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A genus-level supertree of the Dinosauria

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One of the ultimate aims of systematics is the reconstruction of the tree of life. This is a huge undertaking that is inhibited by the existence of a computational limit to the inclusiveness of phylogenetic analyses. Supertree methods have been developed to overcome, or at least to go around this problem by combining smaller, partially overlapping cladograms. Here, we present a very inclusive generic-level supertree of Dinosauria (covering a total of 277 genera), which is remarkably well resolved and provides some clarity in many contentious areas of dinosaur systematics.

Keywords: supertrees; phylogeny; dinosaurs; fossil; Mesozoic

1. INTRODUCTION

In the last few decades, advances in theoretical systematics, as well as in computer sciences, have provided biologists and palaeontologists with tools to investigate the phylogenetic relationships among organisms, yet phylogenetic inference is computationally expensive and analyses of large datasets hardly feasible (Graham & Foulds 1982). This problem is exacerbated in palaeontology, where missing data can lead to an exponential increase in the number of most-parsimonious solutions permitted by a given dataset. However, 'partial phylogenies' (i.e. phylogenies including only a subset of the taxa known to belong to a certain group) are accumulating at an increasing rate, and the Dinosauria represent a typical, if not extreme, example of this trend.

Supertree methods, formally introduced by Gordon (1986), can be implemented to combine such 'partial phylogenies' and obtain more inclusive estimates without the need to pool the original datasets. Accordingly, whenever a collection of 'partial phylogenies' exists, supertrees can represent an alternative to a direct analysis of the primary data (i.e. the pooled dataset).

Several supertree methods have been developed (e.g. Sanderson *et al.* 1998; Wilkinson *et al.* 2001 for review), but only those using matrix representation with parsimony (MRP methods) have software implementation (Swofford 1998; Thorley & Page 2000) and these are currently the only viable choice in supertree reconstruction. Nevertheless, their characterization is still incomplete. In particular, when the source trees are incompatible (i.e. they disagree about the relationships of the taxa that overlap), their behaviour is not completely understood. In these cases, MRP methods can be inaccurate. It is debatable whether MRP estimates are accurate enough to be useful tree-reconstruction methods (Purvis 1995*a*; Wilkinson *et al.* 2001). Yet, there is evidence (Bininda-Emonds & Sanderson 2001) that, if the set of source trees is large enough, the MRP supertree(s) are accurate representations of the information conveyed by the trees in the input set.

The original MRP method of Baum (1992) and Ragan (1992), referred to as component coding-MRP (CC-MRP) in this paper, was used to combine 126 'partial phylogenies' of dinosaurs (covering a total of 277 genera) with the aim of obtaining a single, genus-level supertree. CC-MRP makes use of the fact that a tree can be represented in a matrix by means of a set of binary 'characters'. Following Baum & Ragan (1993), we refer to these 'characters' as matrix elements. Matrix representations of different source trees can be readily combined with missing entries in the matrix elements corresponding to taxa that are not present in the matching source tree. Parsimony analysis of the combined matrix representations yields one or more most parsimonious trees (MPTs), the CC-MRP supertree(s), which comprise all the included taxa (see Baum 1992; Ragan 1992 for more details).

2. MATERIAL AND METHODS

Potential source trees were identified from online searches. Two electronic literature databases were searched for publications with relevant source trees, BFV (Bibliography of Fossil Vertebrates) online (http://eteweb.lscf.ucsb.edu/bfv/bfv_form.html) and Web of Science (http://wos.mimas.ac.uk/). BFV online does not allow the enquirer to confine his search to a limited number of years and it was thus screened over the whole time-span that it covers (1509–1993), while Web of Science was searched for the years 1993–2001. All publications that were likely to include a cladogram were examined. Because the aim of this analysis was to obtain a consensus representation of cladistic views on dinosaur systematics, the earliest of which date back to the beginning of the 1980s (Benton 1990), publications presented before the year 1980 have been excluded *a priori*. Publications after this date were retained when they presented cladogram(s) resulting from an original study, or from the modification of a pre-existing dataset. The list of all retained publications is available (see electronic appendix). For each selected cladogram, a Nexus (Swofford 1998) tree file was produced using MacClade (Maddison & Maddison 1997). Some terminal genera were omitted *a priori* (see electronic appendix, available on The Royal Society's Publications Web site, for the list of the omitted taxa).

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These were either *nomina dubia*, unconstrained taxa, or both. The former are taxa based on material inadequate for diagnosis and for proper phylogenetic analysis. The latter may be valid taxa but they appear only in one source tree and as members of a polytomy. Accordingly, their inclusion adds nothing to the analysis but an increase in the number of possible MPTs. Most original studies included a variable proportion of suprageneric terminal taxa. For analytical proposes, their monophyly was assumed and a standard taxon substitution (Wilkinson *et al.* 2001) was performed. Each suprageneric taxon was substituted with a star tree (i.e. an unresolved polytomy) including either: (i) the taxa embodied in each of them when explicitly given in the original study; or (ii) only its non-controversial members in the case that no such definition was given (see electronic appendix for the minimal non-controversial definition of each suprageneric taxon). When multiple MPTs were presented, strict reduced consensus (RC; Wilkinson 1994) was implemented using RadCon (Thorley & Page 2000) and the tree in the RC profile with the highest cladistic information content (Thorley *et al.* 1998) was retained for the CC-MRP analysis.

Five CC-MRP matrices (see electronic appendix), one scoring all of the 277 included taxa (Matrix I), one for Sauropodomorpha (Matrix II), one for Ornithischia (Matrix III) and two for Theropoda (Matrices IV and V) were produced using RadCon. These have been analysed separately, resulting in one comprehensive (Matrix I) and four compartmentalized (Matrices II–V) supertrees. It is important to note that Matrices II–V are matrices in their own right, not subsamples of Matrix I. They have not been obtained by pruning the excluded taxa, e.g. all theropods and all ornithischians (in the case of Matrix II) from Matrix I, but by pruning the source trees and then recoding them in a new CC-MRP matrix. This approach, implemented here for the first time, to our knowledge, is important because each matrix element is representative of a node in a tree. Thus, pruning a taxon from an MRP matrix will create a matrix that is not representative of the real topology of the pruned tree (figure 1).

Because objective functions for implementing a correct, unequal character-weighting scheme in MRP analyses are still unknown (Bininda-Emonds *et al.* 1999; Bininda-Emonds & Sanderson 2001), equally weighted parsimony was used to analyse the five CC-MRP matrices.

Paup* (Swofford 1998) was used to analyse the data matrices with parsimony and, in order to avoid the problem of being 'bogged down' in sub-optimal tree islands, the following tree-search protocol was applied: (1) 100 heuristic searches were carried out using tree bisection–reconnection (TBR) branch swapping with the 'multrees' option not in effect; random stepwise addition was used to obtain the starting trees for these replicates; (2) the MPTs found were retained and swapped using TBR branch swapping with the 'multrees' option in effect.

A potentially serious problem of MRP supertree methods is their ability to resolve conflict among the source trees by the generation of novel clades (*sensu* Bininda-Emonds & Bryant 1998). Bininda-Emonds *et al.* (1999) and Bininda-Emonds & Sanderson (2001) have likened the appearance of such clades in MRP to their appearance in Total Evidence analyses. However, as shown by Pisani & Wilkinson (2002), this cannot be the case and such novel clades should always be collapsed. No novel clades (*sensu* Bininda-Emonds & Bryant 1998) are present in the dinosaur supertree.

A poorly understood problem in MRP supertree building is how to evaluate the support for the resulting clades. For those who feel that an MRP supertree is naked without some measure of support, following Bininda-Emonds *et al.* (1999) and Liu *et al.* (2001), decay indices (Bremer 1988) are provided. Decay values have been calculated for Matrices II–IV, but because of the size of the resulting supertree, they have not been calculated for Matrix I. However, it is our opinion that this measure cannot be considered really representative of the support for the clades recovered by the supertree. Accordingly, decay values should be interpreted with care. Consider, for example, that novel clades (*sensu* Bininda-Emonds & Bryant 1998), despite being unsupported (Pisani & Wilkinson 2002), have a positive decay index. Thus, new support measures for MRP supertrees are needed and are under development (D. Pisani, unpublished data), but they will not be considered any further in this paper.

3. RESULTS

A total of 34 900 MPTs was found from the analysis of Matrix I before the search had to be aborted because of memory limitations. We suggest that this sample of MPTs, although less than the set of all possible supertrees, is representative of the whole. This is because the topology of their strict consensus agrees perfectly with those of the strict consensus trees summarizing the results obtained from the compartmentalized analyses (Matrices II, III and V), which have been run to completion. It is thus possible to argue that increasing the number of retained MPTs from the analysis of Matrix I will result in a more comprehensive collection of alternative solutions for the polytomies seen in figure 2 and not in the collapse of its resolved areas. The strict consensus of the 34 900 MPTs from the analysis of Matrix I (figure 2) therefore represents the most inclusive estimate that has ever, to our knowledge, been presented of the phylogeny of the Dinosauria.

Contentious issues in dinosaur systematics are resolved in the present supertree. Sauropodomorpha is composed of *Saturnalia* and monophyletic Prosauropoda and Sauropoda (Sereno 1999; Benton *et al.* 2000; *contra* Gauthier 1986). Within Prosauropoda, a monophyletic Melanorosauridae (*Riojasaurus*, *Camelotia* and *Melanorosaurus*) emerges as the sister group of Plateosauria (*Massospondylus*, *Yunnanosaurus* and Plateosauridae). Within Sauropoda, *Barapasaurus* is the sister group to all other Eusauropoda (Upchurch 1998; *contra* Wilson & Sereno 1998) and *Omeisaurus* is more closely related to Neosauropoda than it is to *Shunosaurus* (Wilson & Sereno 1998; *contra* Upchurch 1998). The early dinosaurs *Eoraptor* and the Herrerasauridae are basal theropods (Sereno *et al.* 1993; *contra* Langer *et al.* 1999). Ceratosauria is a monophyletic group containing Coelophysoidea and Neoceratosauria (Sereno 1999; Holtz 2000; *contra* Forster 1999), while torvosaurids are more closely related to derived tetanurans (Avetheropoda) than to spinosaurids (Holtz 2000; *contra* Sereno *et al.* 1994). Therizinosauroidea is the sister group of Oviraptorosauria (Russell & Dong 1993; Holtz 2000; *contra* Sereno 1999), but *Caudipteryx* is a basal member of Paraves: it is excluded from both Oviraptorosauria (*contra* Sereno 1999) and Avialae (*contra* Ji *et al.* 1998), while Metornithes is monophyletic and contains Ornithothoraces, *Avimimus* (Chatterjee 1991; *contra* Holtz 1994) and Alvarezsauridae (Chiappe *et al.* 1996; *contra* Sereno 1999).

Within Ornithischia, *Minmi* and *Gargoyleosaurus* are basal Ankylosauridae (Sereno 1999; *contra* Kirkland

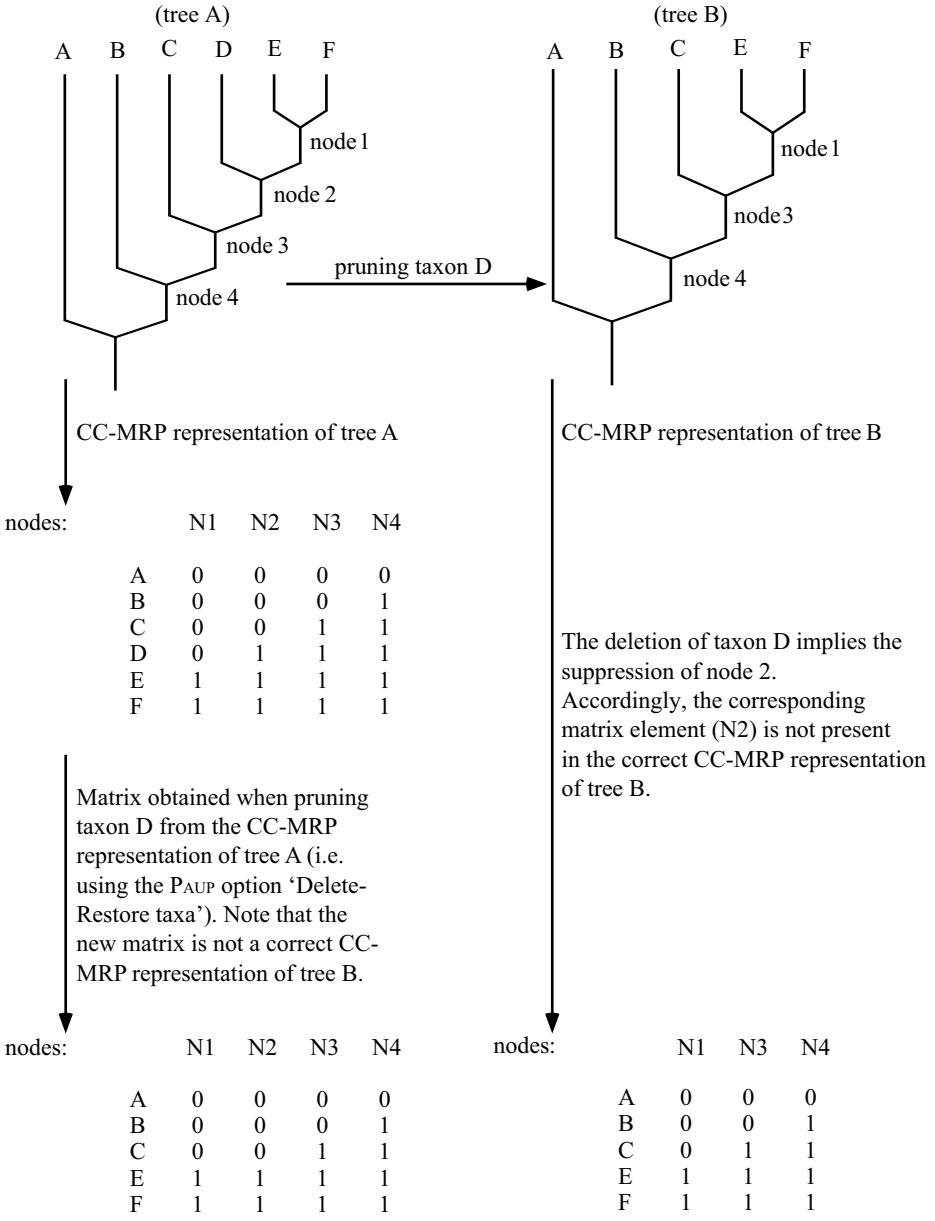
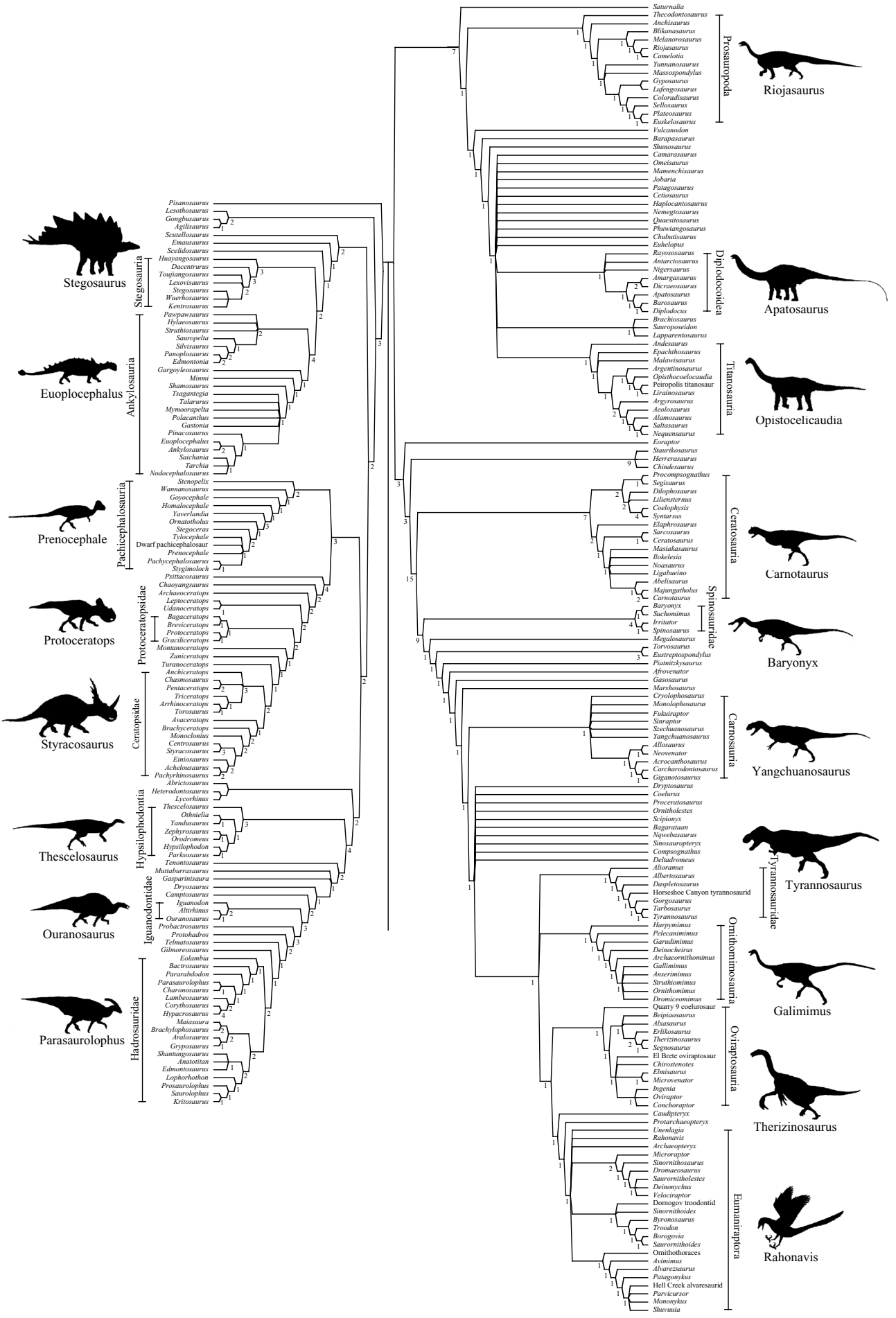


Figure 1. A tree on six leaves (tree A) and its corresponding pruned version (tree B), from which taxon D has been deleted. Pruning taxon D from the CC-MRP representation of tree A results in a matrix that is not the correct CC-MRP matrix representing tree B.

1998). A monophyletic Iguanodontidae (Norman 1998; *contra* Sereno 1999) containing *Iguanodon*, *Altirhinus* and *Ouranosaurus* is recovered, while the Hadrosauridae appears more closely related to *Probactrosaurus* than to Iguanodontidae. *Leptoceratops* and *Udanoceratops* are excluded from Coronosauria (Protoceratopsidae plus Ceratopsoidea) and a monophyletic Protoceratopsidae containing *Bagaceratops*, *Breviceratops*, *Graciliceratops* and *Protoceratops* is recovered (Sereno 2000; *contra* Chinnery & Weishampel 1998).

The present supertree contains three important polytomies. One lies within Sauropoda and the other two within Theropoda: one at the base of Coelurosauria and the other within Coelurosaria, at the base of the Eumaniraptora.

The polytomy within Sauropoda involves the taxa more derived than *Shunosaurus* and is due to both the existence of conflicting hypotheses concerning the relationships of three long-necked Chinese taxa, *Omeisaurus*, *Mamenchisaurus* and *Euhelopus*, and to the poorly constrained position of *Cetiosaurus*. The first problem reflects differences in the results obtained by different authors on the relationships of those taxa. Among the source trees, two classes of cladogram exist. Upchurch (1995, 1998) includes all three Chinese taxa in a clade nested outside Neosauropoda, while Wilson & Sereno (1998; also Sereno 1999) do not include *Mamenchisaurus* and consider *Omeisaurus* and *Euhelopus* to be distantly related. In the supertree, *Omeisaurus* and *Euhelopus* are nested according to the second of these two hypotheses, but *Mamenchisaurus* is free to cluster with either of the two. Implementing RC, two 'rogue' taxa (*Cetiosaurus* and *Mamenchisaurus*) are identified. With their exclusion (figure 3*a*), the following taxonomic statements are true in all the supertrees: (i) *Haplocanthosaurus* falls within Neosauropoda (defined by the node connecting *Diplodocus* and *Saltasaurus*) and is


Stegosaurus
Euoplocephalus
Prenocephale
Protoceratops
Styracosaurus
Thescelosaurus
Ouranosaurus
Parasaurolophus
Stegosauria
Ankylosauria
Pachicephalosauria
Protoceratopsidae
Ceratopsidae
Hypsilophodontia
Iguanodontidae
Hadrosauridae
Pisanosaurus
Lesothosaurus
Gongbusaurus
Agilisaurus
Scutellosaurus
Emausaurus
Scelidosaurus
Huayangosaurus
Dacentrurus
Toujiangosaurus
Lexovisaurus
Stegosaurus
Wuerhosaurus
Kentrosaurus
Pawpawsaurus
Hylaeosaurus
Struthiosaurus
Sauropelta
Silvisaurus
Panoplosaurus
Edmontonia
Gargoyleosaurus
Minmi
Shamosaurus
Tsagantegia
Talarurus
Mymoorapelta
Polacanthus
Gastonia
Pinacosaurus
Euoplocephalus
Ankylosaurus
Saichania
Tarchia
Nodocephalosaurus
Stenopelix
Wannanosaurus
Goyocephale
Homalocephale
Yaverlandia
Ornatotholus
Stegoceras
Tylocephale
Dwarf pachicephalosaur
Prenocephale
Pachycephalosaurus
Stygimoloch
Psittacosaurus
Chaoyangsaurus
Archaeoceratops
Leptoceratops
Udanoceratops
Bagaceratops
Breviceratops
Protoceratops
Graciliceratops
Montanoceratops
Zuniceratops
Turanoceratops
Anchiceratops
Chasmosaurus
Pentaceratops
Triceratops
Arrhinoceratops
Torosaurus
Avaceratops
Brachyceratops
Monoclonius
Centrosaurus
Styracosaurus
Einiosaurus
Achelousaurus
Pachyrhinosaurus
Abrictosaurus
Heterodontosaurus
Lycorhinus
Thescelosaurus
Othnielia
Yandusaurus
Zephyrosaurus
Orodromeus
Hypsilophodon
Parksosaurus
Tenontosaurus
Muttaburrasaurus
Gasparinisaura
Dryosaurus
Camptosaurus
Iguanodon
Altirhinus
Ouranosaurus
Probactrosaurus
Protohadros
Telmatosaurus
Gilmoreosaurus
Eolambia
Bactrosaurus
Pararabdodon
Parasaurolophus
Charonosaurus
Lambeosaurus
Corythosaurus
Hypacrosaurus
Maiasaura
Brachylophosaurus
Aralosaurus
Gryposaurus
Shantungosaurus
Anatotitan
Edmontosaurus
Lophorhothon
Prosaurolophus
Saurolophus
Kritosaurus
Saturnalia
Thecodontosaurus
Anchisaurus
Blikanasaurus
Melanorosaurus
Riojasaurus
Camelotia
Yunnanosaurus
Massospondylus
Gyposaurus
Lufengosaurus
Coloradisaurus
Sellosaurus
Plateosaurus
Euskelosaurus
Vulcanodon
Barapasaurus
Shunosaurus
Camarasaurus
Omeisaurus
Mamenchisaurus
Jobaria
Patagosaurus
Cetiosaurus
Haplocantosaurus
Nemegtosaurus
Quaesitosaurus
Phuwiangosaurus
Chubutisaurus
Euhelopus
Rayososaurus
Antarctosaurus
Nigersaurus
Amargasaurus
Dicraeosaurus
Apatosaurus
Barosaurus
Diplodocus
Brachiosaurus
Sauroposeidon
Lapparentosaurus
Andesaurus
Epachthosaurus
Malawisaurus
Argentinosaurus
Opisthocoelocaudia
Peiropolis titanosaur
Lirainosaurus
Argyrosaurus
Aeolosaurus
Alamosaurus
Saltasaurus
Nequensaurus
Eoraptor
Staurikosaurus
Herrerasaurus
Chindesaurus
Procompsognathus
Segisaurus
Dilophosaurus
Liliensternus
Coelophysis
Syntarsus
Elaphrosaurus
Sarcosaurus
Ceratosaurus
Masiakasaurus
Ilokelesia
Noasaurus
Ligabueino
Abelisaurus
Majungatholus
Carnotaurus
Baryonyx
Suchomimus
Irritator
Spinosaurus
Megalosaurus
Torvosaurus
Eustreptospondylus
Piatnitzkysaurus
Afrovenator
Gasosaurus
Marshosaurus
Cryolophosaurus
Monolophosaurus
Fukuiraptor
Sinraptor
Szechuanosaurus
Yangchuanosaurus
Allosaurus
Neovenator
Acrocanthosaurus
Carcharodontosaurus
Giganotosaurus
Dryptosaurus
Coelurus
Proceratosaurus
Ornitholestes
Scipionyx
Bagaraatan
Ngwebasaurus
Sinosauropteryx
Compsognathus
Deltadromeus
Alioramus
Albertosaurus
Daspletosaurus
Horseshoe Canyon tyrannosaurid
Gorgosaurus
Tarbosaurus
Tyrannosaurus
Harpymimus
Pelecaniminus
Garudimimus
Deinocheirus
Archaeornithomimus
Gallimimus
Anserimimus
Struthiomimus
Ornithomimus
Dromiceomimus
Quarry 9 coelurosaur
Beipiaosaurus
Alxasaurus
Erlikosaurus
Therizinosaurus
Segnosaurus
El Brete oviraptosaur
Chirostenotes
Elmisaurus
Microvenator
Ingenia
Oviraptor
Conchoraptor
Caudipteryx
Protarchaeopteryx
Unenlagia
Rahonavis
Archaeopteryx
Microraptor
Sinornithosaurus
Dromaeosaurus
Saurornitholestes
Deinonychus
Velociraptor
Dornogov troodontid
Sinornithoides
Byronosaurus
Troodon
Borogovia
Saurornithoides
Ornithothoraces
Avimimus
Alvarezsaurus
Patagonykus
Hell Creek alvaresaurid
Parvicursor
Mononykus
Shuvuuia
Prosauropoda
Riojasaurus
Diplodocoidea
Apatosaurus
Titanosauria
Opistocelicaudia
Ceratosauria
Carnotaurus
Spinosauridae
Baryonyx
Carnosauria
Yangchuanosaurus
Tyrannosauridae
Tyrannosaurus
Ornithomimosauria
Galimimus
Oviraptosauria
Therizinosaurus
Eumaniraptora
Rahonavis

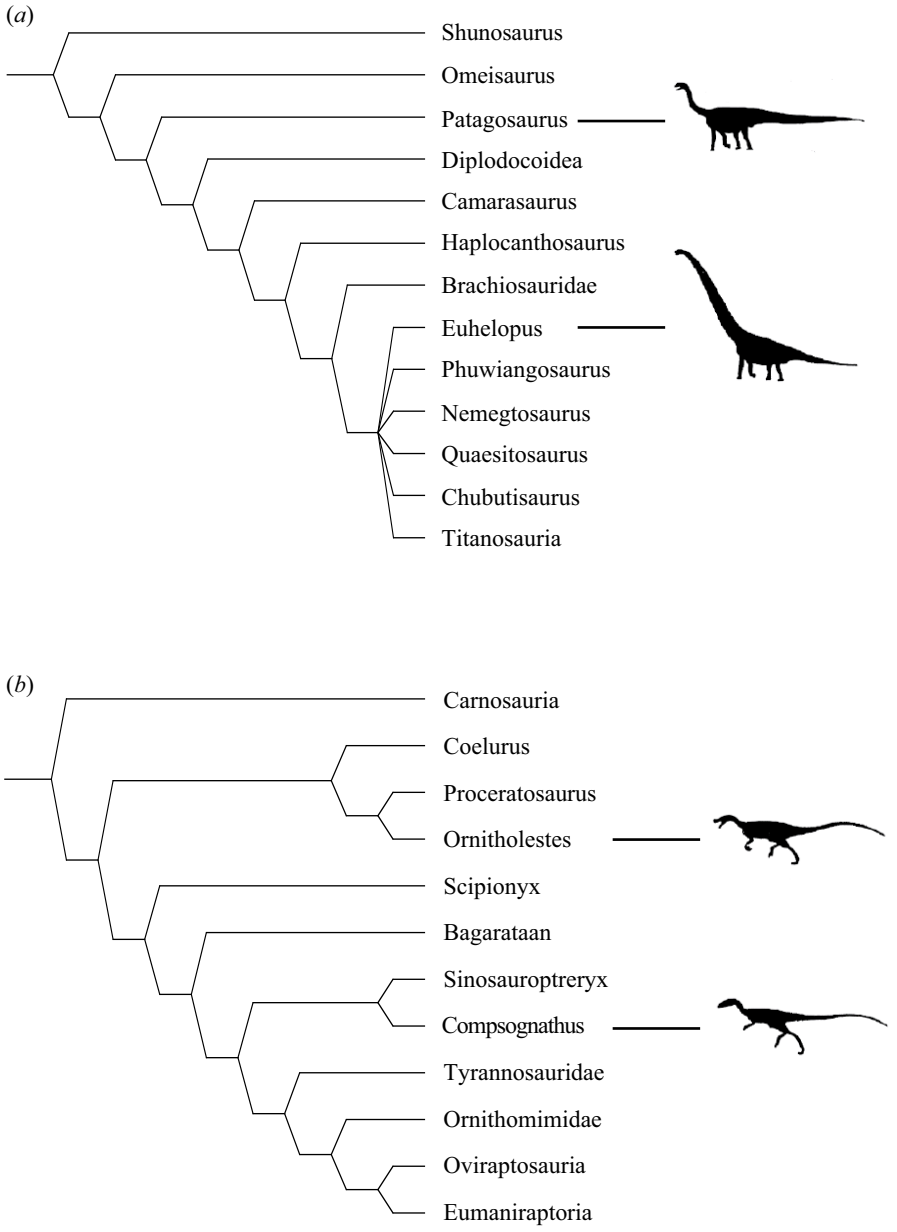


Figure 3. (*a*) Reduced consensus of the 14 323 MPTs of length 356 obtained from the analyses of Matrix II. (*b*) Reduced consensus of the 85 900 MPTs of length 910 obtained from the analysis of Matrix V.

more closely related to *Camarasaurus*, *Brachiosaurus* and Titanosauria than to Diplodocidae; (ii) *Euhelopus*, *Chubutisaurus*, *Phuwiangosaurus*, *Nemegtosaurus*, *Quaesitosaurus* and Titanosauria are more closely related to each other than they are to any other retained sauropod; (iii) *Nemegtosaurus* and *Quaesitosaurus* are more closely related to the derived Titanosauria than they are to Diplodocidae.

Within Theropoda, the polytomy at the base of Coelurosauria is simply caused by a few poorly constrained genera (i.e. genera that are present in few trees and are not tightly bracketed by taxa of a relatively stable position) *Deltadromeus*, *Dryptosaurus* and *Nqwebasaurus*. As above, RC identifies these taxa and their omission allows extra resolution of the supertree (figure 3*b*). Conversely, the variable placement of eumaniraptorians in the source trees seems to be due to real character incongruences (Holtz 2000) and leads to an unresolved polytomy in the supertree topology.

Figure 2. (*Opposite*.) The strict consensus of the 34 900 MPTs of length 1988 obtained from the analysis of Matrix I. Numbers along the branches correspond to the decay values of the supertrees obtained in the compartmentalized analyses (which are not reported).

4. DISCUSSION

Supertree techniques are now becoming commonplace in biology (e.g. Purvis 1995*b*; Bininda-Emonds *et al.* 1999; Liu *et al.* 2001), but this is the first time, to our knowledge, that a supertree method has been implemented to disentangle the phylogeny of a fossil group.

Supertree methods resemble meta-analysis in several respects (see also Sanderson *et al.* 1998). In meta-analysis, formal statistical techniques are implemented to sum up a body of separate (but similar) experiments (Mann 1990).

Similarly, supertree methods exploit either the existence of a one-to-one relation between a tree and its matrix representation (Ragan 1992), or subtrees–tree reconstruction algorithms (e.g. Aho *et al.* 1981; Semple & Steel 2000) to combine a body of different (but partially overlapping) phylogenies. Meta-analysis is like an ordinary scientific review of research, except that ordinary reviews provide a qualitative, and often subjective, assessment of few studies, while meta-analysis promises a quantitative synthesis of all available data (Mann 1990). In the same way, supertree methods introduce objectivity to phylogenetic reviews by quantitatively synthesizing results of previous phylogenetic studies.

Phylogenetic trees should be used as frameworks to test evolutionary hypotheses (Felsenstein 1985; MacLeod 2001). Such frameworks should be (i) obtained independently from the characters where evolution is under investigation; (ii) objective (i.e. they should not represent the personal view of the author); (iii) inclusive of all relevant taxa. Biologists often solve point (i) by testing the evolution of morphological characters on molecular phylogenies, an option unavailable to palaeontologists. However, since phylogenetic supertrees, including MRP supertrees, represent consensus solutions (Pisani & Wilkinson 2002), they are only indirectly based on any particular morphological characters. Moreover, they are objective (point (ii)) and can be very inclusive (point (iii)). Therefore, they should be used as frameworks (see also Lanyon 1993) for evolutionary palaeobiological studies, such as implementation of the comparative method of Felsenstein (1985), or the phylogenetic bracket of Witmer (1995). Recent evolutionary studies within Dinosauria, (e.g. Carrano 2000; Hutchinson 2001*a*,*b*) have generally used those authors' own subjective estimation of the consensus.

With regard to the supertree under discussion, it is important to note that some of its structure can be expected to change in the near future as works in the press, or in progress, are published. In particular, the monophyly of Prosauropoda, Ceratosauria and Metornithes may not be sustained, while *Eoraptor* and Herrerasauridae may be found to be more basal within Dinosauria.

As previously stated, Bremer support values must be interpreted with care when used as a measure of support for a supertree. However, the low values obtained for a high proportion of nodes shows that there is a certain amount of discordance among the source trees, i.e. there is still disagreement among dinosaur systematicians relative to most areas of the trees. This is more noticeable in the Saurischia that have, on average, lower decay values than the Ornithischia. This might indicate that the phylogenetic signal of ornithischians is less masked by homoplasy or may simply reflect greater attention focused upon saurischian phylogeny. Never the less, we are confident with the resolution of conflicts of our supertree.

In conclusion, we hope the dinosaur supertree presented will represent a solid framework for future study of dinosaurian evolution, and will stimulate and direct further systematic studies towards the less well understood areas of dinosaur systematics that are highlighted as polytomies in the supertree.

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