniotes. They have major impacts on hypotheses of character acquisition and transformation. However, it is important to remember that supertree construction is a step away from primary character-based analysis; the raw data here consist of shared nodes in trees. For a detailed consideration of the implications of character distribution and evolution in these significantly different topologies, see Coates *et al.* (2000) and Ruta *et al.* (2003). As suggested elsewhere (Bininda-Emonds *et al.* 2002; Pisani *et al.* 2002), inclusion of multiple trees from closely similar datasets skews the resulting supertree. If, therefore, analysis II is accepted as the most balanced treatment, then the overall pattern retrieved from MRP corroborates the hypothesis of a deep split within Palaeozoic tetrapods. In analysis II, *ca.* 74% of stem-amniote diversity is accounted for by lepospondyls, the relationships of which represent the most outstanding conflict within recent studies. Most strikingly, visual inspection of figure 4 shows that the lissamphibian stem is vastly more diverse, or node-rich, than its amniote counterpart.

There is a fundamental debate about the performance of supertrees relative to character-based trees, especially with regard to the creation of novel topologies that are not supported by any of the primary analyses. In the present work, however, spurious groups have a limited impact on the overall shape of the consensus supertree. Instances of these groups are rare. They are usually found in a small percentage of CC-MRP solutions, and do not cause drastic reshuffling within well-established clades. The degree of overlap between these clades is minimal and involves only one or a few genera (see § 9c). Importantly, conflicting positions of different groups and genera in the source trees do not appear to reduce resolution in the supertree topology. Instead, the latter shows either one of the possible alternative arrangements found in the contributory analyses or a novel arrangement altogether. Notable examples include stereospondyls, lepospondyls and, in the crownward part of the tetrapod stem, various Lower Carboniferous taxa. However, the use of supertrees as substitutes for character-based analyses is problematic if widespread spurious groups are retrieved. Therefore, in

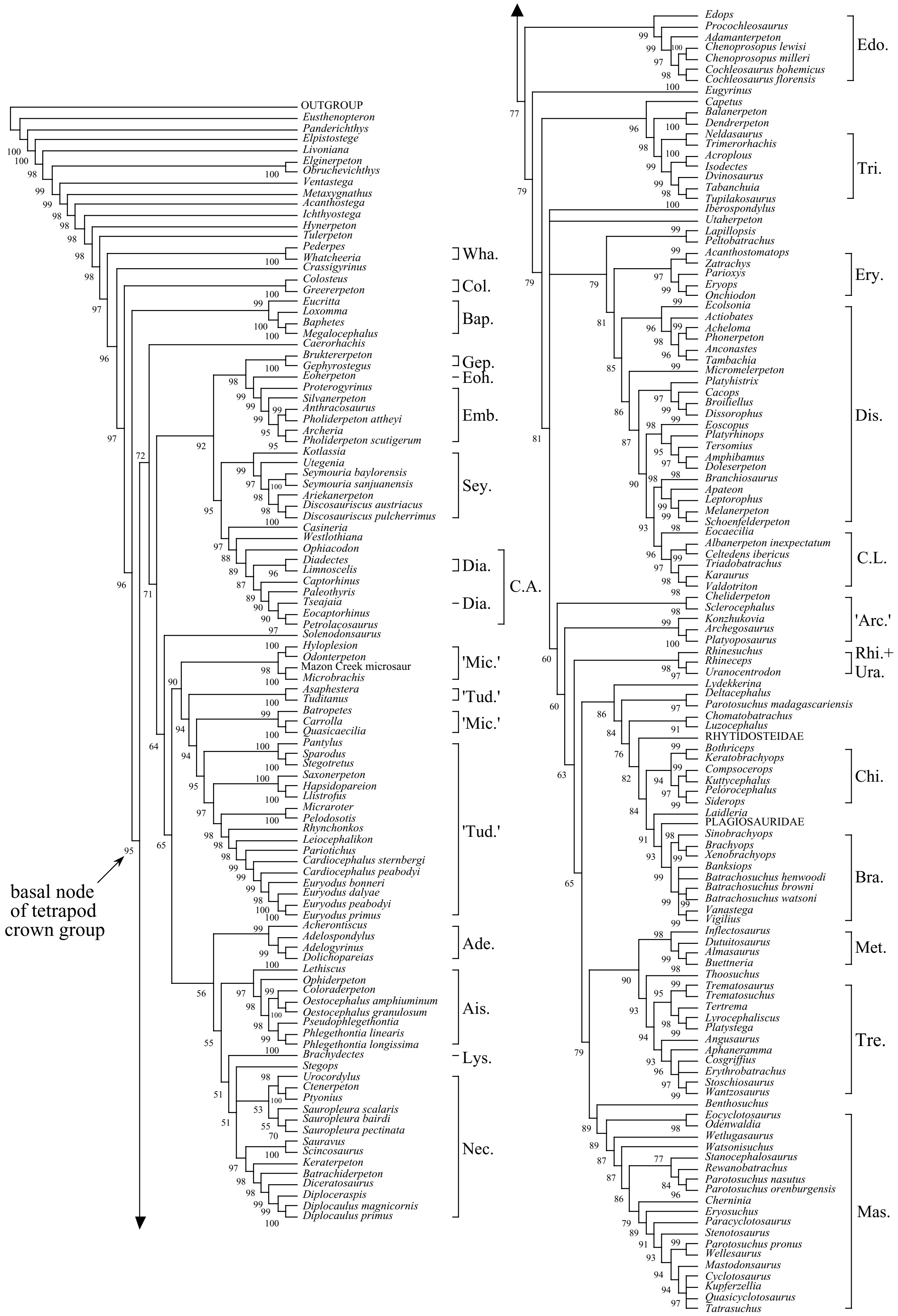

Figure 4. Majority-rule consensus from analysis II (see § 9 for details and figure 2 for abbreviations).

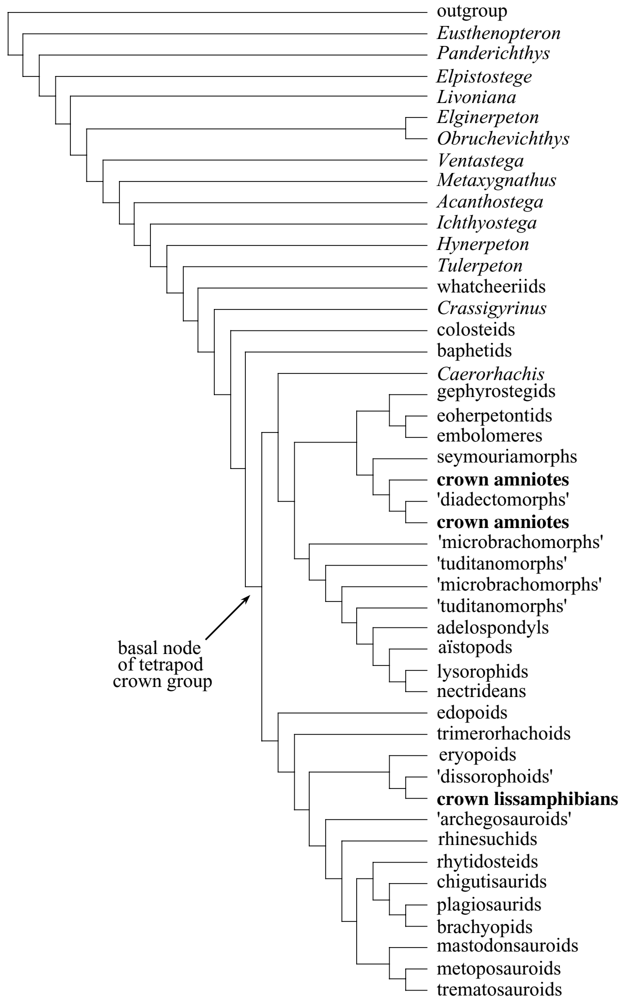

Figure 5. Simplified topology of the majority-rule consensus illustrated in figure 4.

agreement with former suggestions (Pisani & Wilkinson 2002; Pisani *et al.* 2002), such groups ought to be collapsed. Alternatively, genera or species that appear in unusual positions in the supertree (e.g. *Peltobatrachus* and *Lapillopsis*; see § 9c) could be constrained to cluster with the clades to which they belong (in this example, temnospondyls), and multiple analyses should be undertaken to eliminate 'noise' generated by MRP processing. However, discussion of these issues is beyond the scope of this paper.

In conclusion, given the taxonomic range of source trees and the variety of characters used to construct them, supertree methods are the only practical means of generating summaries of primary results. This applies to contributory phylogenies derived from different character sets as well as to the more limited data sources of fossil-based trees. In all cases, the need is to recognize the nature and source of likely 'noise', and to provide a framework within which to address key areas to be targeted by further character analyses.

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