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DAVID W. E. HONE & ERIC BUFFETAUT (Guest Editors)

**Flugsaurier: pterosaur papers in honour of
Peter Wellnhofer**

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Umschlagbild: Reconstitution of a *Rhamphorhynchus* from the Upper Jurassic of Eichstätt, Bavaria. Concept: P. Wellnhofer;
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Contrasting supertree and total-evidence methods: the origin of the pterosaurs

By
David W. E. Hone^{1,2*} & Michael J. Benton²

¹*Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10,
80333 München, Germany*

²*Department of Earth Sciences, University of Bristol, Queens Road, Bristol, BS8 1RJ, UK
Correspondence to: Institute of Vertebrate Palaeontology and Palaeoanthropology, Xizhimenwai Dajie 142,
Beijing 100044, P. R. China*

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Abstract

The two most commonly used approaches for combining data from cladistic analyses are “total evidence methods” (combining available data sets) and “supertree methods” (combining trees produced by those data sets). Here we present a study of the phylogenetics of basal diapsid reptiles using multiple palaeontological data sets, complete with multiple overlapping characters and taxa, in which we performed both total evidence (“supermatrix”) and supertree analyses. The results of the total evidence approach were well resolved, with robust nodes. Two supertrees were also created using Matrix Representation with Parsimony (MRP) methods from the original data and these gave results that conflict with the source trees. However MRP produced unsupported novel clades that are rejected, suggesting that the method may be less reliable than previously thought.

The origin of the pterosaurs within the diapsids has long been debated in the palaeontological literature. Recently it was suggested that the origin of the pterosaurs lay close to the proclertiforms, as opposed to their more usual position among the higher archosaurs. The phylogeny produced here using a total evidence method places the pterosaurs among derived archosaurs. Contrary to some reports, the total evidence method performs significantly better than either MRP supertree method for this study. Although analysis times were similar, the difference in timescale for assembling the different datasets is massive: the total evidence data set took 800 hours to produce, the supertree data set took 1 hour.

Key words: Proclertiformes, Archosauria, supertree, supermatrix, total evidence.

Zusammenfassung

Die beiden am häufigsten benutzten Ansätze für die Kom-

bination von Daten von kladistischen Analysen sind „Total-Evidence-Methoden“ (Kombination verfügbarer Datensätze) und „Supertree-Methoden“ (Kombination von Stammbäumen, die durch jene Datensätze produziert wurden). Hier stellen wir einer Studie der Phylogenie von basalen diapsiden Reptilien unter Verwendung vielfältiger paläontologischer Datensätze inklusive mehrfach überlappender Merkmale und Taxa vor, in welcher wir sowohl Total-Evidence-Analysen („supermatrix“) als auch Supertree-Analysen durchführten. Die Resultate des Total-Evidence-Ansatzes waren gut aufgelöst mit robusten Gabelpunkten. Durch Anwendung von Methoden der Matrix-Darstellung mittels Parsimonie-Analyse (MRP – maximal sparsames Kladogramm) wurden von den ursprünglichen Datensätzen auch zwei Supertrees geschaffen, und diese lieferten Ergebnisse, die mit den Ausgangsstammbäumen in Widerspruch stehen. Jedoch produzierte MRP nicht gestützte, neuartige Klade, die verworfen werden, da anzunehmen ist, dass diese Methode wohl weniger verlässlich ist, als früher gedacht wurde.

Der Ursprung der Flugsaurier innerhalb der Diapsida wurde lange in der paläontologischen Literatur diskutiert. Kürzlich wurde vorgeschlagen, dass der Ursprung der Flugsaurier nahe bei den Proclertiformes lag, im Widerspruch zu ihrer üblicheren Position unter den höheren Archosauria. Die hier mittels der Total-Evidence-Methode entwickelte Phylogenie stellt die Flugsaurier zu den abgeleiteten Archosauria. Im Gegensatz zu einigen Berichten arbeitete die Total-Evidence-Methode für diese Studie bedeutend besser als jede der beiden MRP-Supertree-Methoden. Obwohl die Analysen-Zeiten ähnlich waren, ist der Unterschied im zeitlichen Rahmen für das Eingeben der verschiedenen Datensätze gewaltig: Die Erstellung des Total-Evidence-Datensatzes nahm 800 Stunden in Anspruch, der Supertree-Datensatz erforderte eine Stunde.

Schlüsselwörter: Proclertiformes, Archosauria, Supertree, Supermatrix, Total-Evidence

*Author for correspondence and reprint requests; E-mail: dwe_hone@yahoo.com

1. Introduction

1.1 Supermatrices vs. Supertrees

Total evidence was proposed as a philosophy of systematics by KLUGE (1989) as a way of minimising the effects of homoplasy, and maximising the explanatory power of large or multiple datasets (KLUGE 2004). HUELSENBECK et al. (1996) distinguished three approaches available to systematists with multiple datasets – always to combine data (total evidence approach), never to combine data (taxonomic congruence) or ‘conditional combination’ (combining data only if the levels of data heterogeneity were high). Alternative methods for summarising and combining phylogenetic data have also been sought, the most important of these being the supertree, which stands as a philosophical and practical opposite to the total evidence method (BININDA-EMONDS 2004a, 2004b). Supertrees are assembled by combining trees, not by combining the source data that generate those trees.

The obvious advantage of using a total evidence approach is that, with a consistent method, more data should improve the chances of discovering the one true phylogenetic tree. Moreover, “the relationship between numbers of characters and probability of correctly estimating phylogeny corresponds to our intuition about how phylogenetic methods *should* work” (HUELSENBECK et al. 1996 – their italics). By contrast, supertrees have attracted much criticism both with regard to their philosophical justification and their outcomes. It has been argued that there is a loss of information since combining trees, and not data, leaves the method one step removed from the primary data (GATESY & SPRINGER in BININDA-EMONDS 2004). This manifests itself as three separate problems: differences in signal strength and subsignals between trees (BARRETT et al. 1991; PISANI & WILKINSON 2002), pseudoreplication of data (BININDA-EMONDS 2004a), and the validity of supertrees as phylogenetic hypotheses (BININDA-EMONDS 2004a, b).

Weighted supertree methods (RONQUIST 1996; BININDA-EMONDS & SANDERSON 2001) have been suggested to deal with the problems of signal strength by weighting the supertree matrix characters according to the bootstrap values of the source trees. Consequently, poorly resolved or badly supported trees receive correspondingly lower weighted characters in the supertree matrix and thus have less influence on the resolution of the output supertree.

Recent efforts in cladistics have focused on increasingly large phylogenies in an attempt to reconstruct the “Tree of Life” (e.g. BININDA-EMONDS et al. 1999; KENNEDY & PAGE 2003; PISANI et al. 2002; PURVIS 1995; WILKINSON et al. in LITTLEWOOD & BRAY 2001). This work is patchy, however, with some groups being well-studied but showing conflicts (e.g. mammals) and others being under-represented. The emphasis has been on producing rapid estimates of the phylogeny of large groups of organisms in an attempt to cover as much of the tree as possible.

The most common supertree method is Matrix Representation with Parsimony (MRP), and thus is also the most discussed. MRP was developed independently by BAUM (1992) and RAGAN (1992), and although many methods are available (BININDA-EMONDS 2004a; WILKINSON et al. 2005), MRP has become the most commonly used because it is easily implemented in

readily accessible phylogenetic software (see BININDA-EMONDS [2004a] and WILKINSON et al. [2005] for more comprehensive coverage of this and other supertree methods).

Many recent large-scale phylogenies have been produced using MRP supertree methods. They have a huge advantage over the total evidence method in their speed of assembly and operation. Phylogenies can be combined into supertree matrices in a matter of minutes whereas even a small character data set can take hours to enter into a cladistics program. Total evidence methods are not often used for analysing morphological data sets, though it is increasingly common for molecular data (SALAMIN et al. 2002). However, it has been shown that some supertree methods generate spurious novel clades, invalidating the new phylogeny (PISANI & WILKINSON 2002; WILKINSON et al. 2005). Indeed, a recent study suggests that these problems are common for published supertrees (WILKINSON et al. 2005 – contra BININDA-EMONDS 2003).

The question remains therefore – what is the best method for resolving conflicts in differing phylogenies, and how can this be done efficiently, quickly and accurately? Much work has concentrated on evaluating the different methods in general, but here they are compared directly in an example where there are conflicting phylogenies. In this case the subject is the inter-relationships of the archosauromorph reptiles. Five data sets were combined to form a total evidence “supermatrix” (with 324 characters and 45 taxa) and their individual resultant trees combined into a supertree. Here a supermatrix is defined as a matrix composed of data derived from the works of other authors, and no new data is added by the analyst.

1.2 The prolacertiforms, pterosaurs, and early diapsids

The diapsids, a major division of amniotes that includes birds, crocodylians, lizards, and snakes, diverged into two major clades in the Permian – the archosauromorphs and lepidosauromorphs, some 280 million years ago. Most of the positions of the fundamental branches in the tree are generally agreed upon, but the positions of prolacertiforms and pterosaurs have proved controversial (BENNETT 1996; BENTON & ALLEN 1997; DILKES 1998; EVANS 1988; HONE & BENTON 2007; JALIL 1997).

The pterosaurs, are a difficult clade to place because of their sudden appearance in the fossil record as complete flying animals, and the unique mixture of derived characters they possess. At various times they have been allied with many basal and derived archosaurian clades, though few characters can be found to unite them with any particular clade (BENNETT 1996; UNWIN 2005; HONE 2005) (see Fig. 1). Their complex flight-adapted anatomy, and the fact that the first pterosaurs, from the Late Triassic, some 220 million years ago, already have all those characters, gives few opportunities to compare structures to those of other basal archosaurs or diapsids. The majority of authors (e.g. GAUTHIER 1986; BENTON 1990, 1999; SERENO 1991; BENTON & ALLEN 1997) have concluded that they belong within Ornithodira and are often depicted as the sister group to Dinosauromorpha or *Scleromochlus* (BENTON 1999). Recently, BENNETT (1996) and others (see HONE & BENTON 2007 for a review) have argued that pterosaurs occupy a more basal position within the diapsids, and nest among, or are closely allied to, prolacertiforms.

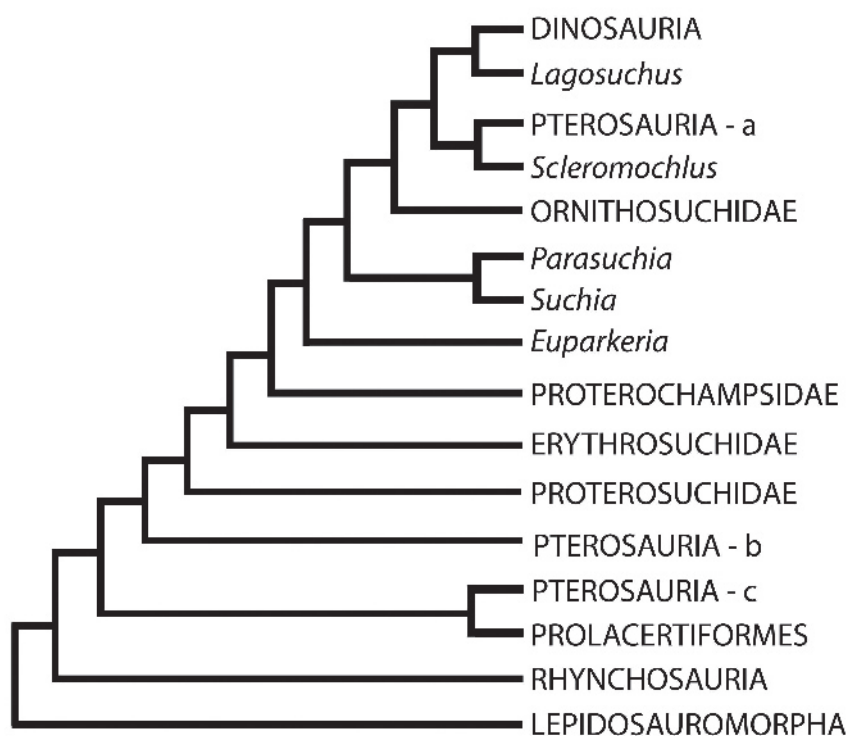


Figure 1: Possible phylogenetic positions of the pterosaurs based on BENNETT (1996). The Pterosauria are shown in three possible positions: (a) as ornithodirans, close to the dinosaurs (b) as basal archosauromorphs, second analysis, or (c) as sister taxa to, or within, the prolacertiforms. Modified from HONE & BENTON (2007).

Phylogenetic relationships and their resolution vary among recent works on the prolacertiforms. EVANS (in BENTON 1988), JALIL (1997), BENTON & ALLEN (1997), and BENNETT (1996) all regard them as a monophyletic group, though the resultant trees are generally poorly resolved and are composed of differing sets of taxa. DILKES (1998) concluded that the prolacertiforms were paraphyletic, notably with *Prolacerta* being excluded from the clade. MODESTO & SUES (2004) arrived at a similar conclusion using a modified version of DILKES' dataset. The results produced by BENNETT (1996) and DILKES (1998) have shown that an emerging consensus on the phylogenetic positions of pterosaurs and prolacertiforms as being only distantly related, is not uniformly accepted. These conflicts make the origins of the pterosaurs an interesting case study for comparing supertree and total evidence methods

The aims of this paper are therefore to (a) compare supertree (weighted and unweighted MRP) and supermatrix methods for a single phylogenetic problem, and (b) assess recent contrasting phylogenetic conclusions concerning prolacertiforms and pterosaurs.

2. Materials and methods

The data sets used here (Appendix A) are an amalgam of five source data sets: EVANS (in BENTON 1988), BENNETT (1996), BENTON & ALLEN (1997), JALIL (1997), and DILKES (1998). These five publications were chosen as recent studies of the groups in question, and contain a large number of taxa and characters. In

order to produce a balanced account of all the available data, a majority-rule matrix was constructed (Appendix B) – i.e. for each cell where two or more authors had coded a character the majority opinion was entered. A “?” indicates either a blank in an original data set or a conflict of coding (i.e. where both 1's and 2's were equally represented by different authors thus leaving no consensus as to the coding of the cell), whereas cells left blank indicate that there were no data available from any source matrix (i.e. a “?” in a matrix was transposed, but blanks indicate that that cell was never examined although for analysis these were replaced with a “?”). Polymorphic coding was not considered as this would have actively removed data from the matrix – numerous conflicts over character coding by different authors would have rendered ‘stable’ character codings as uncertain and left the analysis with less data, not more in the final analysis.

In the case of EVANS (in BENTON 1988) there were approximately 20 “repeat” characters, that is, characters that were listed twice in the matrix (these can be identified in the list by the code “E” followed by two separate numbers). The majority of these repeat characters were identical, but some had a number of differences and these were coded as “?”. It should be noted that this summarising effort is extremely time consuming: all the characters have to be cross-referenced to ensure that they overlap correctly and each cell must be cross-referenced from each data set (a total of over 17000 cells here), though many could be copied directly or were blank (for a character coded by only one author covering a few taxa). The checking was especially time-consuming as no two authors list their taxa in the same sequence or have their characters in any kind of

anatomical order (i.e. starting with the anterior skull and ending with the distal termini of the hindlimbs).

The source publications were chosen as they give a broad overlap of taxa, and a suitable coverage of diapsid and archosaur taxa. This includes basal diapsids, rhynchosaur, prolacerti-forms, advanced diapsids, and saurian outgroups (a number of basal taxa were removed as they were outside the areas of interest for this study, see Appendix A). Minor marginal adjustments were required to avoid replicating taxa or losing data (if a taxon was deleted). *Sphenodon* and Sphenodontia were treated as identical (i.e. merged), as were *Proterosuchus* and Proterosuchidae, and *Rhynchosaurus* and Rhynchosauridae. (See Appendix A for the full list of changes). In the case of BENTON & ALLEN (1997), there were codings for four different *Tanystropheus* species and two *Malerisaurus* species. These

were combined before comparison, (e.g. codings of 1, 1, 0 and ? would be treated as a 1 by the majority rule assumption with the ‘?’ not contributing to the calculation).

In assessing characters for the matrix, the aim was to retain as many characters, and therefore as much data, as possible. Characters were initially compared among the five source publications to find those that overlapped and whose coding could be combined. In addition, there were a number that could be considered redundant relative to one another.

As an example, author A might use the character “long and narrow ribs at a shallow angle to the vertebrae” and author B “extended thin ribs”. Obviously the described character states of the ribs are similar, but the addition of the angle to the first definition means that they cannot be combined directly as described above. However, both characters cannot be used,

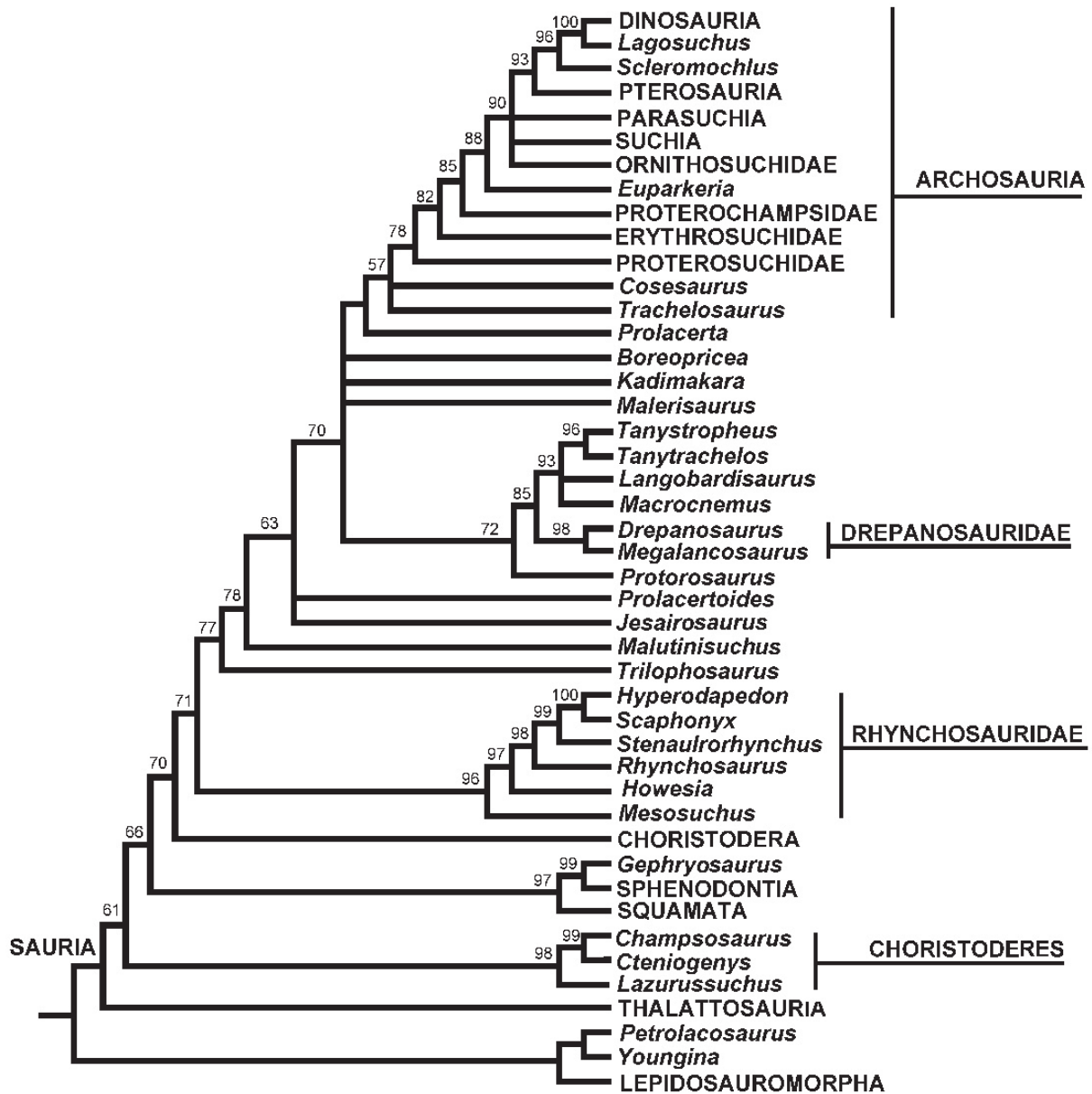


Figure 2: Fifty percent Majority-Rule Consensus Supertree (ST)
The relevant percentage retention values for the MRC are listed in at the relevant nodes.

as much of the information would be replicated. In these situations, the selected character was the one that contained the most information (i.e. had the most number of taxa scored for that character). Some characters were also rescored in order to make the most use of the data. In the above example, if there were three states 0, 1 and 2, with 2 being long, narrow *and* at a shallow angle, the 2's could be re-scored as 1s and compared to the other character ("0" being long, and "1" narrow) with no conflict. Some character choices simply could not be justified either way, being very similar to other characters (or combinations of others) in which case they were excluded. Where these situations occur, they are explained in the character list. In order to render this large data set easier to compare with the source matrices, taxa are listed in alphabetical order, and the characters in anatomical order (i.e. reading from the tip of the snout to the back of the skull, then from front to back down the vertebral column, then forelimbs, and finally hindlimbs, ending at the tips of the toes).

Before the analysis, safe taxonomic deletion (WILKINSON & BENTON 1995) was attempted, but no taxa could be safely deleted. The trees were then constructed in PAUP* Version 4.06b (SWOFFORD 1998) using a heuristic search (the dataset was too large to use an exact method) with stepwise addition and tree-bisection-reconnection (TBR). All characters were used and were unordered, similar to the approach in MRP, and so representing a balanced approach to comparing the methods. Based on previous studies, *Petrolacosaurus* and *Lepidosauromorpha* were selected as outgroups as these represent very basal taxa with the context of the study (cf. EVANS in BENTON 1988). The resultant MPT's were then combined into consensus trees. Both the strict and semi-strict trees were relatively well resolved, however a Majority Rule Consensus tree was retained in order to maximize the amount of phylogenetic resolution available for comment.

The source trees for MRP analysis were constructed in PAUP* using branch-and-bound searches (or heuristic searches where the data sets were too large) using the original data provided by the authors. The same source works were used and all the taxa relevant to the study were included. In the case of EVANS (in BENTON 1988), all the discarded taxa were deleted before the data set was run and the consensus tree calculated (rather than keeping the original tree and deleting the taxa from that, which would not necessarily generate the same tree). In the case of the data from BENTON & ALLEN (1997), the additional species of *Malerisaurus* and *Tanytropheus* were deleted so as to avoid overlap (*Malerisaurus langstoni* and *Tanytropheus longobardicus* were retained as the respective type species). Although not available for safe deletion, *Rhombopholis* was also removed as it was coded for very little data and created many extra MPTs (this was also done in the original study – BENTON & ALLEN 1997).

The supertree matrix was constructed using the matrix representation method available in RadCon (ver 1.1.6) (THORLEY & PAGE 2000), which was then run in PAUP* in order to generate the trees (with a heuristic search due to the large numbers of taxa). MRP is an effective and rapid method of constructing a supertree from the available source trees. Strict consensus trees of the source matrices were used in the construction of this matrix (though all were the same as the semi-strict consensus trees available). The supertree analysis

gave many MPT's, so consensus trees were constructed: strict, semi-strict, and Majority Rule Consensus (MRC). The first two contained very little information as the nodes largely or completely collapsed. However, the MRC tree was much better resolved, and produced broadly similar supertrees. These trees should therefore be considered Consensus Supertrees.

The source trees for the weighted MRP supertree (BININDA-EMONDS & SANDERSON 2001) were constructed in PAUP*. The most parsimonious trees saved and used for the supertree (see above for details) were bootstrapped (10 000 replicates, without replacement, 1000 Max trees were retained) and the support values saved. These were then formatted as TRE files for analysis (with kind assistance from O. BININDA-EMONDS) so that the bootstrap values weighted the characters accordingly (from 0.01 to 1.0). Thus a measure of support is included in the supertree and poorly supported branches receive less weighting than those which are well supported. SuperMRP.pl (BININDA-EMONDS 2005) was then used to produce a 'rooted' MRP matrix (i.e. with an artificial all "0" outgroup added) which was then run in PAUP* to produce the final weighted MRP supertree.

As with the basic supertree, because of the high numbers of taxa, a heuristic search was used. With the exception of the Rhynchosauria, both the strict and semi-strict trees collapsed into unresolved polytomies, so again an MRC tree was produced.

3. Results and discussion

3.1 Supertree and supermatrix methods

The supertree analysis produced a large number of MPTs (33 937). The strict and semi-strict consensus trees were limited in their resolution (largely collapsed), but the majority-rule consensus supertree (ST) is well resolved (see Fig. 2). Many branches are retained above the 90% level, and half of the remainder show values of 75% or more (i.e. are present in percentage of the MPTs).

The weighted supertree analysis did not reach a single most parsimonious tree and was stopped after 60 000 trees were retained (the limit of the computer's memory). This computing limitation did not necessarily affect the outcome of the analysis – it has been identified as both a problem of supertrees (SANDERSON et al. 1998) and also for any analysis with large numbers of taxa and high levels of missing data. Similar 'unfinished' analyses include DAVIES et al. (2004) and RUTA et al. (2003). As with the ST, the weighted MRP supertree had very poor resolution of the strict and semi-strict consensus trees, so again an MRC tree is retained (hereby referred to as the WST). This is also well resolved, with few polytomies (see Fig. 3), although the retention levels of the branches are slightly lower than in the ST (mostly between 75% and 95%).

The supermatrix analysis produced just 121 MPTs of 822 steps (character state changes) each. Both the strict and semi-strict consensus trees are far more resolved than those of the supertree analyses, and the majority-rule consensus tree (MRC) is similarly well resolved (see Fig. 4), and more than two thirds of the branches of the MRC tree are retained at 100%. This indicates that, despite the large amount of missing data, the clades are well supported.

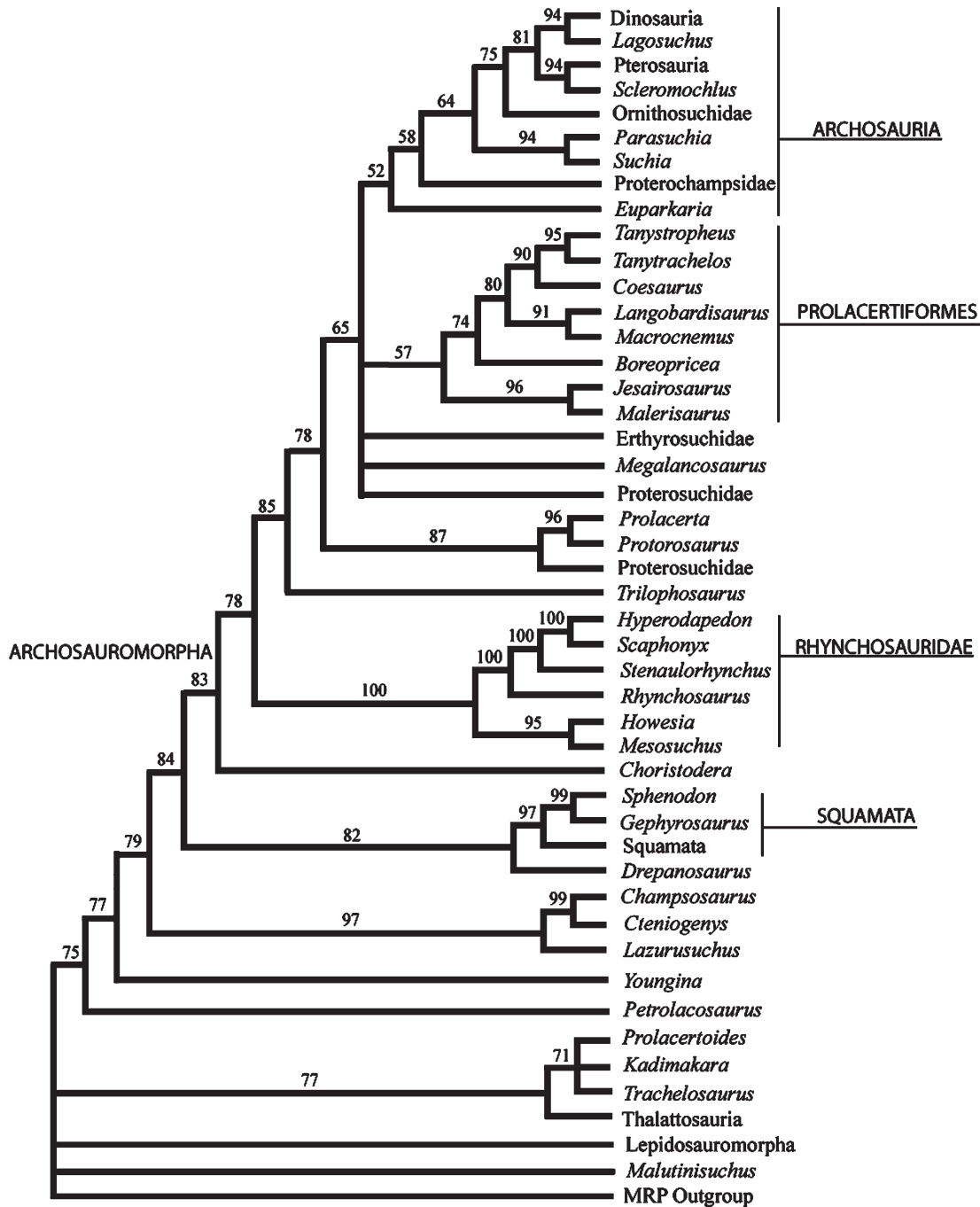


Figure 3: Fifty percent Majority-Rule Consensus Weighted Supertree (WST).
The relevant percentage retention values for the MRC are listed in at the relevant nodes.

In all three trees, some clades are particularly well supported with a high retention or bootstrap values. The ST and SM trees as a whole exhibit a more or less expected pattern of relationships, i.e. they closely match the results of existing studies, including the source trees. The prolacertiforms are relatively well resolved, well supported, and monophyletic. However, in the WST, there are a number of novel rearrangements (i.e. relationships that do not appear in any of the source trees) and disruptions to this pattern, for example a ‘clade’ consisting of *Prolacertoides*, *Kadimakara*, *Trachelosaurus* and *Thalattosauria*. The squamates do not appear in a less derived position than

the choristoderes in any of the source trees, as they do in the ST and WST. This is therefore a novel configuration and thus must be considered as unreliable (PISANI & WILKINSON 2002). Similarly, the Rhynchosauria are not separated from the Archosauria by the Prolacertiformes in any of the source trees as they are here, and this must equally be rejected. Consequently, when compared to the source trees the two primary revisions of the ST and the WST produced by a supertree method, are immediately rejected. In contrast, the topology of the SM tree are predictably similar to the source trees and suffers no such problems.

It has been shown that supertrees perform significantly better with increasing numbers of input trees (BININDA-EMONDS & SANDERSON 2001) and thus the ST and WST may be hindered by a lack of data compared to previous supertree analyses. However, increasing the number of input trees would merely increase bias towards a total evidence approach, which operates equally with any number of input matrices (although clearly larger numbers of matrices would take longer to combine, and low numbers of characters combined with high numbers of taxa would also limit effectiveness).

There is a potential problem with supermatrix analyses in that the results may have less resolution (fewer resolved nodes; lower bootstrap values for some nodes) than the source trees. However, this can occur with any normal cladistic analysis (especially one with large amounts of missing data) and they do still hold the potential to resolve conflicts in the competing source trees and present new hypotheses of relationships. Moreover, a supermatrix may be the only way to resolve a monophyletic / paraphyletic argument between two results produced from data sets of equal size – the only other alternative is a third independent data set. Similarly, any strongly supported, but conflicting, trees are best resolved with a total evidence method (DE QUEIROZ et al. 1995). However, as noted by SANDERSON et al. (1998), the total-evidence method is time consuming, and if the characters and taxa do not overlap significantly, it is easy to be left with a matrix consisting mostly of question marks. Consequently, the results will be poorly constrained at best, and many MPTs may be produced.

With such a high number of characters, character atomization is a potential problem for supermatrix analyses. Character atomization occurs when characters are broken down to such a degree that they are no longer independent of one another. For example, the shape of the acetabulum and head of the femur could be coded separately, whereas their shapes are, in many ways, mutually determining. As a result, some branches receive heightened support simply because one character has been divided into several, all with identical codings. In molecular studies, this may occur where codings for genes and gene products overlap and so reinforce each other, as one is conditional on the other. Character atomization may also occur in morphological analyses or as a result of coding for functional morphology, as the morphological features have been modified to fulfill a single function (SMITH 1994: p. 38).

Hidden redundancy in character lists is always a risk. For example, the characters ‘frontal is longer than nasal’ and ‘nasal is shorter than frontal’ are identical, and yet although an unskilled anatomist should spot that both are identical, it is unlikely that they would observe that both are also probably redundant with ‘orbit is longer than high’ (where the antero-posterior dimension of the orbit is associated with the same dimension of the frontal bone). Here, the redundancy could be missed unless specialist anatomical knowledge is brought into play, since the two forms of the characters might well have been presented by different authors, and they sound rather different. However, such cases are rare, at least in the present analysis – based on a careful query of all characters.

The results of this study show that, as may be expected, MRP methods are capable of producing spurious results (PISANI & WILKINSON 2002, WILKINSON et al. 2005). The two primary novelties (the basal position of the choristoderes relative to

the squamates, and the displacement of the Rhynchosauria from Archosauria) found by MRP on the ST and WST trees have both been demonstrated to be spurious and unreliable in this analysis. Here, they do not reflect the source trees and so must be rejected (PISANI & WILKINSON, 2002). In contrast, the SM method produces a well-structured tree with some strong branches (high bootstrap values) and well-defined clades. This would suggest that the prolacertiforms are indeed monophyletic and that the rhynchosaurians are the sister group to the crown-group archosaurs.

3.2 The relationships of the prolacertiforms and pterosaurs

The relationships of the prolacertiforms as a whole are well resolved in both the ST and SM trees, though less so in the WST (taxa such as *Drepanosaurs* and *Prolacertoides* are missing from the clade labelled in Fig. 3 indicating that it is polyphyletic according to the taxa traditionally make up the clade). However, their paraphyly in the ST tree aside, they exhibit very different topologies between the trees. The SM MRC tree has one large polytomy, (polytomies are common in previous analyses of the prolacertiforms), and the majority of taxa show similar relationships to those seen in the source trees. However, in the ST tree, the topology corresponds more closely to a Hennigian comb. Taxa roughly match the positions of their counterparts in the source trees, but they differ from the arrangement in the SM tree. Given the large variation in the source trees, neither of these results can be treated as preferable to the other. Even the supposed paraphyly of the prolacertiforms evident in the ST tree cannot be discounted, as this configuration was recovered by DILKES (1998). In the WST tree, *Prolacerta* is not included in the prolacertiforms (as found by DILKES 1998), but of greater importance is the separation of *Megalancosaurus* and *Drepanosaurus* – a well established sister-taxon relationship (both are drepanosaurids known from numerous near-complete fossils). The former forms part of a polytomy basal to the prolacertiforms and in a polytomy with the archosaurs. *Drepanosaurus* however, has a new position significantly further down the tree and joins the squamates – a highly suspect relationship not found in any source tree.

Aside from the most basal taxa, all three trees differ in the topology and relationships of important clades (Figs 2–4). In addition to the details reported for the prolacertiforms, most of the major diapsid clades show marked variation in their relationships among the three trees. The SM tree reflects results reported by the majority of previous authors, although the Rhynchosauria might be expected to lie basal to the Prolacertiformes (JALIL 1997). The ST and WST trees in contrast, the Choristodera are basal to the Squamata. In both trees the prolacertiforms are paraphyletic, reflecting DILKES (1998), wherein *Prolacerta* is separate and more derived than the prolacertiforms. However, here in the ST the prolacertiforms are dispersed within the tree and in the WST *Prolacerta* is basal to this clade, and not derived with respect to it.

The Pterosauria lie as sister group to the Dinosauria or *Scleromochlus* + Dinosauria (as ornithomirans) in both the ST and WST trees. This result matches the primary analysis of BENNETT (1996) and is clearly the source of their

position as this was the only source tree that included them. However, they remain among the more basal archosaurs in the SM tree, although they are well separated from the prolacertiforms. This is similar to the secondary analysis recovered by BENNETT (1996) and so is hardly unexpected, but clearly the addition of further characters and taxa to this analysis has not resulted in pterosaurs taking a more basal position (i.e. close to or among the basal diapsids).

BENNETT (1996) asserted that certain hindlimb characters of pterosaurs are non-homologous to, but convergent with, those of the higher archosaurs (See HONE & BENTON 2007). Nonetheless, as a simple test of BENNETT's (1996) suggestion, the supermatrix analysis was repeated with the successive removal of the appendicular characteristics (both forelimb, hindlimb, pectoral and pelvic girdles, and then just hindlimb and pelvic girdle). In both cases the

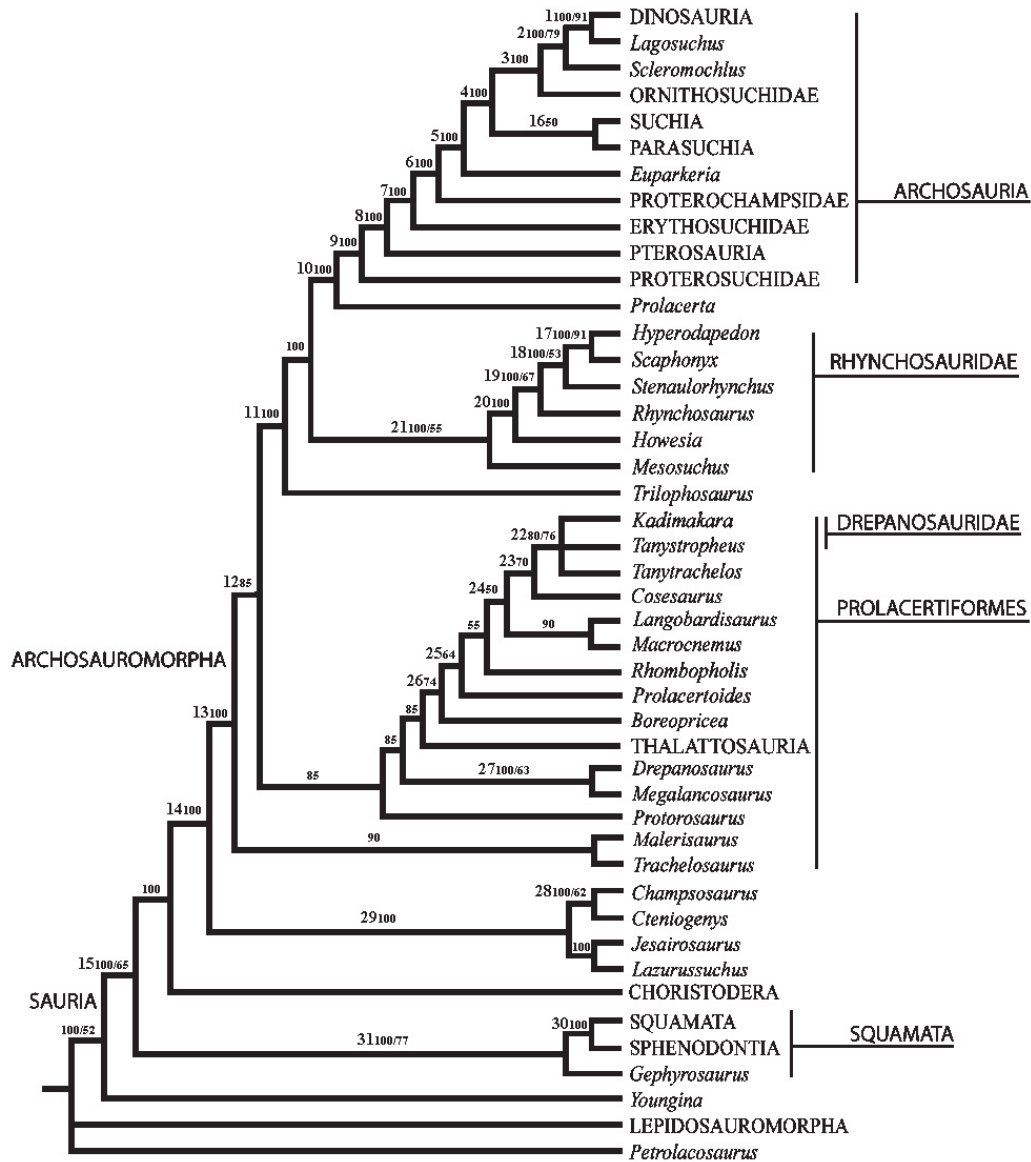


Figure 4: Fifty percent Majority-Rule Consensus Supermatrix Tree (SM).

Bold numbers refer to nodes and branches (lying on top of the branch before the node in question, (e.g. 1 refers to the node for DINOSAURIA / *Lagosuchus*), in some cases the branch to an individual taxon is referred to and here the number is placed after the taxon on the right-hand side. The defining characters associated with each node are listed in appendix 2B. Bootstrap figures (as a percentage, 10 000 replicates with replacement) are also given where relevant after the MRC figure, e.g. 99/65 is a node with 99% appearance on the MRC tree with a 65% retention when bootstrapped.

Pterosauria remained in the same location as in the original supermatrix analysis, basal to the Erythrosuchidae, and did not pair with more basal taxa, just as BENNETT (1996) showed. However, without character deletion, the only valid standpoint

in our view, reanalysis of BENNETT's (1996) data matrix results in pterosaurs appearing as a sister group of dinosauromorphs, the 'normal' result. Since these variations mirror the topologies seen in the SM tree, it appears that limb characters are not a key

part of the evidence for the phylogenetic relationships of the pterosaurs. Therefore, hindlimb characters may be considered homologous between the pterosaurs and dinosauriforms: supporting the traditional view. This is in spite of their more basal position than might be expected which can be attributed to the very high levels of missing data in the supermatrix. The pterosaurs are recovered in a more basal position in the SM tree than might be expected, but still more derived than the possibilities recovered by BENNETT (1996) and others.

According to BININDA-EMONDS (2004a) the WST tree should prove more reliable than a simple MRP tree. However, as with the ST, the WST can be rejected because of the appearance of novel arrangements of taxa, including some combinations of taxa present in the WST that do not even appear in the ST. Although the weighting of input trees should significantly reduce the problems of over-weighting large trees and / or poorly supported trees, it also appears to mar the clarity of the results. In this study, the problem of a novel rearrangement of clades not seen in any source tree (e.g. the choriosteres appearing both more basal to, and more derived than, the Squamata) rules out the ST tree for empirical reasons. However, this does not necessarily invalidate the method, even if it poses a serious question over reliability (as also shown by PISANI & WILKINSON [2002], and WILKINSON et al. [2005]) it merely allows us to reject a single tree produced by that method. The WST tree generates both novel rearrangements of clades and a large number of what must be spurious clades.

The archosaurs and rhynchosaurs are well defined as they appear in only one source tree. However, all the other clades have produced novel and / or spurious relationships whose origins are harder to determine. This appears to be a function of how well represented each taxon is in the MRP matrix (i.e. the number of occurrences in source trees). Experimentation in which basal taxa were selected as outgroups rather than an all '0' MRP outgroup produce similar results (i.e. many novel clades and pairings) and often resulted in inversions of well-supported relationships (e.g. archosaurs basal all other clades). The generation of novel clades by MRP and weighted MRP methods is a complex problem associated with weighting, missing data and MRP algorithms that require further investigation. As noted by O. BININDA-EMONDS (pers. comm.), this is a problem for MRP trees as consensus methods alone, and not if they are considered as simply a way of producing a 'best fit' of the input trees.

3.3 Analysis times

Reconstructing large palaeontological cladograms is evidently problematic. While the total evidence approach here produces strong results, it is extremely time-consuming. In particular when multiple overlapping data sets are concerned, the time necessary to compare all taxa and characters is very great and thoroughly testing for redundant characters is an extremely time-consuming operation. Even aligning non-overlapping data sets can take inordinate amounts of time and then, as ever, with a high number of taxa, analysis is limited to heuristic searches by cladistic programs that do not guarantee to find all, or indeed any of the MPTs. Given the levels of missing data in an 'average' paleontological data set it is not surprising that many MPTs are often generated.

In short, while they may be reliable, supermatrix methods are time-consuming and they have the potential to find large numbers of sub-optimal trees.

In contrast, MRP methods have sharply contrasting characteristics. They provide a rapid result – source trees can be fed directly into RadCon and the supertree matrix can be generated in minutes, although analysis time for both methods depends on the specifics of the matrix. However, the results of this study suggest that the reliability of the MRP technique is poor and, as discussed above, not enough is yet known about how MRP manipulates some branches and can produce spurious results (PISANI & WILKINSON 2002; WILKINSON et al. 2005) and by extension how MRP optimises matrix conflicts. As with the above approach, large numbers of sub-optimal trees may be generated with high numbers of taxa.

This leads to the conclusion that neither method provides a good balance between speed and accuracy. If source trees agree, then supertrees are quick and reliable, but if not, they are unlikely to discover the one 'true' phylogeny as represented by the underlying data (WILKINSON et al. 2005). Therefore, if speed is to remain the primary factor in choosing a method of assembling multiple datasets, a much greater level of investment is required in understanding and improving MRP as a supertree method, or moving on to other methods, though their effects must be explored. As the situation stands, MRP is unsuitable for resolving conflicting source trees and total evidence methods require too much time to be efficient for large morphological analyses.

4. Conclusions

The results of these studies suggest that, as proposed by DILKES (1998) and MODESTO & SUES (2004), *Prolacerta* is not a member of the Prolacertiformes. However, the remaining taxa that make up the Prolacertiformes can be considered a monophyletic sister group to the Archosauria. The clade should be renamed and redefined accordingly (see also HONE & BENTON 2007). The results of this study do not support a close relationship between the Pterosauria and the Prolacertiformes but instead confirms the results of previous studies that they are derived archosaurs, and are probably form the clade Ornithodira, with the dinosauriforms.

This result is recovered using a very large dataset comprising of hundreds of characters and using multiple techniques. No analysis this large has previously been published concerning the origins of pterosaurs and despite the supermatrix not being a 'traditional' cladistic datamatrix, a number of characters are still recovered supporting this derived position of pterosaurs. Far more work is still required on this subject however, as much data is missing from the supermatrix which could be filled based on specimen work as its lack is due to non-overlapping datasets and not inapplicable coding or missing parts of fossil specimens.

In comparing supertree and supermatrix methods, it can be concluded that problems inherent in supertree construction are highly significant. The trees were relatively well resolved, but previously well supported branches (in the original source trees) were lost, and robustly supported hierarchies reversed. In contrast, the total-evidence approach produced a well-resol-

ved tree with relatively strong branch support. However, the considerable amount of time that had to be committed to the supermatrix approach (estimated at about 800 hours to create the data set, versus just one hour for the supertree and only three hours for the weighted supertree – the supermatrix data also took significantly longer to analyse) seriously weakens the applicability of the technique. However, the time issue is unlikely to be so severe with molecular data.

In coming years, as demand grows for ever-larger segments of the tree of life, and especially for complete trees consisting of perhaps hundreds or thousands of species, supertree methods seem at the present time to be the only approach that can produce results. Improvements to the MRP technique or its replacement by another method, are probably a more fruitful strategy than further emphasis on total evidence methods. Even though total evidence methods at present are methodologically superior to supertree methods, the time-consuming elements are those that involve specialist human input – namely the careful combination of separate matrices, and checking for redundancy of taxa and characters, and especially the latter. Those processes can never be automated.

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Appendices:

A

Characters used in phylogenetic analysis

All the characters from the source matrices are listed below. All that were removed from the analysis have been marked as such and are given no number. All are in anatomical sequence. The descriptions for each are taken in unmodified form from the publications hence the variation in whether or not they are listed with character states. Where these are given they are placed in brackets with slashes denoting the different states (with 0 always first).

Abbreviations:

- A = Absent
- L = Long
- R = Reduced
- P = Present
- S = Short
- N = No
- Y = Yes

Therefore, 'Femur (L/R/S) D23' would denote that a long femur was coded as 0, a reduced one as 1 and a short one as 2. The character was used by Dilkes and was number 23 in his data set.

The original authors of characters have been coded as follows for simplicity:

BENNETT (B), BENTON & ALLEN (BA), DILKES (D), EVANS (E – EVANS listed her characters in sections A1–4, B1–8 etc. Here we retain the more conventional system of numbering them consecutively, but a conversion is given below for ease of comparison), and JALIL (J).

Representation of taxa in the source matrices is as follows:

TAXA	EVANS	JALIL	BENNETT	BENTON & ALLEN	Dilkes
<i>Boreopricea</i>	#	#		#	
<i>Champsosaurus</i>					#
<i>Choristodera</i>	#	#			
<i>Cosesaurus</i>	#	#		#	
<i>Cteniogenys</i>					#
<i>Dinosauria</i>			#		
<i>Drepanosaurus</i>	#				#
<i>Erythrosuchidae</i>			#		
<i>Euparkeria</i>			#		
<i>Gephyrosaurus</i>	#				#
<i>Howesia</i>	#				#
<i>Hyperodapedon</i>					#
<i>Iguana</i>		#			
<i>Jesairosaurus</i>		#			
<i>Kadimakara</i>	#	#		#	
<i>Lagosuchus</i>			#		
<i>Langobardisaurus</i>				#	
<i>Lazarussuchus</i>					#
Lepidosauromorpha			#		
<i>Macrocnemus</i>	#	#			
<i>Malerisaurus</i>	#	#		#	
<i>Malutinisuchus</i>		#			
<i>Megalancosaurus</i>	#			#	#
<i>Mesosuchus</i>	#				#
Ornithosuchidae			#		
Parasuchia			#		
<i>Petrolacosaurus</i>					#
<i>Prolacerta</i>	#	#		#	#
Prolacertiformes			#		
<i>Prolacertoides</i>	#	#			
Proterochampsidae			#		
Proterosuchidae			#		
<i>Proterosuchus</i>	#	#			#
<i>Protorosaurus</i>	#	#		#	#
Pterosauria			#		
<i>Rhombopholis</i>				#	
<i>Rhynchosaurus</i>		#			#
Rhynchosauria			#		
Rhynchosauridae	#				
<i>Scaphonyx</i>					#
<i>Scleromochlus</i>			#		
Sphenodontia		#			
Squamata	#				
<i>Stenaulorhynchus</i>					#
Suchia			#		
<i>Tanystropheus</i>	#	#		#	#
<i>Tanytrachelos</i>	#	#		#	
Thalattosauria	#				
<i>Trachelosaurus</i>	#	#			
<i>Trilophosaurus</i>	#	#		#	#
<i>Youngina</i>	#	#			#

The following taxa were deleted from the EVANS dataset:

Araeoscelis, Aphelosaurus, Mesenosaurus, Coelurosauravus, Claudiosaurus, Heleosaurus, Galesphyrus, Blomosaurus, Noteosuchus, Palaeagama, Heleosuchus, Hovasaurus, Acerosodontosaurus, Thadeosaurus, Kenyasaurus, Tangasaurus, Saurosternon, Kuehneosauridae, Diphydontosaurus, Planocephalosaurus, Clevosaurus, Homeosaurus, Malutinisuchus, Kallimodon, Pleurosauridae, Paliguana, Kudnu, Colubrifer, Iguana, Aenigmatosaurus, Lacertulus.

EVANS conversion:

A	1	–	4
B	5	–	12
C	13	–	26
D	27	–	33
E	34	–	64
F	65	–	69
G	70	–	90
H	91	–	97
I	98	–	119
J	120	–	145
K	146	–	174
L	175	–	194
M	195	–	200
N	201	–	205
O	206	–	216
P	217	–	226

Cranial Characters:

1. Symphysis (P/A)	D127
2. Skull (midline > than max. width / less)	D1
- Metakinetic Skull	B9
<i>ALL 1s</i>	
3. Skull height (less than 1/3 length / = or + 1/3 length)	B31
- Skull shape (rounded in cross-section / subtrapezoidal)	B32
<i>AUTAPOMORPHY</i> Lepidosauromorpha	
4. Skull low and narrow with short and narrow postorbital region (N/Y)	J38
5. Elongation of temporal and antorbital regions	E164
6. Length of snout (<50% of total length / >)	D2, E91, J64
- Long gavial-like snout	E224
<i>AUTAPOMORPHY</i> Choristodera	
- Premaxilla size (S/L)	B1
<i>AUTAPOMORPHY</i> Lepidosauromorpha	
7. Chisel-like premaxillary region	E156
8. Dorsomedial process of premaxilla (extends beyond narial openings / reduced)	BA1, E51
9. Premaxilla (horizontal ventral margin / down-turned ventral margin)	D6
10. Shape of maxillary ramus of premaxilla (extends as posterodorsal process to form caudal border of naris Y/N)	D8, E70, J25
11. Premaxilla extends anterolaterally to form slender rostrum	E201
12. Enlarged posterolateral process on premaxilla	E212
13. Prominent subnarial process of premaxilla (A/P)	B2
14. Premaxilla and prefrontal (no contact / contact)	D7
- Premaxilla contacts frontals, separates nares in midline	E203
<i>AUTAPOMORPHY</i> Choristodera	
15. External nares confluent, no median dorsal process on premaxilla	E206
16. Confluent nares	E217
17. External nares location (marginal / midline)	D11
18. External nares (separate / single, medial naris)	D10
19. External nares shape (rounded / elongate)	D12
- External nares are placed posteriorly	E202
<i>AUTAPOMORPHY</i> Thalattosauria	

- Slender nasals, fused in midline	E218
<i>AUTAPOMORPHY</i> Choristodera	
20. External naris elongated anteroposteriorly and close to midline (N/Y)	E218 / 86, J26
21. Single median naris	E66
22. Form of suture b/w premaxilla and maxilla above dentigerous margin (simple vertical or diagonal contact / notch present in maxilla)	D17
23. Maxilla (horizontal ventral margin / convex ventral margin)	D16
24. Tall maxilla	E37
25. Number of grooves on maxilla (none / one / two)	D62
26. Septomaxilla (P/A)	D14
- Septomaxilla elaborated to protect vomeronasal organ	E177
<i>AUTAPOMORPHY</i> Squamata	
27. Contact between vomer and maxilla (A/P)	D38
28. Contact between ectopyerygoid and maxilla (A/P)	D40
29. Nasals taper anteromedially	E50, J49
- Vomers (long and broad / reduced)	B39
<i>AUTAPOMORPHY</i> Lepidosauromorpha	
30. Shape of cranial margin of nasal at midline (strongly convex with little anterior process / transverse with little convexity)	D13
31. Nasals longer than the frontals (N/Y)	BA2, D18, E94, J61
32. Lacrimal (L/S or A)	J15
33. Lacrimal fails to meet nasal	D15, E35, J50
- Lacrimal contact with nasal (P/A)	BA5
<i>CANNOT JUSTIFY</i>	
- Lacrimal fails to reach external nares	E14
<i>CANNOT JUSTIFY</i>	
34. Lacrimal (contacts nasal and reaches external naris / does not contact or reach)	D15
35. Lacrimal extent (element runs forward from the orbit / restricted to the orbital rim in lateral view)	BA6
36. Prefrontal-nasal structure: orientated anteroposteriorly to internasal suture or anterolaterally directed	J1
- Long pre-frontals meet in midline, separate nasals from frontals	E219
<i>AUTAPOMORPHY</i> Choristodera	
- Frontoparietal suture (interdigitating / straight)	BA3
<i>AUTAPOMORPHY</i> <i>Boreoprincea</i>	
37. Ratio of frontals and parietal (>1.0 / <1.0)	D19
38. Shape of dorsal surface of frontal next to sutures with postfrontal and parietal (flat to slightly concave / depressed with deep pits)	D20
39. Fused postorbitofrontal	E225
40. Postfrontal (L/S/A)	B33
41. Shape of dorsal surface of postfrontal (flat to slightly concave / depressed with deep pits)	D21
42. Postfrontal dimensions (substantial tripartite element / short lacking clear process)	BA7, E30
43. Postfrontal enters upper temporal fenestra, loss of postorbital / parietal contact	D24, E195
44. Narrow parietal	E162 / 174
45. Fused parietals	E175
46. Parietal foramen lost or at frontoparietal suture	E207
47. Transverse frontoparietal suture	E176
48. Median contact of parietals (suture present / parietals fused with loss of suture)	D25
49. Parietal table (broad / constricted without sagittal crest / sagittal crest present)	D26
50. Parietals (do not send caudal process onto occiput / do)	B34
- Shape of median border of parietal (level with skull table / drawn downwards to form ventrolateral flange)	D28, E20
<i>AUTAPOMORPHY</i> <i>Petrolacosaurus</i>	
51. Postparietals (P/A)	B35, D29, E123 / 29, J14
52. Postparietals (paired / fused)	B35
53. Postparietals (L/S)	J3
54. Postorbital and parietal contact (P/A)	D22
55. Posterior process of postorbital (does not extend beyond back of lower temporal fenestra / extends back beyond the posterior margin of the lower temporal fenestra)	BA8
56. Postorbital with posterior process extending back beyond end of upper temporal fenestra	E99

57. Ratio of lengths of anteroventral and posterodorsal processes of postorbital (>1.0 / <1.0) D23
58. Reduction of ventral ramus of squamosal: cotyle for quadrate head BA9, B5, E54
59. Loss of ventral ramus of squamosal E178 / 209, J54
- Frequently ventral peg of squamosal fits into quadrate notch E183
- AUTAPOMORPHY Squamata*
60. Anteroventral process of squamosal (broad ventrally with distal width that is approx. equal to dorsoventral height / narrow ventrally with distal width less than dorsoventral height / absent) D34
61. Otic notch B46
- Slender stapes E75 / 130
- AUTAPOMORPHY Petrolacosaurus*
62. Stapes lacks foramen B19, E87
63. Posterior process of jugal extending posteriorly nearly to back of skull (N/Y) J28
64. Lateral surface of jugal above maxilla (continuous / lateral shelf present) B8, D33
65. Subtemporal process of jugal (robust / slender) B38, D32, J42
66. Postorbital ramus of jugal (extends to middle of lower temporal fenestra / extends well posterior to the centre of lower temporal fenestra) B4
67. Posterior process of jugal (P/A) BA10, E210
68. Reduced rod-like quadratojugal under lower temporal fenestra contacts jugal E100
69. Posterior process of jugal extends beyond midpoint of lower temporal fenestra E72
70. Contact b/w ectopterygoid and jugal (restricted with area of contact approx. equal to or less than contact b/w ectopterygoid and pterygoids / ectopterygoid expanded caudally) D39
- Ectopterygoid (broadly contacts the maxilla and narrowly contacts the jugal in ventral view / more or less broadly contacts the jugal behind the posterior limit of the maxilla) B10
- CANNOT JUSTIFY*
71. Shape of ectopterygoid along suture with pterygoids (transversely broad / posteroventrally elongate and does not reach lateral corner of transverse flange / posteroventrally elongate and reaches corner of transverse flange) D42
72. Entepicondylar foramen (P/A) E192, J32
- Ventral extent of quadrate (abductor chamber S/L) B8
- AUTAPOMORPHY Lepidosauromorpha*
73. Quadratojugal shape; an indicator of whether there is a complete lower temporal bar (low and with anterior process / tall with reduced anterior process) BA11
74. Quadratojugal L-shaped and or situated behind upper temporal fenestra (N/Y) J27, B7
75. Tall quadratojugal with reduced anterior process E84
76. Loss of quadratojugal and quadratojugal foramen E179
77. Quadratojugal (P/R/A) BA12, J43, E43, E121, D35
78. Quadrate (covered laterally / exposed laterally) D36, E23
- Greatly reduced quadrate / pterygoid overlap E181
- CANNOT JUSTIFY*
79. Quadrate emargination (A/P) D37, J5, E26
- Reduction in quadrate / quadratojugal conch E168
- CANNOT JUSTIFY*
80. Quadrate tall, more than half height of lower temporal fenestra E85
81. Upper temporal fenestra E1, D3, B44
- Upper temporal fenestra slit-like or obliterated E204
- AUTAPOMORPHY Thalattosauria*
82. Post-temporal fenestra D53, B15, J65
- Suborbital fenestra E2
- ALL 1's
- Lower temporal fenestra E3, D4
- ALL 1's*
83. Posterior border of lower temporal fenestra bowed B45, E31
84. Antorbital fenestra (A/P) B45, D18, E27
85. Elements contributing to lateral border of suborbital fenestra (ectopterygoid, palatine and maxilla / or ectopterygoid and palatine contact to exclude maxilla) D41
- Antorbital fenestra position (separate from naris / close to naris) B42
- AUTAPOMORPHY Lepidosauromorpha*
86. Prominent antorbital fossa surrounding antorbital fenestra (A/P) B43
87. Lower temporal arcade (A/P) J13
88. Parasphenoid-basisphenoid in the side wall of braincase (N/Y) J68

- Preorbital region consisting of maxillae, pterygoids, palatines and nasals (elongate/not elongate)	B3
<i>AUTAPOMORPHY</i> Lepidosauromorpha	
89. Posterior margin of skull table deeply emarginated, lies well forward relative to quadrate	E205
90. Paraoccipital foramen	J7
- Paraoccipital process touches suspensorium	E74 / 125
<i>AUTAPOMORPHY</i> <i>Petrolacosaurus</i>	
- Loss of postsplenial	E15
<i>AUTAPOMORPHY</i> <i>Petrolacosaurus</i>	
91. Pineal foramen (present or large / reduced or absent)	B14, BA4, E71
92. Parapineal foramen (P/A)	D27
93. Development of retroarticular process	E24, J8
- Reduction in retroarticular process	E169
<i>AUTAPOMORPHY</i> <i>Sphenodon</i>	
94. Tabulars (P/A)	B6, D30, J2
95. Cleithrum (P/A)	B23, D93, J9
96. Coronoid (P/A)	B48
97. Stapedial (P/A)	J6
- Epipterygoid reduced to slender column	E180
<i>AUTAPOMORPHY</i> Squamata	
- Paroccipital process, supratemporal and parietal closely associated and providing support for head of the quadrate	E182
<i>AUTAPOMORPHY</i> Squamata	
- Paraoccipital process (ends freely / reaches suspensorium)	D52
<i>AUTAPOMORPHY</i> <i>Petrolacosaurus</i>	
98. Paroccipital process distally expanded	E184
- Metotic fissure divided to give separate opening for cranial nerve 9 and perilymphatic duct	E185
<i>AUTAPOMORPHY</i> Squamata	
- Complete vidian canal	E186
<i>AUTAPOMORPHY</i> Squamata	
99. Orientation of basipterygoid processes (anterolateral / lateral)	D43
- Loss of supraglenoid buttress	E16
<i>AUTAPOMORPHY</i> <i>Petrolacosaurus</i>	
100. No ectepicondylar groove or foramen	E33, J21
101. Absence of supratemporal	B36, BA13, D31, E208 / 220
102. Supratemporal (when present) lies deep	E188
103. Ossified lateraosphenoid	B40, D50
104. Pila antotica	J69
105. Complete abducens canal and dorsum sellae	E133
106. Foramen for entrance of internal carotid arteries (lateral wall of braincase / ventral surface of parasphenoid)	D45
107. Club-shaped ventral ramus of opisthotic (A/P)	B12, D46
- Paraoccipital process of the opisthotic (do not contact suspensorials / contact suspensorial with tapered distal ends / contact with vertically expanded distal ends)	B12
<i>CANNOT JUSTIFY</i>	
108. Lateral surface of prootica (continuous and slightly convex/crista prootica present)	D47, J70
109. Anterior inferior process of prootica (A/P)	D48
110. Coracoid process	D94
111. Abducens foramina	D49
112. Position of occipital condyle	D51
113. Supraoccipital	D54
114. Pyriform recess	C11
115. Exoccipital and opisthotic (separate / fused)	B37
116. Depth of lower jaw measured at max. height of adductor fossa relative to length of jaw from tip to articular (<25% / >25%)	D70
117. Jaw symphysis	D71
118. Jaw occlusion	D65
- Propalinal jaw action	E71
<i>AUTAPOMORPHY</i> <i>Sphenodon</i>	
119. Occipital condyle anterior to craniomandibular joint (N/Y)	J66
120. Divergence of dentaries cranial to symphysis (A/P)	D72

121. Dentary-coronoid-surangular profile (horizontal to convex / concave caudal to coronoid)	D73
122. Number of tooth rows on dentary (one / two / more)	D64
123. Dentary-splenic mandibular symphysis length (distally positioned / present along $\frac{1}{3}$ of lower jaw)	B47
124. Posterior process of dentary extends beyond coronoid	E147
125. Pterygoids (join cranially / remain separate)	D126
126. Angular reduced to less than $\frac{1}{3}$ rd lateral height of jaw	E136
127. Retroarticular process entirely formed by articular (N/Y)	D74, J18
128. Uprturned retroarticular process (A/P)	D75
129. External mandibular fenestra	B49, D76
130. Premaxilla with acrodont teeth	D9, E65
131. Maxillary tooth plate (A/P)	D60
132. Location of maxillary teeth (only on occlusal surface / on occlusal and lingual surfaces)	D63
133. Palatal elements covered by a shagreen of teeth	B54, E222
134. Teeth on palatine ramus of pterygoids (present in two fields / present in one field / present in three fields / absent)	D68, E170
- Enlarged palatine tooth row, roughly parallel to maxilla	E146
<i>CANNOT JUSTIFY</i>	
135. Teeth on transverse flange of pterygoids (single row / multiple / absent)	B53, D69, E124
136. Location of maxillary teeth (only on occlusal surface / on occ. and lingual surfaces)	D63
137. Number of tooth rows on maxilla (single / multiple)	D61
138. Posterior dental teeth lie anterior to posterior maxillary teeth	B18, BA14, E95, J62
139. Tooth implantation	B2, D55, E132
140. Thecodont teeth	E223
- Alternating acrodont teeth	E149
<i>AUTAPOMORPHY Sphenodon</i>	
- All thecodont teeth in adult	E154
<i>AUTAPOMORPHY Sphenodon</i>	
141. Pterygoid flange teeth	BA16
142. Reduction in pterygoid teeth	E25
- Posteromedial flanges on maxillary teeth	E152
<i>AUTAPOMORPHY Sphenodon</i>	
- Anterolabial flanges on dentary teeth	E151
<i>AUTAPOMORPHY Sphenodon</i>	
- Teeth mediolaterally expanded	E172
<i>AUTAPOMORPHY Trilophosaurus</i>	
143. Teeth circular or square in cross-section	E173
144. Teeth oval or compressed	D59, B17
145. Marginal teeth laterally compressed and serrated	B50, D57, E28
146. Recurved teeth	B16, D58, E96, J63
- Postereolateral flanges on some palatine teeth	E157
- Prominently flanged and striated teeth on posterior region of the maxilla	E158
- No caniniform teeth	E17, D56
- No parasphenoid teeth	E22
147. Vomerine teeth (P/A)	D66, E187
148. Palatine teeth (P/A)	D67
149. Crown of marginal teeth (single point / tricuspid)	D136
150. Enlarged anterior dentary teeth project upward between upper tooth rows in more or less prominent diastema, often accompanied by more or less prominent notch between premaxilla and maxilla (A/P)	B51
- Three or fewer premaxillary teeth on each side	E155
<i>EXCESS OF TOOTH CHARACTERS</i>	
- Four or fewer premaxillary teeth on each side	E153
<i>EXCESS OF TOOTH CHARACTERS</i>	
151. Seven or fewer premaxillary teeth on each side	BA15, E150
Axial Characters:	
152. Atlantal intercentrum (normal / enlarged)	B99
153. Odontoid prominence on atlas pluerocentrum (A/P)	D133
154. Division of presacral vertebral column into cervical, cervicodorsal and dorsal regions (A/P)	B102

155. Dimensions of cervical neural spine (tall with height and width approx. equal / long and low with height < width)	BA20, D82, E34, J40
156. Number of cervical vertebrae (7 or fewer / more than 7)	BA17, E98
157. Number of cervical vertebrae (fewer than 10 / 10 or more)	BA18, J56
158. Postaxial cervical intercentra (P/A)	D79
159. Relative length of mid and posterior cervical and dorsal vertebral centra (cervical centra subequal in length to dorsals / cervical centra longer than dorsals)	BA19
160. Distal ends of cervical neural spines (no expansion / expansion present in form of flat table)	D143
161. Length of centra of cervical vertebrae 3-5 (shorter than those of mid-dorsal v / subequal / greater)	B100
162. Centra of cervical vertebrae 3-6 (no more than moderately inclined / steeply inclined)	B101
163. Cranial margin of cervical neural arch (straight / notched to form overhang)	D134
164. Cervical vertebrae longer than dorsals	E4
165. Twelve cervical vertebrae	E59, J56
166. Longest cervical vertebra lies at end of series	E61
167. Cervical centra shorter than mid-dorsals	D81, E67 / 196
- Cervical intercentra form hypapophyses	E189
<i>AUTAPOMORPHY</i> Squamata	
- Mammillary processes on neural spines of posterior cervical and anterior dorsal vertebrae	E7
<i>AUTAPOMORPHY</i> <i>Petrolacosaurus</i>	
168. Loss of trunk intercentra	BA24, D80, E32, J67
169. Neural arches of mid-dorsals (shallowly excavated / deeply excavated)	D84
170. Dorsal neural spine height (tall / low with height < length)	BA23, D85, E101
171. Ovoid spine-table on top of neural spine (A/P)	BA21
172. Transverse processes of trunk vertebrae well developed (N/Y)	B21 E88 / 214, J31
173. Number of sacral vertebrae (0-2 / 3+)	B56
- Fifth metatarsal at least double length of second sacral centrum	E113
<i>ALL "0"s</i>	
174. Intercentra of postaxial presacral vertebrae (P/A)	B55
175. First caudal (separate from sacrum / incorporated into sacrum)	D128
176. Caudal zygapophysis (inclined / nearly or fully vertical)	D129
177. Distal ends of caudal neural spines (not expanded / expanded)	D139
178. Tall neural spines in dorsal and anterior caudal region	D88, E119
179. Caudal autotomy	E134
- Loss of caudal anatomy	E165
<i>ALL "0"s</i>	
- Caudal zygapophyseal facets (disposed no more than 45-60 degrees from horizontal / nearly vertical)	B103
<i>AUTAPOMORPHY</i> Dinosauria	
180. Postcloacal bones (A/P)	B129, BA48, E62, J60
181. Diapophysis and parapophysis (parapophysis in anterior dorsal vertebrae transfers from centrum to neural arch)	B58
- Swollen neural arches with deep lateral excavations	E5
<i>AUTAPOMORPHY</i> <i>Petrolacosaurus</i>	
- Strong ventral keels on cervical and anterior dorsal vertebrae	E6
<i>AUTAPOMORPHY</i> <i>Petrolacosaurus</i>	
182. Haemal spines large and plate like	B127, D91, E118
183. Curvature of haemal spines (no curvature / cranial curvature present)	D141
184. Platycoelous vertebrae	E213
185. Spine tables (A/P)	B57
- Neural spines with specialised intervertebral facets	E105
<i>AUTAPOMORPHY</i> <i>Youngina</i>	
186. Neurocentral surfaces (closed in adult / open in adult)	D131
187. Intervertebral articulation formed by zygosphenes-zygantrum (N/Y)	E135, J20
188. Ossified epiphyses with discrete centres	E138
- Elongation of vertebral column by addition of pre-sacrals	E166
<i>AUTAPOMORPHY</i> Thalattosauria	
189. Vertebrae non-notochordal in adult (N/Y)	B20, D83, E76, J29
190. Coracoid (large plate / small with sub-circular profile)	B105
191. Ratio of lengths of caudal transverse processes and centra (<1.0 / >1.0)	D89, J36

- Slender and tapering cervical ribs at low angle to vertebrae (A/P)	B22, BA22, D77, E92
<i>CANNOT JUSTIFY</i>	
192. Ribs run back parallel to the cervical vertebral column	E92
193. Cervical rib accessory process (A/P)	D78, E93, J37
194. Tapering cervical ribs	E97, J41
195. Long slender cervical ribs	E36
- 19-28 pairs of caudal ribs	E114
<i>ALL "0"s</i>	
196. One or more cervical ribs are single headed	E197, J30
- Elongate one-piece ribs	E215
<i>ALL "0"s</i>	
197. Last few dorsals with fused ribs	BA25, E60
198. Posterior dorsal vertebrae with fused ribs (N/Y)	J57
199. Dorsal ribs holocephalous (N/Y)	D86, J19
200. Second sacral rib (not bifurcate / bifurcate with caudal process pointed bluntly / bifurcate with caudal process truncated sharply)	D87
201. Proximal caudal ribs (recurved / project laterally)	D90
202. Sacral and caudal ribs (fused to centra / free)	D132
203. Gastralia (A/P)	D92, E190
204. Lumbar region (not differentiated / ribs of last few presacrals project laterally and are not expanded / ribs of last presacrals fused or lost, project laterally and are not expanded distally)	D137
205. Anterior caudal ribs expanded distally	E106
206. Dorsal body osteoderms (A/P)	B60
207. 1-1 alignment between dorsal body osteoderms and vertebrae (A/P)	B61
-19-28 pairs of caudal ribs	E114
<i>ALL "0"s</i>	
208. 9-10 pairs of caudal ribs	E117
209. Ribs attach laterally to sternum	E198
210. Sternum arises as two plates	E199
211. Interclavicle T-shaped or cruciform	E200/ 226
Appendicular Characters:	
212. Low scapula	D99, E39
213. Scapula low in lateral view, mostly ventral	E115, J45
214. Scapula subequal to coracoid	BA26, E116
215. Short scapula, reduced coracoid	E160
216. Anteroposterior width of scapula (broad / narrow)	B62, D99, J44
217. Clavicle (P/A)	B104
- Anterior border of scapulocoracoid with 2 emarginations	E191
<i>AUTAPOMORPHY Squamata</i>	
- Enlarged coracoid process for triceps	E8
<i>AUTAPOMORPHY Petrolacosaurus</i>	
218. Single coracoid	B105, E13
219. Glenoid fossa of scapulocoracoid (faces laterally / faces posteroventrally)	B106
220. Coracoid tubercle (not displaced dorsally / lies close to glenoid fossa and coracoid foramen)	B63
221. Forelimb length (greater than or equal to half of hindlimb / less than half)	B107
- Limbs reduced with respect to presacral vertebral column	E163
<i>ALL "0"s</i>	
222. Archosaur humerus (A/P)	B64
223. No entepicondylar foramen on humerus	BA27, D 68 / 107, E78
224. Humerus with strong entepicondyle	E102
- Humerus greater than or equal to length of femur	D106, E107
<i>AUTAPOMORPHY Hyperodapedon</i>	
225. Medial margin or proximal humerus (weakly arched / strongly arched)	B65
226. Deltopectoral crest (extends less than ¼ down humerus / extends more)	B66
- Distal end of humerus (wider than proximal end / narrower)	B67
<i>ALL "0"s</i>	
227. Ectepicondylar foramen or groove of humerus (P/A)	B68
229. Deltopectoral crest shape (crescentic / subrectangular)	B108
- Apex of deltopectoral crest (less distally placed on humerus / more)	B109

AUTAPOMORPHY <i>Lepidosauromorpha</i>	
- Radius equal or subequal to length of humerus	E10
AUTAPOMORPHY <i>Petrolacosaurus</i>	
- Twisted radius	E103
AUTAPOMORPHY <i>Lagosuchus</i>	
230. Radius longer than ulna (split into 3 states – Longer / Equal / Shorter)	BA28, E104
- Ulna lacks olecranon and sigmoid notch	E21
AUTAPOMORPHY <i>Cosesaurus</i>	
231. First distal carpal lost or fused	BA31, E40, J46
232. Loss of intermedium in carpus	BA29, E41, J47
233. Medial centrale meets fourth distal carpal in adult	E109
234. Medial centrale double lateral centrale	E110
- Proximodistal expansion of ulnare and intermedium	E12
AUTAPOMORPHY <i>Petrolacosaurus</i>	
- No foramen between intermedium and ulnare	E79
AUTAPOMORPHY <i>Petrolacosaurus</i>	
235. Centralia in the manus (P/A)	BA30, E48, J51
236. Lateral centrale of manus (P/ Small or A)	J10
237. Lateral manus centrale meets second distal carpal	E193
238. Relative lengths of metacarpals 3 and 4 (3 shorter than 4 / 3 equal in length to or longer than 4)	BA32, E137, J55
239. Relative lengths of metacarpals 1 and 5 (shorter than 2 and 4 / similar to 2 and 4)	BA33, E136
240. Medial centrale in carpus (P/A)	J33
241. Fourth metacarpal shorter than third	E55
242. Distal condyles of metacarpal I (perpendicular to long axis / offset / offset so ungual is enlarged)	B72
243. Manus length (> or = to half of tarsus and pes / less)	B70
244. Manual asymmetry (digit IV stoutest and longest and other diminishing / I and II stouter)	B71
245. Ilium with reduced contribution to acetabulum	D102, E42, J48
246. Ilium short in relation to ischium	BA34, E63
247. Ilium with strong pubic flange	D110, E139
248. Dorsal margin of ilium	D102
249. Iliac spine (A/P)	B73, E159
250. Preacetabular buttress on ilium (A or insignificant / well developed)	BA35
251. Narrow, elongated, waisted pubis	E161, BA37
252. Anterior apron of pubis (A/P)	D104
253. Pubis and ischium (puboischadic plate and broad contact b/w pubis and ischium / plate absent and bones shot and broad / plate absent, bones elongate)	B74, D144
254. Pubis length (shorter than ischium / longer)	B76
- Enlarged lateral and distal pubic tubercles	E9
AUTAPOMORPHY <i>Petrolacosaurus</i>	
255. Pubic acetabular margin recess (A/P)	B77
256. Thyroid foramen in pelvis (A/P)	BA36, D100, E52 / 129, J22
- Acetabulum (elongate / circular)	D101
AUTAPOMORPHY <i>Petrolacosaurus</i>	
257. Acetabulum (imperforate / perforate)	B111
258. Length of ischium relative to width of acetabulum (short / posteroventrally elongate)	B75
259. Relative contributions of pubic elements to acetabulum (primarily the ilium / approx. equal contributions from each element)	D105
260. Hindlimb posture (sprawling / semi-erect or erect)	B78
261. Relative proportions of femur (distal width/total length <0.3 / >0.3)	D111
262. Bird-like distal end of femur (A/P)	B112
263. Femoral shaft curvature (not markedly sigmoid / sigmoid / bowed anteriorly)	B79, BA38, E18
264. Lesser trochanter of femur (A/P)	B80
265. Fourth trochanter of femur (absent / mound-like / sharp flange)	B81
- Distal articular surface of femur level	D110, E19
AUTAPOMORPHY <i>Petrolacosaurus</i>	
266. Prominent cnemial crest on tibia (A/P)	B82
267. Fibular anterior trochanter (crest-shaped and lowed / knob-shaped and robust)	B83
268. Fibular distal end width (less than proximal end / greater)	B84
269. Fibula thin and strongly tapered distally (A/P)	B114
270. Tibia equal or subequal to length of femur	B113, BA39, E11

271. Ectepicondylar foramen (P/A)	D108
272. Medial centrale of carpus (P/A)	D109
273. Perforating foramen (between astragalus and calcaneum / between distal ends of tibial and fibula)	BA40, D115, E44 / 145, J59
274. Hemicylindrical calcaneal condyle (A/P)	B91
275. Astragalus-calcaneum articulation (concave-convex absent / present)	B88, D113, E90 J34
276. Lepidosaurian ankle joint (A/P)	D114, J24
277. Lateral tuber of calcaneum (A/P)	B120, BA41, D116, J35
278. Astragalocalcaneal canal	B90
279. Centrale (P and does not connect to tibia / P and contacts tibia)	D117
280. Centrale (P and contacts distal tarsal 4 / P and does not contact)	D118
281. Pedal centrale (P/A)	B94, BA42, E53, J53
282. Astragular tibial facet (concave / saddle shaped)	B85
283. Ascending process of astraglus fitting between fibula and tibia (A/P)	B117
284. Astagalar posterior groove (P/A)	B119
Astraglus (not transversely widened / widened)	B116
285. Astragalar tibial and fibular facets (separated / adjacent)	B86
286. Dorsal and ventral astragalocalcaneal facets (subequal in size / ventral facet much larger than dorsal)	B89
287. Astragalus and calcaneum unfused or fused	J23
288. Lateral pes centrale fused to astragalus	E141
289. Shape of astragalus (L-shaped with broad base / elongate)	B116 / 118, D135
290. Astragalus and calcaneum fuse in juvenile	E140
291. Crocodyloid tarsus (A/P)	B87
292. Advanced mesotarsal ankle (A/P)	B115
293. Calcaneal facets for fibula and distal tarsal (separated / contiguous)	B92
294. Calcaneal tubercle orientation (orientated less than 45 degrees, shaft taller than broad / orientated > than 45, shaft broader than tall)	B93
295. Pedal stance (plantigrade / digitigrade)	B122
296. Pes centrale displaced laterally	E82
297. Pes (functionally pentadactyl or tetradactyl / functionally tridactyl)	B123
298. Reduction in length of foot	E56
299. Maximum of five ossified tarsals	E49, J52
300. Only four ossified tarsals	E64
301. Three proximal tarsals with centrale integrated into proximal row	E69
302. Loss of fifth distal tarsal (P/A or reduced)	D121, E81, J11
- Fifth distal tarsal lost or fused	B98 / 126, E112 / 143
<i>CANNOT JUSTIFY</i>	
303. Fourth distal tarsal has dorsal process meeting recess in astragalocalcaneum	E120
304. Distal tarsal IV transverse width (broader than III / subequal to III)	E121
305. Loss of second distal tarsal	BA44, D120, E194
306. Loss of first distal tarsal; first metatarsal meets astragalocalcaneum	E142
307. Loss of first distal tarsal	BA43, D119, E45, J58
308. First distal tarsal enlarged	E111
309. Reduction in length of metatarsals	E167
310. Metatarsal 5 shape (L-shaped / symmetrical and very short)	BA46
311. Fifth metatarsal hooked in one plane	D122, E89, J12
312. Fifth metatarsal hooked in two planes	E144
313. Fifth metatarsal very short and geometrical	E57
314. Fourth metatarsal is at least 3X length of fifth metatarsal	BA45, E46
315. Fourth metatarsal elongated, forms at least 40% of digit 4	E83
316. Metatarsal III length (less than ½ tibial length / more than ½)	B125
317. Ratio of lengths of metatarsals I and IV (>0.4 / <0.4 and >0.3 / <0.3)	D123
Metatarsals II, III, and IV (unequal in length with IV longest / subequal with III longest)	B95
318. Metatarsus configuration (spreading / compact)	B124
319. Long ground phalanx on digit	E58
320. Phalanges short in relation to metapodials	E68
321. Pedal digit III (shorter than IV / longer)	B96
322. Ratio of lengths of digits 3 and 4 (<0.8 / >0.8 and <0.9 / >0.9)	D124
323. Relative length of second phalanx on digit 5 of foot (short / long)	BA47

324. First phalanx of the fifth toe elongated (as long as the metacarpals of digits I-IV) (N/Y)
- Phalanges of pedal digit V (four / fewer)
AUTAPOMORPHY *Boreopricea*

D138, J71
B97

B

Data Matrix

Boreopricea

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Champsosaurus

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Choristodera

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Cosesaurus

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Ctenioygenys

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Dinosauria

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Drepanosaurus

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Erythrosuchidae

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Euparkeria

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Gephyrosaurus

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Howesia

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Hyperodapedon

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Jesairosaurus

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Kadimakara

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Lagosuchus

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Langobardisaurus

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Lazurussuchus

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Lepidosauromorpha

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Macrocnemus

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Malerisaurus

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Megalancosaurus

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Mesosuchus

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Ornithosuchidae

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Parasuchia

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Petrolacosaurus

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Prolacerta

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Prolacertoides

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Proterochampsidae

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Proterosuchidae

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Protosaurus

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Pterosauria

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Rhombopholis

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Rhynchosauridae

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Scaphonyx

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Scleromochlus

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Sphenodontia

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Squamata

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Stenaulorbhynchus

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Suchia

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Tanystropheus

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Tanytrachelos

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Thalattosauria

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Trachelosaurus

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Trilophosaurus

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Youngina

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?01?????000?00?00?0?0111?1010?0?0?0?1?????0000?000?000?0??0? 00?????00000?00?00000?00?0?0?0??00

C Further Tree Information

The diagnostic characters related to each node are listed below. Some characters are listed multiple times due to multiple character states which therefore change in several locations. Where no node is marked, it has no defining characters.

Supermatrix Tree (SM) (Figure 4)

- 1 – 151, 160, 217, 229, 283, 297: 2 – 189, 219, 221, 295, 316, 318: 3 – 220, 242, 244, 264: 4 – 50, 113, 207, 293, 294: 5 – 60, 85, 184, 222: 6 – 230, 244, 321: 7 – 95, 128, 243: 8 – 149: 9 – 102, 113, 173, 249: 10 – 81: 11 – 26: 12 – 242: 13 – 79: 14 – 12: 15 – 28, 36, 53, 61, 87, 93, 94, 96, 236: 16 – 286: 17 – 2, 25, 115: 18 – 25, 248, 252, 261: 19 – 84, 116, 119, 280: 20 – 23, 30, 130: 21 – 14, 38, 117, 136, 301, 320: 22 – 163: 23 – 313, 319: 24 – 213, 214, 259: 25 – 29: 26 – 155, 212: 27 – 176, 182, 248, 252: 28 – 152, 185, 202: 29 – 1, 174: 30 – 209, 210: 31 – 178, 186, 253, 271, 303.

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Autor(en)/Author(s): Hone David W. E., Benton Michael J.

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