Sauropod dinosaur phylogeny: critique and cladistic analysis

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Sauropoda is among the most diverse and widespread dinosaur lineages, having attained a near-global distribution by the Middle Jurassic that was built on throughout the Cretaceous. These gigantic herbivores are characterized by numerous skeletal specializations that accrued over a 140 million-year history. This fascinating evolutionary history has fuelled interest for more than a century, yet aspects of sauropod interrelationships remain unresolved. This paper presents a lower-level phylogenetic analysis of Sauropoda in two parts. First, the two most comprehensive analyses of Sauropoda are critiqued to identify points of agreement and difference and to create a core of character data for subsequent analyses. Second, a generic-level phylogenetic analysis of 234 characters in 27 sauropod taxa is presented that identifies well supported nodes as well as areas of poorer resolution. The analysis resolves six sauropod outgroups to Neosauropoda, which comprises the large-nostrilled clade Macronaria and the peg-toothed clade Diplodocoidea. Diplodocoidea includes Rebbachisauridae, Dicraeosauridae, and Diplodocidae, whose monophyly and interrelationships are supported largely by cranial and vertebral synapomorphies. In contrast, the arrangement of macronarians, particularly those of titanosaurs, are based on a preponderance of appendicular synapomorphies. The purported Chinese clade 'Euhelopodidae' is shown to comprise a polyphyletic array of basal sauropods and neosauropods. The synapomorphies supporting this topology allow more specific determination for the more than 50 fragmentary sauropod taxa not included in this analysis. Their distribution and phylogenetic affinities underscore the diversity of Titanosauria and the paucity of Late Triassic and Early Jurassic genera. The diversification of Titanosauria during the Cretaceous and origin of the sauropod body plan during the Late Triassic remain frontiers for future studies. © 2002 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2002, **136**, 217–276.

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INTRODUCTION

Sauropods were the largest terrestrial vertebrates – their estimated body mass exceeds that of other large dinosaurs by an order of magnitude (Peczkis, 1994; Alexander, 1998). Despite the potential biomechanical constraints at this extreme body size, sauropods were the dominant megaherbivorous group throughout 140 million years (Myr) of the Mesozoic, constituting approximately one-fourth of known dinosaur genera (Dodson & Dawson, 1992). Sauropod generic diversity increased through time, with peaks in the Late Jurassic of North America and the Late Cretaceous of South America (based on Hunt *et al*., 1994). The North American diversity peak may have extended into the

Cretaceous, as new discoveries of sauropods from Oklahoma (Wedel, Cifelli & Sanders, 2000a, b), Arizona (Ratkevitch, 1998), and Utah (Britt *et al*., 1998; Tidwell, Carpenter & Brooks, 1999) attest. The dearth of sauropod remains on poorly known southern landmasses may also be to due poor sampling rather than a lack of fossil remains. Recent discoveries in Africa (Jacobs *et al*., 1993; Russell, 1996; Monbaron, Russell & Taquet, 1999; Sereno *et al*., 1999), Madagascar (Sampson *et al*., 1998; Curry Rogers & Forster, 2001), and Indo-Pakistan (Chatterjee & Rudra, 1996; Jain & Bandyopadhyay, 1997; Malkani, Wilson & Gingerich, 2001) have begun to reduce this bias.

All known sauropods have a distinct, easily recognizable morphology: a long, slender neck and tail at either end of a large body supported by four columnar limbs (Fig. 1). The anatomical details of this architecture are unique to sauropods and have furnished the
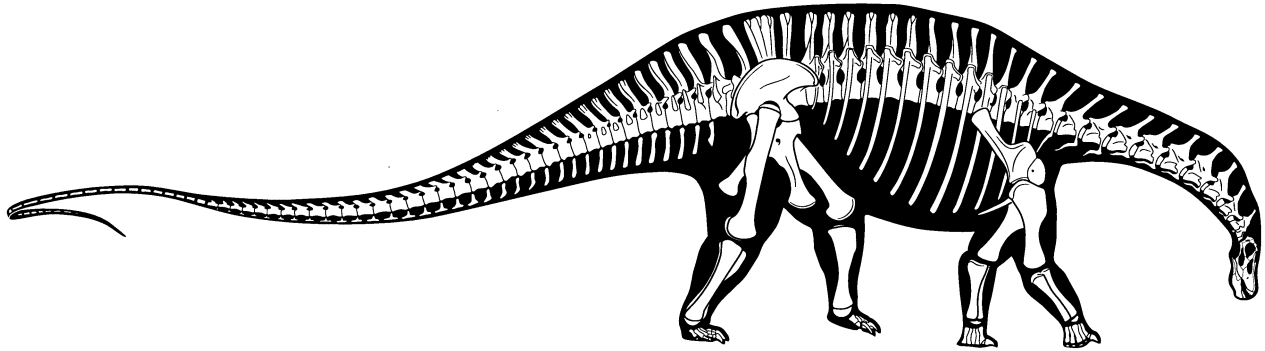
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Figure 1. Silhouette skeletal reconstruction of *Dicraeosaurus hansemanni* in right lateral view. The reconstruction is based on a partial skeleton (HMN skeleton m), which includes a partially articulated vertebral series from the axis to the 18th caudal vertebra (including ribs and chevrons), a pelvis, and a hindlimb lacking the pes (Janensch, 1929b; Heinrich, 1999: fig. 19). Elongate, biconvex distal caudal centra were collected at sites s and dd, but the length of this series is unknown (McIntosh, 1990: 392). The presence of a 'whiplash' tail of 20 or more elongate, biconvex caudal centra is equivocal for *Dicraeosaurus* (Wilson *et al*., 1999: 594). A 'whiplash' of intermediate length has been reconstructed here. The forelimb was based on a second specimen (HMN skeleton o) preserving a scapula, coracoid, humerus, and ulna in association with caudal vertebrae, a pelvis, and a partial hindlimb (Heinrich, 1999: fig. 6). Missing elements of the manus and pes were based on those of *Apatosaurus* (Gilmore, 1936); missing cranial elements were based on *Diplodocus* (Wilson & Sereno, 1998: fig. 6A).

basic evidence of their monophyly (e.g. Marsh, 1878, 1881; Romer, 1956; Steel, 1970; Gauthier, 1986; McIntosh, 1990). Based on comparisons with the saurischian outgroups Prosauropoda and Theropoda (Gauthier, 1986; Sereno *et al*., 1993), early sauropod evolution was characterized by an increase in body size, elongation of the neck, and a transition from bipedal to quadrupedal progression. These and many other sauropod synapomorphies must have arisen during the 15–25 million-year interval defined by their hypothesized divergence from other saurischians 225–230 Myr ago (Mya) (Flynn *et al*., 1999) and their first appearance in the fossil record, 206–210 Mya (Buffetaut *et al*., 2000; Lockley *et al*., 2001) (Fig. 2).

A broad range of variation is present within this basic body plan, providing a basis for more than 70 named sauropod genera. Of these, the few that are known from cranial remains indicate at least two different general skull morphs (Fig. 3). One sauropod subgroup, Diplodocoidea, has a long, low skull with a rectangular muzzle that terminates in a reduced set of pencil-like teeth. In contrast, macronarians such as *Brachiosaurus* and *Camarasaurus* have tall skulls with large, laterally facing nostrils and rounded jaws invested with large, spoon-shaped teeth. Cranial material of the basal titanosaur *Malawisaurus* (Jacobs *et al*., 1993), the isolated skull of *Nemegtosaurus* (Calvo, 1994; Wilson, 1997), and newly discovered material (Calvo, Coria & Salgado, 1997; Martinez, 1998) suggest a distinct skull morphology for titanosaurs that can be interpreted as a variation on the basic macronarian skull morph. The recently
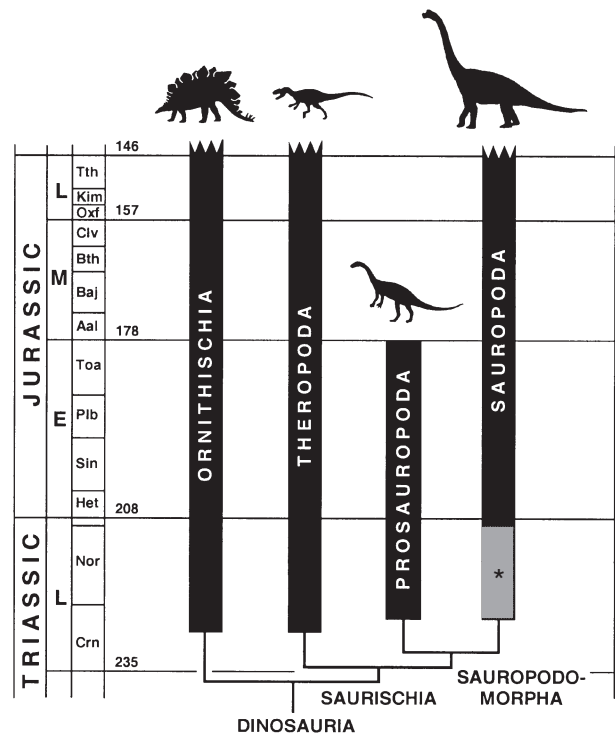

Figure 2. Temporal distribution and relationships of major lineages of dinosaurs during the Triassic and Jurassic. The asterisked grey bar represents the ghost lineage preceding the first appearance of sauropods in the fossil record. The diagnostic features of Sauropoda evolved during this implied 15–25 million year interval. Icons from Wilson & Sereno (1998) and Sereno (1999); timescale based on Harland *et al*. (1990).
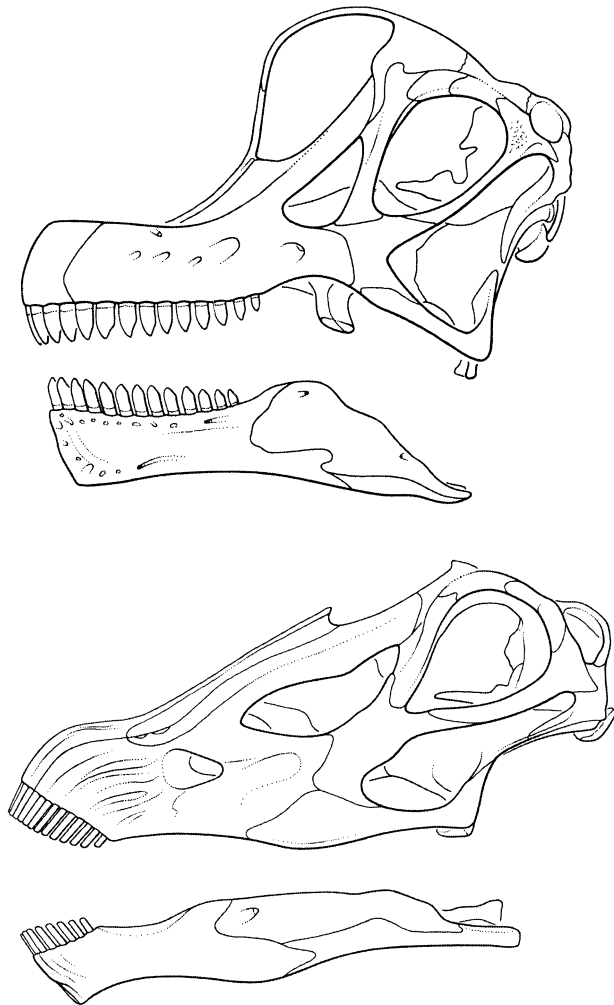
Figure 3. Macronarian and diplodocoid skull types, as represented by *Brachiosaurus* (top) and *Diplodocus* (bottom), respectively. Skulls are in left lateral view. Based on Wilson & Sereno (1998: figs 6A, 8A).

Figure 4. Vertebral laminae in cervical (top) and dorsal (bottom) vertebrae of *Diplodocus*. Both vertebrae are in right lateral view. Modified from Hatcher (1901: pl. 3, fig. 14; pl. 7, fig. 7). Abbreviations based on Wilson (1999a): acpl = anterior centroparapophyseal lamina; c = coel; cpol = centropostzygapophyseal lamina; cprl = centroprezygapophyseal lamina; di = diapophysis; hpo = hyposphene; nsp = neural spine; pa = parapophysis; pc = pleurocoel; pcdl = posterior centrodiapophyseal lamina; pcpl = posterior centroparapophyseal lamina; podl = postzygodiapophyseal lamina; poz = postzygapophysis; ppdl = parapophyseal diapophyseal lamina; prdl = prezygodiapophyseal lamina; prpl = prezygoparapophyseal lamina; prz = prezygapophysis; spdl = spinodiapophyseal lamina; spol = spinopostzygapophyseal lamina; sprl = spinoprezygapophyseal lamina. Scale bar = 20 cm.

described skull of *Rapetosaurus* (Curry Rogers & Forster, 2001), which was preserved in association with definitive titanosaur postcrania, confirms this assessment.

The sauropod vertebral column varies both in its length and morphology. The number of presacral vertebrae ranges from 24 to 31, the sacrum consists of between four and six co-ossified vertebrae, and the tail includes from 35 to more than 80 vertebrae. The presacral centra and neural arches of sauropods are characterized by numerous bony struts that connect the costovertebral and intervertebral articulations, centrum, and neural spine (Fig. 4). These bony struts, or vertebral laminae, enclose discrete fossae that in life may have been filled by pneumatic diverticulae, or outpocketings of lung epithelium (Britt, 1997; Wedel
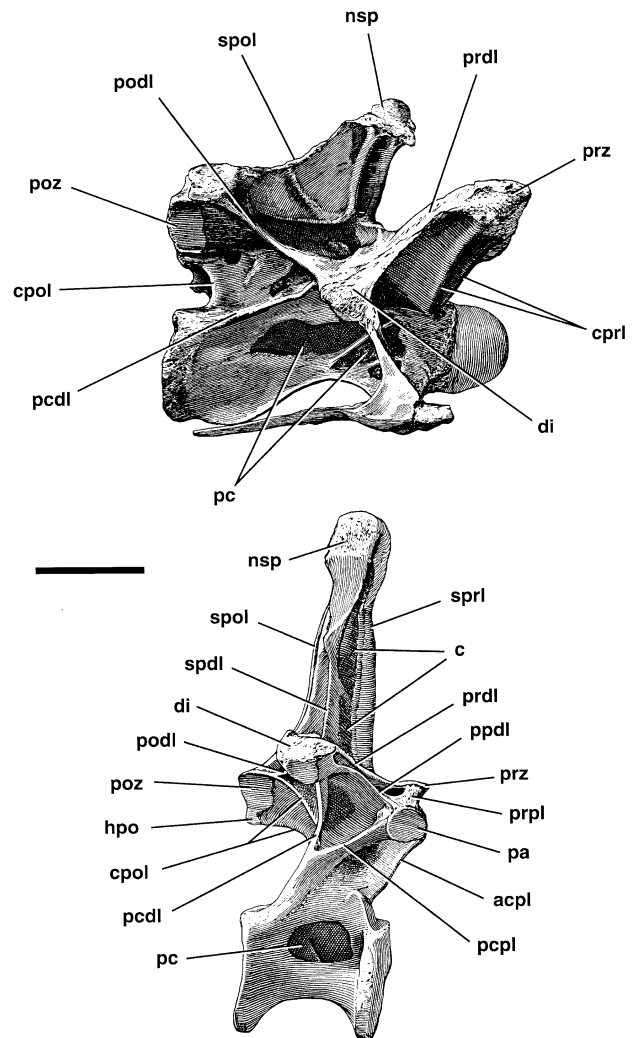
et al., 2000b). The architecture of these vertebral laminae is particularly complex in sauropods compared to that in other saurischians and phylogenetically informative at higher and lower levels (Bonaparte, 1999;

Wilson, 1999a). Sauropods are also characterized by various tail specializations, including the fusion of the distalmost three or four caudal vertebrae into a bony tail club in *Shunosaurus* (Dong, Peng & Huang, 1989), and the short series of mobile, biconvex caudals in neosauropods, which is modified into a 'whiplash' tail in diplodocids (Holland, 1906) (Fig. 5).

Aside from variation in the number of carpal, tarsal, and phalangeal elements, sauropod appendicular elements appear more conservative than other parts of the sauropod skeleton. Titanosaurs may be an exception, as limb specializations were particularly important in the acquisition of their derived 'wide-gauge' limb posture (Wilson & Carrano, 1999).

Major questions surrounding sauropod evolutionary history can be evaluated in the context of a hierarchy of relationships based on the distribution of morphological features within the group. Interest in sauropod relationships has produced quite disparate views of sauropod descent, which necessarily imply different evolutionary histories for the group. The present analysis is an attempt to better our understanding of the lower-level relationships of Sauropoda by evaluating character data from previous analyses, as well as novel character information generated from collections research. The first section of this paper will elucidate points of similarity and difference between recent cladistic analyses, focusing specifically on coding assumptions, scoring, and topology in the two most recent and thorough cladistic treatments of sauropods. This section will underscore the main differences in these views of sauropod relationships, as well as produce a core of characters for use in subsequent analyses. The second section of the paper will analyse a wide range of anatomical characters across a broad sampling of genera to generate a hypothesis of the lower-level relationships of Sauropoda.

ABBREVIATIONS

Institutions. AMNH, American Museum of Natural History, New York; HMN, Museum für Naturkunde der Humbolt-Universität, Berlin; ISI, Indian Statistical Institute, Calcutta; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan.

RECENT CLADISTIC ANALYSES

HIGHER-LEVEL CONSENSUS AND SUMMARY

In an effort to achieve a general consensus of the higher-level relationships of sauropod dinosaurs, topologies of the cladistic analyses of Calvo & Salgado (1995), Upchurch (1995), Salgado, Coria & Calvo *et al.* (1997), Upchurch (1998), and Wilson & Sereno (1998) are compared here. Consensus trees were generated

from the published topologies, which differ considerably in the number of taxa and characters included (Table 1). For ease of comparison, lower-level taxa were subsumed into higher taxa where appropriate (Fig. 6), and the topologies of these five simplified hierarchies were compared in both strict and 50% majority-rule consensus cladograms (Fig. 7). The minimum number of topological rearrangements separating each of the topologies is listed in Table 2.

A strict consensus tree generated from the five analyses preserves only one internal node, Eusauropoda, comprising nine unresolved taxa (Fig. 7). The 50% majority-rule consensus tree offers more resolution, maintaining two additional nodes, Neosauropoda and Titanosauriformes (Fig. 7). Unresolved taxa in the 50% majority-rule tree correspond to *Barapasaurus*, the Chinese taxa that Upchurch (1995, 1998) places in 'Euhelopodidae', *Haplocanthosaurus*, and *Camarasaurus*. Variant interpretations for each of these taxa are outlined below.

The phylogenetic position of *Barapasaurus* amongst non-neosauropods differs only in the analyses of Upchurch (1995, 1998) and Wilson & Sereno (1998). Upchurch considered *Barapasaurus* more basal than *Shunosaurus*, whereas Wilson & Sereno resolved *Barapasaurus* as more closely related to neosauropods than is *Shunosaurus*. Because neither Calvo & Salgado (1995) nor Salgado *et al.* (1997) included more than two basal sauropod taxa, their placement of *Barapasaurus* is consistent with either hypothesis. *Barapasaurus* is known from more than 205 postcranial elements (Jain *et al.*, 1979), but only a fraction of these has been described and fewer illustrated. Miss-
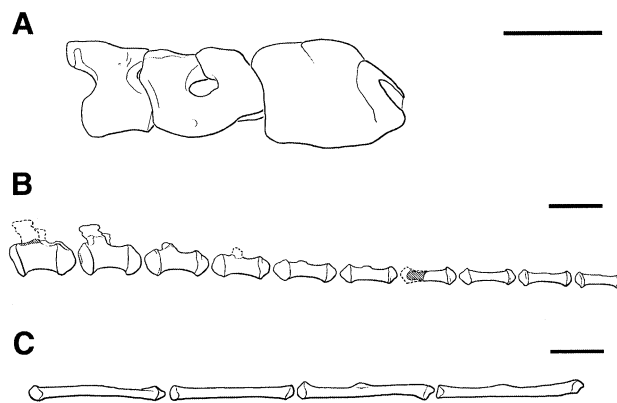

Figure 5. Tail specializations in sauropod dinosaurs. A, bony tail club of *Shunosaurus*; B, short, biconvex distal caudal vertebrae of a unnamed titanosaur from Argentina; C, 'whiplash' tail vertebrae of *Diplodocus*. A–C modified from Dong *et al*. (1989: fig. 1), Wilson *et al*. (1999: fig. 2), and Holland (1906: fig. 29), respectively. Scale bars = 10 cm.

Table 1. Comparison of tree statistics for five recent cladistic analyses of sauropod dinosaurs. Analyses are listed in chronological order. Abbreviations: CI = consistency index; MPT = most parsimonious trees; RI = retention index. Two different CI and RI values were reported by Wilson & Sereno (1998: 54, fig. 44). The correct values (from the figure) are listed here

Analysis	Taxa	Characters	MPT	Steps	CI	RI
Calvo & Salgado (1995)	13	49	1	85	0.655	0.787
Upchurch (1995)	21	174	?	?	?	?
Salgado *et al.* (1997)	16	38	2	54	0.81	0.932
Wilson & Sereno (1998)	10	109	1	153	0.81	0.86
Upchurch (1998)	26	205	2	346	0.553	0.737
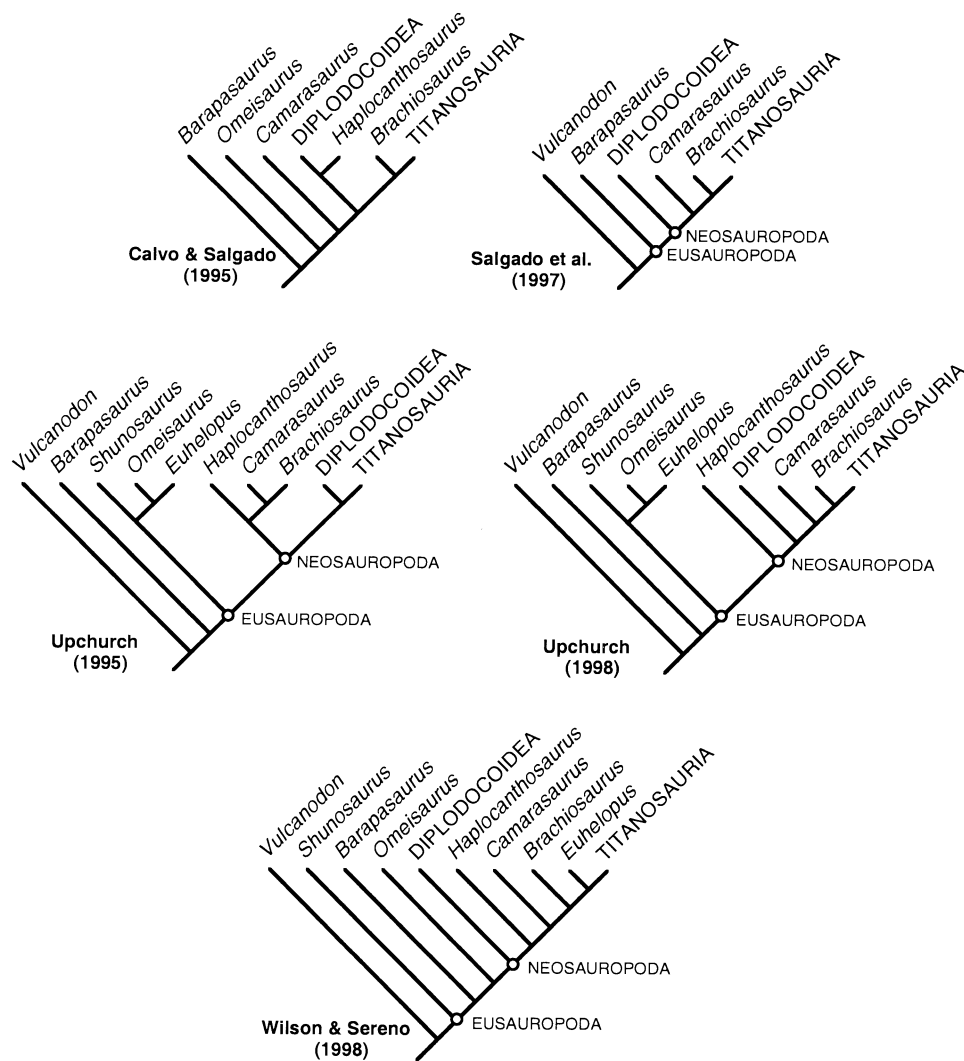
Figure 6. Five recent cladistic hypotheses of sauropod relationships. Each has been simplified for ease of comparison and to reflect higher-level groupings.

ing information, then, may play an important role in the lack of phylogenetic resolution for *Barapasaurus*. Wilson & Sereno (1998) identified six synapomorphies nesting *Barapasaurus* more closely to neosauropods than is *Shunosaurus*, whereas Upchurch identified only two features that unambiguously maintain *Shunosaurus* as more derived than *Barapasaurus*, one of which is homoplastic (CI = 0.167).

Table 2. Comparison of topologies of five recent cladistic analyses of sauropod dinosaurs. Numbers denote the number of higher-level topological differences between the most parsimonious trees in each analysis. Total number of topological differences with other analyses: Calvo & Salgado (1995) – 9; Upchurch (1995) – 12; Salgado *et al*. (1997) – 4; Wilson & Sereno (1998) – 10; Upchurch (1998) – 7

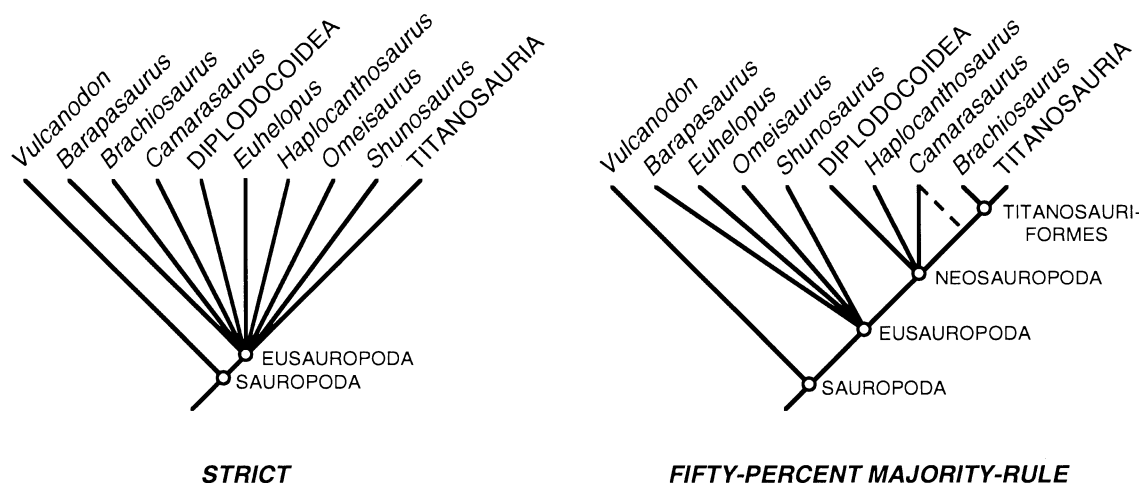|	C & S (1995)	U (1995)	S (1997)	W & S (1998)	U (1998)
C & S (1995)	–	3	2	2	2
U (1995)	–	–	2	5	2
S (1997)	–	–	–	0	0
W & S (1998)	–	–	–	–	3
U (1998)	–	–	–	–	–

Figure 7. Strict (left) and 50% majority-rule (right) consenses of the five recent cladistic hypotheses shown in Figure 6. Dashed line indicates increased resolution after rescoring two characters in the data matrix of Calvo & Salgado (1995).

The Chinese taxa *Shunosaurus*, *Omeisaurus*, and *Euhelopus*, in contrast, are among the most complete sauropod genera known, so missing data cannot be invoked to explain radically different interpretations of their descent. Three analyses, Upchurch (1995, 1998) and Wilson & Sereno (1998), include these three Chinese taxa (see Fig. 6). A fourth, *Mamenchisaurus*, was included by Upchurch (1995, 1998) but not by Wilson & Sereno (1998). Upchurch's analyses found support for the monophyly of these Chinese taxa and placed them as the sister-taxon to Neosauropoda in the clade Eusauropoda. Wilson & Sereno (1998), in contrast, resolved these same Chinese taxa as a polyphyletic assemblage, with *Shunosaurus* as the basal eusauropod, *Omeisaurus* as the outgroup to Neosauropoda, and *Euhelopus* as the sister-taxon to Titanosauria in the clade Somphospondyli.

Different topologies predict different timing and sequence of phylogenetic branching in a group's evolutionary history, so measures of stratigraphic congruence may help resolve topological conflict (Wagner,

1995). The minimum implied gaps for both phylogenies were calculated and compared (Fig. 8). Both the Wilson & Sereno (1998) and the Upchurch (1998) hierarchies require four missing lineages, three of which accrue during the Early and Middle Jurassic. These hierarchies, however, differ in the total implied gap as well as the distribution of that gap. The Wilson & Sereno (1998) hypothesis predicts a larger gap (85 Myr) than does the Upchurch (1998) topology (75 Myr). Scaled to total lineage duration (140 Myr), these minimum implied gaps represent 61% and 54% of sauropod history, respectively. This discrepancy is due to differing interpretations of basal sauropod taxa. Because it is stratigraphically costlier to resolve the Middle Jurassic *Shunosaurus* as more basal than the Early Jurassic *Barapasaurus*, Upchurch's (1998) hypothesis implies less stratigraphic debt than does that of Wilson & Sereno (1998). Both hypotheses accumulate the majority of their stratigraphic debt in the Early and Middle Jurassic, which may indicate that these levels have not been adequately sampled (Wagner, 1995). The apparently simultaneous evolu-
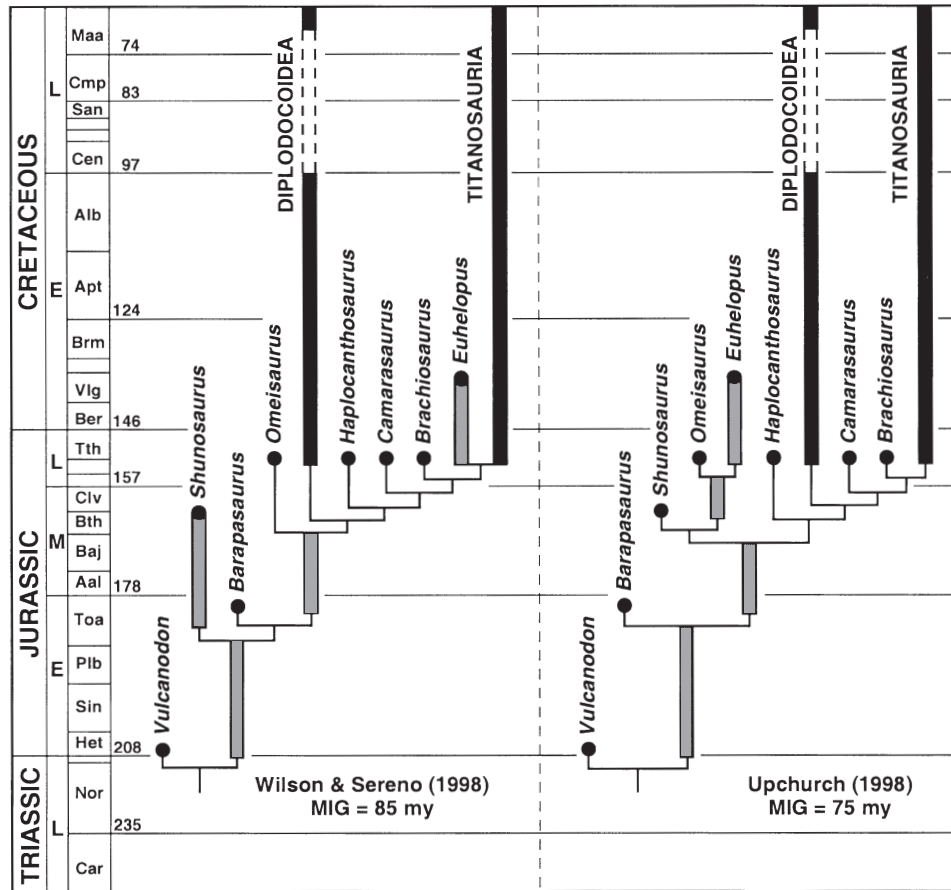
Figure 8. Minimum implied gap (MIG) predicted by the topologies of Wilson & Sereno (1998), left, and Upchurch (1998), right. Grey bars indicate missing lineages as implied by sister-taxon relationships. The dashed bar denotes an missing interval for Diplodocoidea that is implied by the late appearance of the controversial species *Antarctosaurus wichmannianus* (Huene, 1929), here regarded as a rebbachisaurid (see Table 13). Timescale based on Harland *et al*. (1990).

tion of all other neosauropods in the Late Jurassic (Kimmeridgian–Tithonian) underscores this assessment – better sampling of earlier intervals will help resolve the origin of neosauropod lineages as well as that of basal eusauropod taxa. Thus, neither missing anatomical data nor missing stratigraphic information account for differing interpretations of the Chinese 'euhelopodids' by Wilson & Sereno (1998) and Upchurch (1998). The cause for the fundamental difference between these two analyses must be sought in the character evidence each has brought to bear on the problem (see 'Character distributions' in Upchurch, 1998).

Lack of consensus on the phylogenetic affinities of *Haplocanthosaurus* is less the product of disagreement than a general admission of ignorance. All but Upchurch (1998) agree that *Haplocanthosaurus* falls within the clade that includes diplodocoids and macronarians (Neosauropoda), but its position within Neosauropoda is not well supported by any analysis. In

fact, no analysis boasts a decay index greater than two for the node linking *Haplocanthosaurus* to other sauropod taxa. While Calvo & Salgado (1995) interpreted *Haplocanthosaurus* as a basal diplodocoid, Upchurch (1995) interpreted it as the sister-taxon to *Brachiosaurus* and *Camarasaurus*. Later, Upchurch (1998) interpreted it as the outgroup to Neosauropoda, and Wilson & Sereno (1998) interpreted it as a basal macronarian. It is possible that the lack of cranial and distal limb remains precludes alignment of *Haplocanthosaurus* with either of the two main neosauropod lineages. This unresolved situation awaits description of more complete remains referred to the genus (Bilbey, Hall & Hall, 2000).

Calvo & Salgado (1995) placed *Camarasaurus* as the outgroup to a clade that includes titanosauriforms, *Haplocanthosaurus*, and diplodocoids (they did not indicate the node Neosauropoda on their cladogram). All other analyses resolved *Camarasaurus* as a close relative of the neosauropod *Brachiosaurus*. Of

these, all but Upchurch (1995) regard *Camarasaurus* and *Brachiosaurus* as successive sister-taxa to Titanosauria, in the clade Macronaria. Rescoring two characters in the Calvo & Salgado (1995) matrix, however, changes their preferred topology to one that nests *Camarasaurus* within Neosauropoda as the sister-taxon to *Brachiosaurus* and Titanosauria. This change increases the resolution of the 50% majority-rule consensus cladogram (Fig. 7, dashed line). The first character, width of the supraoccipital (Calvo & Salgado character 12), was rescored from the primitive state (50% of skull width) to the derived state (less than 30% of skull width) based on a subadult *Camarasaurus* skull that preserves this suture (Wilson & Sereno, 1998: fig. 7). The second, absence of the hyposphene–hypantrum articulation in anterior dorsal vertebrae (character 23), was also erroneously scored as primitive for *Camarasaurus*, as well as for several other sauropods – *Camarasaurus* (Osborn & Mook, 1921: pl. 73), *Omeisaurus* (He, Li & Cai, 1988: fig. 27), *Apatosaurus* (Gilmore, 1936: pl. 25), *Diplodocus* (Hatcher, 1901: pl. 7), *Barosaurus* (Lull, 1919: 15) and *Dicraeosaurus* (Janensch, 1929a: pl. 1).

In summary, the series of phylogenetic analyses in recent years has led most researchers to a consensus on the fundamental relationships of sauropod dinosaurs. *Vulcanodon* is the most primitive sauropod, placed as outgroup to a paraphyletic series of basal sauropods that includes *Shunosaurus*, *Barapasaurus*, and *Omeisaurus*. Neosauropoda is acknowledged as consisting of two clades, Diplodocoidea and Macronaria. The majority of analyses agree that Macronaria includes *Camarasaurus*, *Brachiosaurus*, and Titanosauria. Although the position of *Haplocanthosaurus* is poorly resolved, this may be the result of missing information. The fundamental higher-level topological disagreement involves the position of the Chinese sauropods. To better discriminate between the differing interpretations of Chinese sauropods, the recent cladistic appraisals of sauropod relationships by Wilson & Sereno (1998) and Upchurch (1998) will be critiqued in the following discussion. The purpose of these critiques is to elucidate differences in coding assumptions, scoring, and topology, with the goal of achieving a consensus of sauropod relationships and producing a core of characters for use in lower-level analyses of sauropod relationships. The analyses by Russell & Zheng (1994), Calvo & Salgado (1995), Upchurch (1995), and Salgado *et al.* (1997) were discussed in Wilson & Sereno (1998: 3–8) and will not be treated here.

WILSON & SERENO (1998)

Wilson & Sereno (1998) presented an analysis of 109 characters in 10 taxa representative of sauropod
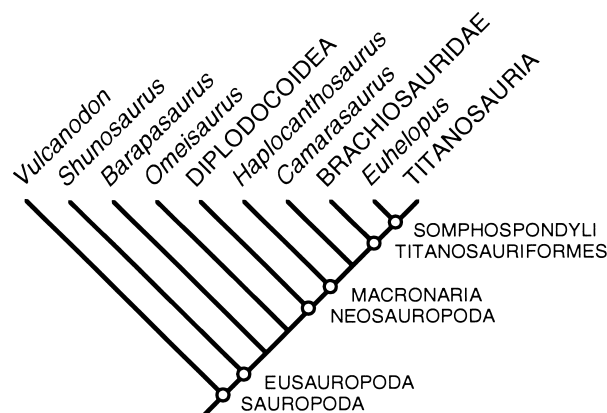

Figure 9. Higher-level relationships of sauropods based on Wilson & Sereno (1998).

diversity. A series of basal taxa was resolved as successive sister-taxa to Neosauropoda, the clade comprising Diplodocoidea and Macronaria (Fig. 9). Within Macronaria, *Haplocanthosaurus* and *Camarasaurus* were positioned as outgroups to Titanosauriformes, the clade that includes Brachiosauridae, *Euhelopus*, and Titanosauria (the latter two form the clade Somphospondyli). Several nodes in the resultant topology were determined to be stable; the position of other taxa, such as *Haplocanthosaurus* and *Barapasaurus*, were deemed less stable (Wilson & Sereno, 1998: 54). Because Wilson & Sereno focused on the higher-level relationships among sauropods, several taxa were not included, and some suprageneric taxa were used as terminals. These and other aspects of Wilson & Sereno (1998) are discussed below.

Higher-level terminal taxa

The use of higher-level terminal taxa in phylogenetic analysis can be advantageous because it enables the systematist to develop analyses of broad taxonomic scope using fewer operational taxonomic units. Where inclusion of all genera spanning a certain taxonomic scope mandates use of heuristic search methods, use of fewer, higher-level terminal taxa may allow exact tree-building methods. These advantages, however, may be countered by several disadvantages that stem from paraphyly of and variation within higher-level terminal taxa.

A basic assumption of cladistic analysis is that terminal taxa are monophyletic (Gaffney, 1977: 89), although the rationale for this has not been specified (Bininda-Edmonds, Bryant & Russell, 1998). An example of the effects of paraphyletic terminal taxa on cladistic analyses is provided by Carpenter, Miles & Cloward (1998). Their study of the phylogenetic rela-

Table 3. Rescored characters from the matrix published by Wilson & Sereno (1998). Character state abbreviations: '0' = primitive; '1', '2', '3' = derived; '?' = unknown; italicization indicates variation within the terminal taxon

Taxon	Character	Original	Rescored
Titanosauria	5, 32	1	*1*
Shunosaurus, *Omeisaurus*, *Camarasaurus*	36	1	0
Brachiosauridae, *Euhelopus*	36	1	0
Diplodocoidea	36	2	1
Titanosauria	36	3	*2*
Shunosaurus, Theropoda, Prosauropoda	58	0	1
Titanosauria, Diplodocoidea	70	3	*3*
Diplodocoidea	87, 88, 106	0	?
Prosauropoda, Theropoda	96	0	1
Brachiosauridae	102	0	1
Titanosauria	106	0	*0*

tionships of the Late Jurassic *Gargoyleosaurus* within Ankylosauria (*c.* 30 genera) employed only two other terminal taxa, Ankylosauridae and Nodosauridae. This choice of terminals allows only three hypotheses of relationships – *Gargoyleosaurus* could be the sister-taxon to either or both Ankylosauridae or Nodosauridae. As Wilkinson *et al*. (1998: 423) noted, "use of aggregate in-group terminal taxa (nodosaurids and ankylosaurids) . . . precludes placement of *Gargoyleosaurus* within either of these clades." In other words, the terminal taxa chosen by Carpenter *et al*. would be judged paraphyletic if the true phylogeny nests *Gargoyleosaurus* within either of them.

Variation can result in the incorrect coding of character states for a higher-level terminal taxon that represents several genera (Weins, 1998). Higher-level clades necessarily include genera that can be distinguished from one another, implying that no one genus represents the ancestral condition of that clade for all characters. Variant characters may be autapomorphies (unique to a genus), synapomorphies (shared by genera within the suprageneric taxon), or homoplasies (shared by genera outside the suprageneric taxon). If autapomorphies or synapomorphies predominate, then the presumed primitive condition for a suprageneric terminal taxon may be too transformed, precluding recovery of its true relationships. On the other hand, predominance of homoplastic characters can link a suprageneric taxon to another on the basis of characters that are not the result of common ancestry. These pitfalls are mitigated by ancestral coding based on prior phylogenetic analysis of the suprageneric terminal taxon (Bininda-Edmonds *et al*., 1998).

Wilson & Sereno (1998) employed three higher-level groups in their analysis: Diplodocoidea, Brachiosauridae, and Titanosauria. Although few would dispute their monophyly, potential danger rests in coding higher-level taxa that exhibit ingroup variation. Wilson & Sereno (1998: appendix, underscored entries) listed five features as varying within terminal taxa in their analysis. A re-evaluation of the matrix identified nine other features that vary within terminal taxa. Of these, character polarity can be safely established for six entries. Characters 5, 32, 36, 70, and 106 of Wilson & Sereno vary within Titanosauria; character 70 varies within Diplodocoidea. Polarity cannot be determined for the remaining three characters (87, 88, 106) in the absence of a lower-level analysis of Diplodocoidea. Observations on all variant characters are summarized in Table 3 and discussed in more detail below. Character numbers appearing in parentheses refer to those of Wilson & Sereno (1998).

Although most titanosaurs have a deep radial fossa on the anterolateral aspect of the ulna (character 5) (*Ampelosaurus* – Le Loeuff, 1995; *Alamosaurus*, USNM 15560), a comparably shallow radial fossa characterizes some saltasaurids (*Neuquensaurus* – Huene, 1929: pl. 11, figs 1D, 2B; *Saltasaurus* – Powell, 1992: fig. 32; *Opisthocoelicaudia* – Borsuk-Bialynicka, 1977: pl. 7, fig. 5). Based on the relationships within Titanosauria (Salgado *et al*., 1997) the shallow radial fossa is assumed to vary within Titanosauria and does not represent the primitive condition for the group.

Spatulate crowns (character 32) vary within Titanosauria, although this was not noted in the matrix. Broad crowns were hypothesized to be primitive for Titanosauria (Wilson & Sereno, 1998: 6) because they are present in *Malawisaurus*, which is considered to be a basal titanosaur (Jacobs *et al*., 1993). The narrow crowns present in other titanosaurs appears to be a derived condition, independent of that of diplodocoids.

The occlusal pattern on the crown (character 36) should be scored as polymorphic for titanosaurs

because some *Nemegtosaurus* teeth have V-shaped wear whereas others have low-angled planar wear (Nowinski, 1971: pl. 8, fig. 3). Note that Wilson & Sereno (1998: 22) did not test the phylogenetic affinities of *Nemegtosaurus*; rather, they assumed it was a titanosaur in their description of terminal taxa. It is also noted here that there is discordance between the description of states and the matrix entries for character 36 in Wilson & Sereno (1998). There is no '0' entry for character 36, and each derived state (except the 'not applicable' state) is one state number higher than it should be (e.g. taxa that are scored '1' should have been scored '0'). Aside from the polymorphism mentioned above, however, the scoring is appropriate.

Similarly, variation in the number of dorsal vertebrae (character 70) within titanosaurs and diplodocoids was not indicated in the matrix, although discussion of the increase in presacral vertebral number within sauropods indicates that counts vary for these two terminal taxa (Wilson & Sereno, 1998: fig. 47). In both cases, the higher dorsal vertebral count (i.e. 12) was assumed to be primitive for the higher-level terminal taxon, because most neosauropods retain this number.

The presence of bifid presacral vertebrae (character 106) was coded mistakenly as invariant within Titanosauria and Diplodocoidea, although the condition is known to vary within both groups (Wilson & Sereno, 1998: fig. 48). *Opisthocoelicaudia* is the only titanosaur with bifid spines, a feature that has been hypothesized to evidence its close affinity to *Camarasaurus* (Borsuk-Bialynicka, 1977; McIntosh, 1990). Given this singular variation in a nested taxon, however, undivided presacral neural spines can be regarded as the primitive condition for Titanosauria. Conversely, whereas most diplodocoids have bifid presacral neural spines, rebbachisaurids are known to possess single neural spines. Wilson & Sereno (1998) presumed bifid presacral spines were primitive for Diplodocoidea, although the possibility that Rebbachisauridae is the most primitive subgroup suggests that single spines may be primitive for Diplodocoidea. Thus, the primitive condition for Diplodocoidea is unknown and can only be discovered by including more subgroups as terminals in a lower-level analysis (see 'Rescoring the matrix', below).

Two features diagnosing Macronaria, open haemal arches (character 87) and coplanar distal ischia (character 88), were scored as primitive for diplodocoids although the rebbachisaurid *Rayososaurus* displays the derived state in both cases (Calvo & Salgado, 1995: 22, fig. 14; Calvo, 1999: 22). As noted for bifid neural spines (character 106), Rebbachisauridae could represent either the primitive or the derived condition for the group, and characters 87 and 88 should be scored as unknown or polymorphic for Diplodocoidea (see 'Rescoring the matrix', below).

Multistate coding assumptions

The 109-character matrix of Wilson & Sereno (1998) included 32 cranial, 24 axial, and 53 appendicular features. All but six characters were binary; three cranial and three axial features were multistates. All multistates were left unordered, but explicit justification was not given for this choice. The cranial multistate features included the position of the external nares (character 18), the cross-sectional shape of the tooth crowns (character 32), and the occlusal pattern (character 36); the three axial multistate features code number of cervical, dorsal, and sacral vertebrae (characters 37, 70, and 2, respectively). Each of these features has been placed in one of four multistate types, each of which may warrant its own coding assumptions (Table 4). The four multistate types are discussed below.

The first type of multistate character records variation in the number of serially homologous elements, such as vertebrae, phalanges, or teeth. Ordering this type of multistate character assumes incremental increases and decreases in the number of segmental elements. That is, a change from 12 to 17 cervical vertebrae requires passing through 13, 14, 15, and 16-vertebrae stages, each costing a step. This multistate coding assumption may be appropriate if vertebral and phalangeal elements are added sequentially (i.e. if the 7th vertebra condenses prior to formation of the 8th). Assumption of unordered changes for this character type, in contrast, means that transformations between any two states costs one step. This coding assumption seems appropriate if vertebral or phalangeal condensations can change the number of resultant segmental units without requiring intermediate stages. Vertebral segment identity may be controlled by a single *Hox* gene. The cervicodorsal transition in many tetrapods, for instance, appears to be defined by the expression boundary of the *Hoxc-6* gene (Burke *et al.*, 1995). Thus, development is not

Table 4. Four categories of multistate characters and recommended codings for Wilson & Sereno (1998). Multistate character types are discussed in text

Type	Character	Suggested coding
I: number	37: cervical vertebrae 70: dorsal vertebrae 2: sacral vertebrae	none
II: size	–	–
III: position	18: external nares	ordered
IV: variation	32: tooth cross-section shape 36: occlusal pattern	unordered

yet informative to the coding strategy of serially homologous structures. As indicated in Table 4, no particular coding is recommended for characters 37, 70, and 2 from Wilson & Sereno (1998).

The second type of multistate character records differences in the size of a structure, either in absolute or relative terms. Partial ordering of this multistate type may be justified on developmental evidence. A structure that increases in size during development passes through intermediate stages or states. If this is considered to be the means by which a structure becomes 'large' in a group's evolutionary history, then ordering of size increases is justified. For size reduction, however, ordering may not be justified. An evolutionary transition from 'large' to 'small' may not require intervening stages. A structure need not reach maximum size before it is reduced; its growth may simply be arrested. Thus, size-related characters may be ordered on the way 'up' (gains accumulate), but left unordered on the way 'down' (losses can occur in a single step). Maddison & Maddison (1992) call this an 'easy loss' character, which can be coded in a step matrix (Table 5). Forey *et al*. (1992: fig. 4.9) refer to this character type as one in which the Wagner parsimony criterion is employed for accumulations and the Fitch parsimony criterion for reversals. No multistates of this type were used by Wilson & Sereno (1998).

The third type of multistate documents variation in the position of an element in space relative to another structure. Ordering may be warranted 'up' and 'down' between states of this multistate type, presuming a 'migrational' rather than a 'discontinuous' model for positional change of anatomical elements. For example, retraction of the internal naris in crocodylians is presumed to occur as a posterior migration of the choanae on the palate, rather than them occupying a terminal position throughout early development and later appearing in a fully retracted position within the pterygoids (e.g. Larsson, 1999). Ordering of this and other migrational characters seems justified. The position of the external nares (character 18 of Wilson &

Sereno), may be justified as an ordered multistate. Although Wilson & Sereno coded this feature as unordered, parsimony resolved the most advanced state (nares retracted to a position above the orbit) as derived from the next most advanced state (nares retracted to a position level with orbit). Ordering of this character has no effect on the overall pattern of relationships.

The fourth multistate type records variation that cannot be interpreted reasonably as transformational. For example, characters 57 and 59, which describe occlusal pattern (V-shaped, high angled planar, low angled planar) and crown morphology (elliptical, D-shaped, or cylindrical cross section), respectively, suggest no character transformation series and were left unordered.

Rescoring the matrix

A total of nine cells from the Wilson & Sereno (1998) character-taxon matrix were rescored. The justifications for these changes are briefly summarized below in order of their appearance in the matrix (see Table 3 for list of rescored characters and states).

Wilson & Sereno (1998) scored the basal sauropod *Shunosaurus* and both sauropod outgroups as lacking the interprezygapophyseal lamina on posterior cervical and anterior dorsal vertebrae (character 58). A recent reevaluation of the nomenclature and distribution of vertebral laminae in saurischian dinosaurs, however, has shown that the interprezygapophyseal lamina actually characterizes all saurischians (Wilson, 1999a: 650). *Shunosaurus*, Theropoda, and Prosauropoda should be rescored as derived for this character. As discussed above (in 'Higher-level taxa'), Diplodocoidea includes taxa that are variable for three characters (87, 88, 106). Although Wilson & Sereno (1998) scored the group as derived in each case, Diplodocoidea should be scored as variable ('?') given the potential basal position of Rebbachisauridae. The outgroups Prosauropoda and Theropoda were scored as having a basipterygoid hook on the pterygoid (character 96), a feature that was determined to have been lost later in sauropod evolution. Both outgroups, however, lack this feature, and should be rescored as derived (Galton, 1990: fig. 15.2; Sereno & Novas, 1993; fig. 8). Brachiosauridae was regarded as primitively lacking somphospondylous bone texture in the presacral vertebrae, a feature that characterizes *Euhelopus* and Titanosauria. *Brachiosaurus*, however, clearly possesses somphospondylous presacral centra (Janensch, 1947: figs 4–8; 1950: figs 70–73) as do other brachiosaurids (*Sauroposeidon* – Wedel *et al*., 2000a: 113, fig. 4).

Each of these changes was emplaced, and the rescored matrix was reanalysed. The resultant topology,

Table 5. Step-matrix coding for an 'easy loss' multistate character that has three derived states (Maddison & Maddison, 1992). Gains accumulate for size increases, but losses can occur in a single step

From\to	0	1	2	3	4
0	0	1	2	3	4
1	1	0	1	2	3
2	1	1	0	1	2
3	1	1	1	0	1
4	1	1	1	1	0

as well as that produced by a 50% majority-rule consensus of trees two steps longer, was identical to that reported by Wilson & Sereno (1998).

Although an attempt was made to cite all previous mention of diagnostic features considering taxa known at time of publication, several citations were omitted by Wilson & Sereno (1998). They are listed here for completeness. Marsh (1878: 412) listed fore and hind limbs nearly equal in size (character 1), reduction of the fourth trochanter of the femur (character 11), and plantigrade hindfoot posture (character 52) in his original diagnosis of Sauropoda. In a revised diagnosis of the group Marsh (1881) noted that opisthocoelous presacral centra (characters 38 and 59) characterizes sauropods. Later, in his classification of the Dinosauria, Marsh (1882: 83) added loss of distal tarsals (character 13) to his diagnosis of the group.

It is also noted here that Wilson & Sereno (1998: fig. 20F) incorrectly labelled the medial view of the ulna as 'posterior'.

UPCHURCH (1998)

Upchurch (1998) presented a revision of his 1995 analysis with an expanded character-taxon matrix that included five additional genera – *Patagosaurus*, *Rebbachisaurus*, *Lapparentosaurus*, *Phuwiangosaurus*, and *Andesaurus* – and 31 additional characters for a matrix scoring 205 characters in 26 sauropod taxa. Upchurch's 1998 analysis is important because it included more taxa and more characters than any previous treatment of Sauropoda. His heuristic analysis of the data matrix produced two most parsimonious trees, which differed only in the relationships of the 'euhelopodid' genera *Omeisaurus*, *Mamenchisaurus*, and *Euhelopus* (Fig. 10A). This resultant topology, however, differs considerably from that of his 1995 analysis. Specifically, the topology of the 1998 analysis recognizes the fundamental division of neosauropods into two groups – diplodocoids and a clade Upchurch refers to as 'brachiosaurs' – that was proposed by Salgado *et al.* (1997) and supported by Wilson & Sereno (1998).

The results of Upchurch (1998) will be evaluated in four ways. First, suboptimal trees will be generated in an effort to determine the relative robustness of nodes. Second, character coding assumptions and their effect on the results of the analysis will be assessed. Two alternate matrices will be produced: one with unordered multistate characters, the other employing different coding strategies for multistate characters. The resultant topologies will be compared to that reported by Upchurch (1998). Third, character evidence supporting the monophyly of the Chinese sauropods *Shunosaurus*, *Omeisaurus*, *Mamenchisaurus*, and

Euhelopus will be evaluated to determine the robustness of 'Euhelopodidae'. Last, a Templeton test will be used to determine whether the Upchurch (1998) matrix can reject a topology in which 'Euhelopodidae' is paraphyletic.

Suboptimal trees

Reanalysis of the published matrix yielded slightly different results than those reported by Upchurch (1998) – two additional most parsimonious trees were produced that differ in the relationship of *Rebbachisaurus* to other diplodocoids. These topological differences resulted from an erroneous entry in the published matrix: *Nemegtosaurus* should be coded as '0' for character 20 (Upchurch, pers. comm.). When this error was corrected, the matrix yielded the results reported by Upchurch (1998).

Upchurch's most parsimonious tree resolves two Lower Jurassic taxa, *Vulcanodon* and *Barapasaurus*, as sister-taxa to Eusauropoda, the clade that includes the Chinese family 'Euhelopodidae' and the globally distributed clade Neosauropoda. 'Euhelopodidae' includes four Middle Jurassic-to-Early Cretaceous taxa whose relationships were not completely resolved. The relationships within Neosauropoda, however, were fully resolved. The Jurassic forms *Patagosaurus*, *Cetiosaurus*, and *Haplocanthosaurus* form a paraphyletic grade of 'cetiosaurs' that fall outside a group uniting Diplodocoidea and the clade including *Camarasaurus*, *Brachiosaurus*, and 'Titanosauroidea'. Upchurch's term 'Brachiosauria' for the latter clade will not be used here, as the name Macronaria has been used previously to refer to the same group (Wilson & Sereno, 1998). Similarly, the name 'Titanosauroidea' (Upchurch, 1995, 1998) will be dropped in favour of Titanosauria, the first name applied to the same group (Bonaparte & Coria, 1993; Salgado *et al.*, 1997; Wilson & Sereno, 1998).

Upchurch's (1998) topology differs from that presented in his 1995 analysis by only four rearrangements, which involve *Mamenchisaurus* or *Euhelopus*, *Opisthocoelicaudia*, *Camarasaurus*, and *Brachiosaurus*. The phylogenetic repositioning of these latter two genera has significant implications for the higher-level relationships of neosauropods. Whereas Upchurch (1995: fig. 8) placed *Brachiosaurus* and *Camarasaurus* (with *Haplocanthosaurus*) as the sister-group to his narrow-crowned clade of diplodocoids and titanosaurs, the revised analysis (Upchurch, 1998: fig. 19) resolved *Camarasaurus* and *Brachiosaurus* within the diplodocoid–titanosaur clade, as successive sister taxa to Titanosauria. In an effort to distinguish between the two scenarios these analyses imply – one, a single origin of narrow tooth crowns, the other their
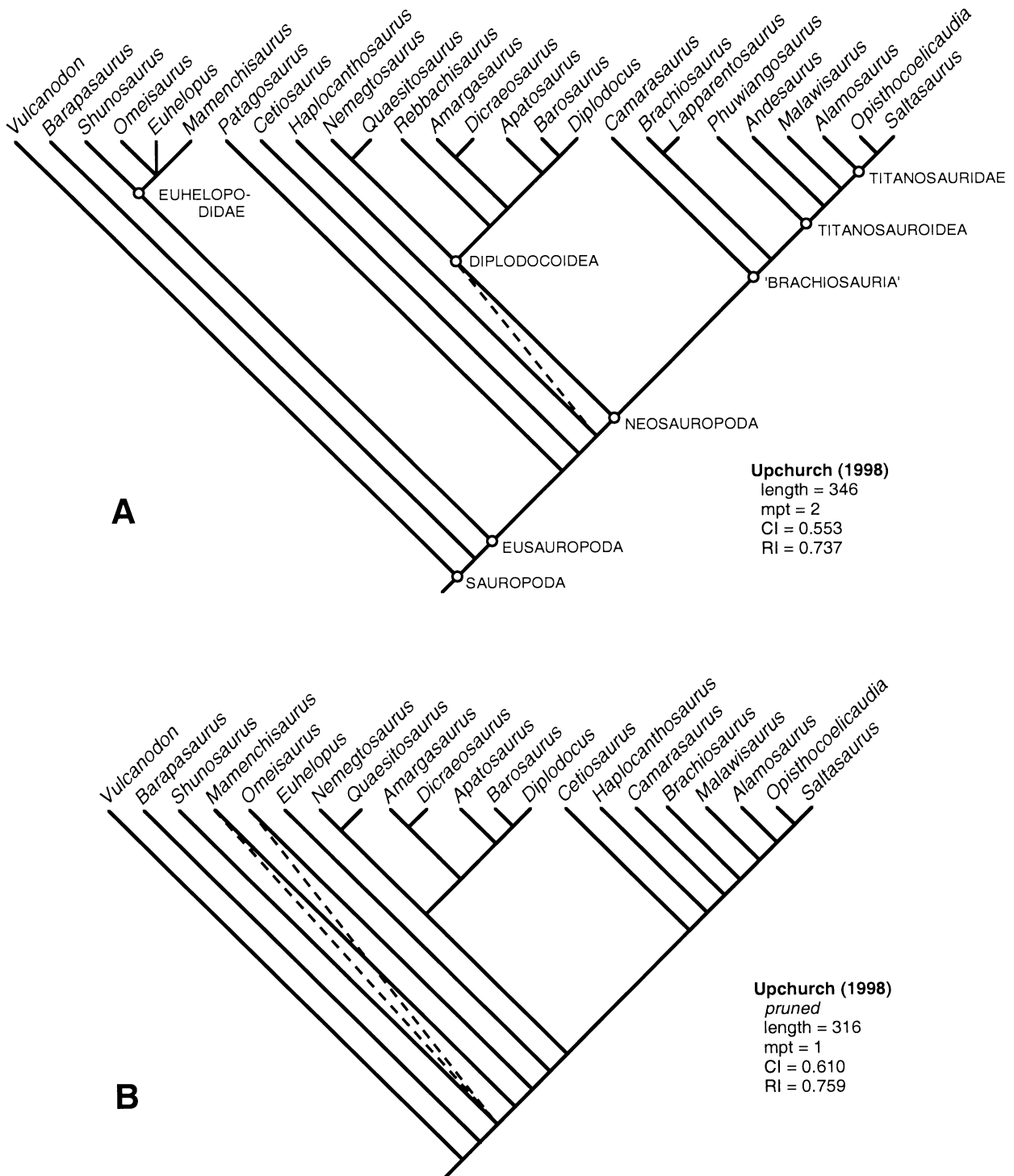
Figure 10. Upchurch (1998). A, fully resolved most parsimonious tree; B, most parsimonious tree produced with taxa pruned to match those of Upchurch (1995). Dashed lines indicate nodes that collapse in a 50% majority-rule consensus of trees two steps longer than the most parsimonious tree.

independent evolution – Upchurch's two analyses are compared here. Because his 1995 analysis did not include a character-taxon matrix or a list of characters and states, direct comparison of the data is not possible. Instead, topologies will be compared.

The five taxa not included in the 1995 analysis were deleted from the 1998 matrix and the 'pruned' data were re-run. Re-analysis produced a single most parsimonious tree that differs in two important ways from that reported by Upchurch (1998) (Fig. 10B). First, the tree produced by the pruned matrix resolves the four 'euhelopodids' as successive sister-taxa to Neosauropoda, implying a paraphyletic 'Euhelopodidae'. Second, the pruned matrix places *Cetiosaurus* and *Haplocanthosaurus* as sequential outgroups to 'Brachiosauria' rather than as outgroups to the rest of neosauropods. Both topological differences present in the pruned matrix are consistent with the topology presented by Salgado *et al.* (1997) and Wilson & Sereno (1998). Three additional steps (generating 489 trees) are required to achieve the Upchurch (1998) topology, which resolves a monophyletic 'Euhelopodidae' and places *Cetiosaurus* and *Haplocanthosaurus* as basal neosauropods. A 50% majority-rule consensus of trees three steps longer than the most parsimonious tree recovers all nodes but those three uniting *Shunosaurus*, *Omeisaurus*, and *Mamenchisaurus* to other eusauropods. Upchurch's 1995 topology first appears as one of the more than 32 700 trees that are nine steps longer than the most parsimonious tree produced by the pruned data.

What are the implications of the topological differences produced by removal of taxa from Upchurch's (1998) original matrix? It is implicit from tree-building algorithms that removal of taxa or characters may have a dramatic effect on overall tree topology (e.g. Wiley *et al.*, 1991; Swofford, 1993). For example, inclusion or exclusion of the taxon Sauropterygia from analyses of sauropsid relationships determines the placement of Testudines within Diapsida or Parareptilia, respectively (Rieppel & Reisz, 1999). In addition to reflecting the structure of the data, such results suggest that polarity of character transformations play a crucial role in placement of certain taxa, and that certain taxa play an important role in establishing polarity. Topological rearrangements following exclusion of five terminal taxa from Upchurch (1998) are restricted to two taxa: 'euhelopodids' and *Haplocanthosaurus*. The phylogenetic position of these two taxa are determined by relatively few characters whose polarity is not strongly supported.

Multistate coding assumptions
The revised matrix of Upchurch (1998) contains 24 multistate characters; 20 were ordered and four were left unordered. Upchurch coded the ordered characters in step matrices that are identical to additive binary coding (e.g. Wiley *et al.*, 1991). Upchurch (1998: 46) justifies his use of additive binary coding this way: "[t]his method is operationally equivalent to the use of an ordered multistate character coded within a single column" but is advantageous because "it can increase the information content of the matrix when missing data is common." Partially missing data, however, can be incorporated into single-column multistate coding just as easily as into binary additive coding. For example, a partially preserved taxon scorable as derived for two of three binary additive characters can simply be coded as '2' in a single multistate character. If desired, the cell can be flagged in the matrix to indicate that the entry represents a partially preserved feature.

Additive binary coding imposes ordered change on characters. What is the justification for this choice, and how does character ordering affect cladogram topology and character support? Two alternative coding assumptions were imposed on the Upchurch (1998) matrix to evaluate the effect of character ordering on the tree topology. The first assumed unordered changes for all characters, and the second assumed unordered change for only cervical count characters. A completely unordered dataset was created by identifying additive binary characters, recoding them into a single column, and scoring residual columns as unknown ('?'). 'Partially missing' information was coded with the highest state preserved. Fifteen equally parsimonious trees were obtained from a matrix of completely unordered characters (Fig. 11A). Although most nodes in this unordered analysis are identical in those of the original, there are several differences. The most striking is that 'Euhelopodidae' is paraphyletic when characters are unordered.

Because ordering may be justified for some characters, the second set of coding assumptions allowed ordering for multistates coding size (type II) and position (type III) of bony elements (Table 6). Additionally, all multistates coding changes in the number of bony elements (type I) were left ordered, except the cervical count characters (C75–79), which were left unordered. The additive binary set coding cervical counts was translated into a single multistate character and the matrix re-analysed. In heuristic search using simple stepwise addition yielded 12 equally parsimonious trees (343 steps). However, use of random addition sequence (100 replicates) recovered an additional tree island that yielded a single most parsimonious tree only 342 steps long (Fig. 11B). Importantly, 'euhelopodid' genera are resolved as a paraphyletic series. Despite the loss of this arrangement in a suboptimal trees (Fig. 11B, dashed lines), this alteration of Upchurch's matrix underscores the dependency of 'euhelopodid' monophyly on ordered neck characters.
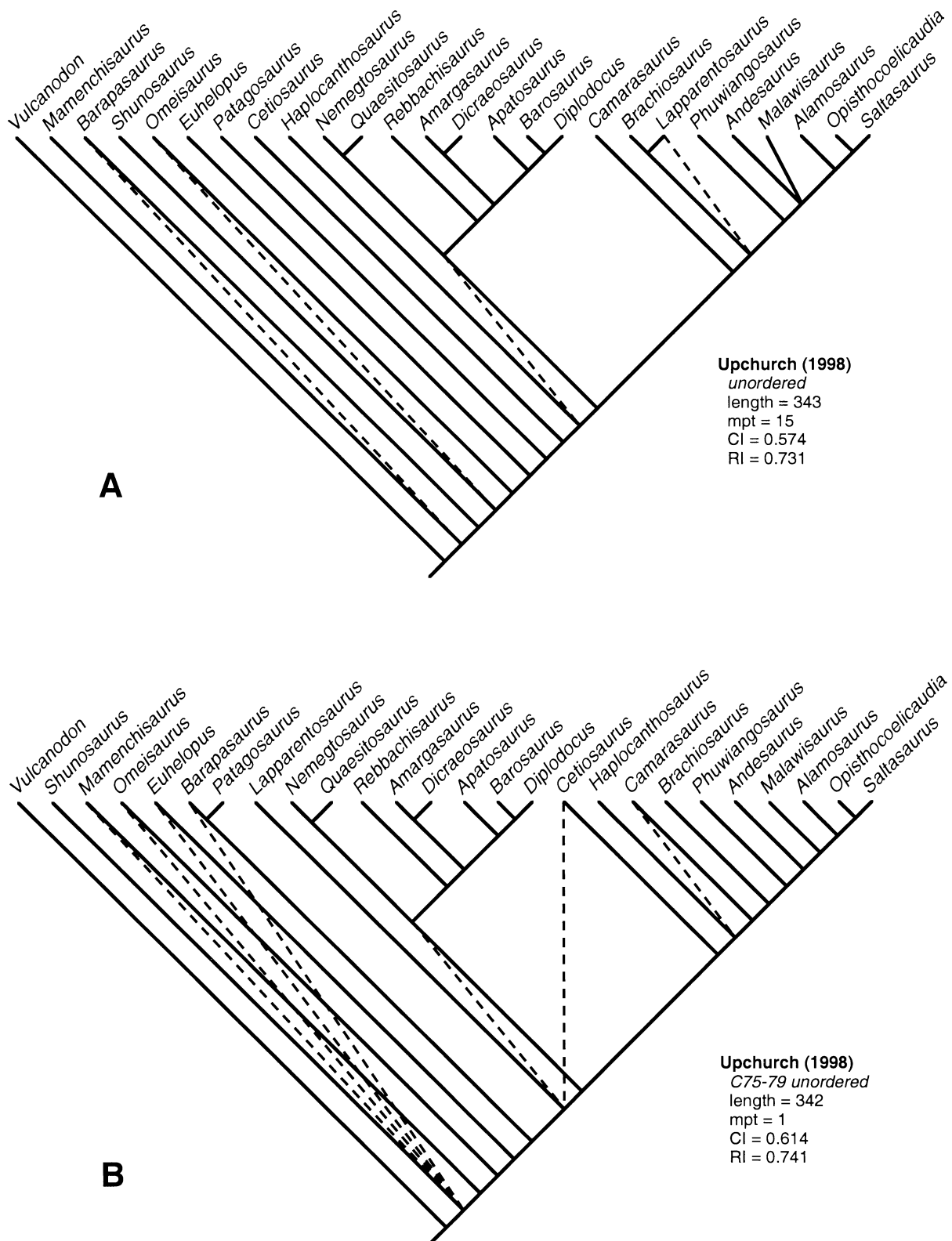
Figure 11. Upchurch (1998) continued. A, 50% majority-rule consensus of 15 trees produced when all characters are left unordered. B, most parsimonious tree when only characters C75–C79 are left unordered. Dashed lines indicate nodes that collapse in a 50% majority-rule consensus of trees two steps longer than the most parsimonious tree.

Table 6. Suggested recodings for four categories of multistate characters from Upchurch (1998). Three characters coded as ordered by Upchurch (1998) are here considered independent characters because they pertain to different regions of the skeleton (C81–82, C145–146, C155–156)

Type	Character	Suggested coding
I: number	C75–79, cervical vertebrae	none
	C120–122, sacral vertebrae	
	C163–165, distal carpals	
	C170–171, manual phalanges	
	C200–201, pedal phalanges	
II: size	C15–16, maxillary flange	'easy loss'
	C47–48, ectopterygoid process of pterygoid	
	C62–63, external mandibular fenestra	
	C69–70, tooth crowns	
	C97–98, dorsal pneumatopores (pleurocoels)	
	C125–126, dorsal neural spines	
	C129–131, procoely on caudal centra	
	C147–148, cranial process of chevrons	
	C158–159, forelimb–hindlimb ratio	
III: position	C2–3, external naris	ordered
	C26–27, infratemporal fenestra	
	C73–74, caudal margin of tooth row	
IV: variation	–	–

Character distributions

Upchurch (1998) defended 'euhelopodid' monophyly on the basis of eight features, seven of which were resolved by his analysis as unambiguous. Re-examination of character distributions reveals that of these eight, four are shared by a broad distribution of sauropod taxa, three are judged as not present in all 'euhelopodid' genera, and one is resolved as unique to 'euhelopodids'. The coding and distribution of each among Sauropoda are discussed below in anatomical order.

"Caudal end of prefrontal in dorsal view... is acute, subtriangular, and inset into the rostrolateral corner of the frontal" (character 28). Upchurch scored 'euhelopodids', *Rebbachisaurus* (based on *Rayososaurus*), and diplodocids with the derived state for this feature (character CI = 0.33). The prefrontal of *Diplodocus* and *Apatosaurus* does have an unusual posteromedially oriented hook at its posterior extreme (Berman & McIntosh, 1978: fig. 3a, d), but this feature characterizes neither 'euhelopodids' nor *Rayososaurus*. Published dorsal views of the skull of *Omeisaurus* indicate that the prefrontal is rounded posteriorly, without any trace of the hook that characterizes diplodocids (He *et al.*, 1988: figs 8, 9). Similarly, based on published illustrations and personal observations, the condition in *Shunosaurus* appears primitive (Zhang, 1988: fig. 8). *Euhelopus* was scored on the basis of an ele-

ment that Mateer & McIntosh (1985: fig. 1C, D) identified as a conjoined frontal and prefrontal. This element, however, is probably incorrectly identified, as the frontal portion of the element has neither the roughened orbital margin nor the anterolaterally orientated ventral ridge that forms the inner margin of the orbit (pers. observ.). The presence of a hooked prefrontal is restricted to the diplodocids *Apatosaurus* and *Diplodocus*.

Thirteen or more cervical vertebrae (character 76). Upchurch (1998) assumed ordered changes for all vertebral count characters and resolved the presence of 13 cervical vertebrae as diagnostic for 'Euhelopodidae'. This is despite the fact that only *Shunosaurus* was scored as possessing 13; *Omeisaurus*, *Mamenchisaurus*, and *Euhelopus* were scored as having 17. Ordering of this and other vertebral count features predispose them to act as synapomorphies for taxa that do not share the same character state. In addition to dependence on a particular coding assumption, two other considerations weaken support for increased cervical count being unique to 'euhelopodids'. First, presence of 13 cervical vertebrae is an ambiguous synapomorphy of 'euhelopodids' because vertebral counts are not known for the basal sauropods *Vulcanodon*, *Barapasaurus*, *Patagosaurus*, and *Cetiosaurus*. Therefore, an increase to 13 cervical vertebrae could have arisen in more basal nodes on the cladogram. Second,

the presence of 13 or more cervical vertebrae characterizes nearly all known sauropods and has been considered to be the primitive condition for Eusauropoda (Wilson & Sereno, 1998: fig. 47). Of the sauropods scored by Upchurch, only *Camarasaurus* was scored as primitively lacking 13; 'euhelopodids', *Brachiosaurus* and diplodocids were scored as derived, and all other sauropods were scored as unknown. Had other derived sauropods been scored appropriately (e.g. *Haplocanthosaurus*, Hatcher, 1903), the presence of 13 cervical vertebrae would be resolved as primitive for Eusauropoda. Based on its ambiguous character distribution among basal sauropods, generality within more derived sauropods, and dependence on an ordered coding strategy, presence of 13 or more cervical vertebrae cannot be held as a 'euhelopodid' synapomorphy. Presence of 17 cervical vertebrae (characters 77–79), however, is unique to *Omeisaurus*, *Euhelopus*, and *Mamenchisaurus*, regardless of coding strategy. Although some argue that *Omeisaurus* has only 16 (e.g. McIntosh, 1990), a large increase in the number of cervical vertebrae can be regarded as a potential synapomorphy of this 'euhelopodid' subgroup.

"Height : width ratio of cranial cervical centra . . . is approximately 1.25" (character 85). This is the only feature clearly shared by *Shunosaurus*, *Omeisaurus*, *Euhelopus* and *Mamenchisaurus* to the exclusion of other known genera. The distribution of this character amongst other basal sauropods (e.g. *Barapasaurus*, *Vulcanodon*, *Patagosaurus*), however, remains unknown.

'Centroparapophyseal lamina' present on middle and posterior dorsal vertebrae (character 105). There are two laminae that may connect the centrum and parapophysis: one projects forward from the parapophysis to the anterior portion of the centrum (anterior centroparapophyseal lamina, acpl), and the other projects backward to the posterior portion of the centrum (posterior centroparapophyseal lamina, pcpl). Upchurch (1998: 60) states that this lamina "supports the parapophysis from below and behind", identifying it as the pcpl. This feature was scored as derived for 'euhelopodids' and all neosauropods except *Camarasaurus* (character CI = 0.33). Salgado *et al.* (1997: 19) list the presence of a pcpl as a synapomorphy of Titanosauria, contending that it is absent in all other sauropods. Wilson (1999a) reevaluated the distribution of vertebral laminae in sauropods, and found that the pcpl characterized all titanosaurs (as stated by Salgado *et al.*, 1997), as well as *Brachiosaurus* (Janensch, 1950: fig. 53), *Euhelopus* (Wiman, 1929: pl. 3, fig. 4.; pl. 4, fig. 2), *Apatosaurus* (Gilmore, 1936: pls. 25, 33), and *Diplodocus* (Osborn, 1899: fig. 7). No pcpl was identified in *Shunosaurus*, *Dicraeosaurus*, or *Omeisaurus* from the figures in Zhang (1988),

Janensch (1929b), and He *et al.* (1988), respectively. Wilson (1999a) considered presence of a pcpl an unambiguous synapomorphy of Titanosauriformes, independently acquired in diplodocids.

Size of the 'cranial process' (characters 147–8) and presence of a 'ventral slit' (character 149) in middle and distal chevrons. All are homoplastic but unambiguous synapomorphies of 'Euhelopodidae'. Coding for the characters 148 and 149 is identical, and character 147 differs from these two only in coding *Camarasaurus* derived. Character 147 codes the presence of the 'cranial process', whereas the second (character 148) codes a "prominent cranial process resulting in craniocaudal length of the chevron greatly exceeding its height." Together, these two binary characters act as an ordered three-state character (Table 6). Presence of an enlarged cranial process and a ventral slit are surely independent, despite their identical codings. Other dinosaurs have chevrons that have anteriorly and posteriorly elongate blades but lack a ventral 'slit' (e.g. *Deinonychus*; Ostrom, 1969: fig. 41). Upchurch's treatment of negative evidence for all three characters is problematic. For example, *Patagosaurus*, *Cetiosaurus*, *Brachiosaurus*, and *Haplocanthosaurus* were scored as primitive for all three characters, but distal tails are not known for any of these taxa. In some taxa, only the distal tail bears chevrons with cranially directed processes (e.g. *Camarasaurus*, Gilmore, 1925: pl. 14). Isolated chevrons of *Barapasaurus* are forked and have a ventral slit (pers. observ.), but the distribution of caudals that have this type chevron is unknown. Scoring *Barapasaurus* with the derived condition and sauropods lacking distal tails as unknown resolves this feature as a basal sauropod synapomorphy that was reversed in Titanosauriformes. Upchurch (1998: 87) mentions this possibility.

'Parasagittally elongate ridge on dorsal surface of the cranial end of the sternal plate' (character 157). This is the second of two features that Upchurch (1998) resolved as unambiguously unique to 'euhelopodids'. Unlike the other unambiguous 'euhelopodid' synapomorphy (character 85: height/width ratio of cranial cervical centra), however, this feature cannot be scored in *Euhelopus*, *Mamenchisaurus*, or in the basal sauropods *Vulcanodon* and *Barapasaurus*. Moreover, no 'longitudinal ridge' could be identified from figures of *Omeisaurus* (He *et al.*, 1988: fig. 42) or *Shunosaurus* (Zhang, 1988: fig. 44). However, both have a small prominence at the anterior extreme of the sternal plate. This prominence is present in most sauropods (e.g. *Apatosaurus* [Marsh, 1880]: fig. 2B and *Alamosaurus* [Gilmore, 1946: pl. 9]) and may represent a synapomorphy of Eusauropoda.

Reexamination of character distributions reduces support for the endemic Chinese group 'Euhelopo-

didae' to a single, ambiguous synapomorphy – cervical centra that are slightly taller than wide. Other proposed synapomorphies of the group either have ambiguous distributions (cannot be scored in basal taxa), are shared by other sauropod subgroups, or are dependent on an assumption of ordered transformations. Slightly better support exists for the monophyly of all 'euhelopodids' but *Shunosaurus*. *Mamenchisaurus*, *Omeisaurus*, and *Euhelopus* are united on the basis of two features representing four evolutionary steps – presence of 17 cervical vertebrae (characters 77–79) and elongate cervical centra (character 80). As was the case for 'Euhelopodidae', however, support for this clade depends on an assumption of ordered changes, as trees produced from a completely unordered matrix attest (Fig. 11).

'Euhelopodidae'? The notion that Chinese sauropods are closely related and should be grouped in a common family or subfamily has a long history that commenced once more than one genus was adequately known. In his initial description of *Omeisaurus*, the second well-preserved Chinese sauropod, Young (1939: 309) grouped it together with *Helopus* (now *Euhelopus*; Romer, 1956: 621) in the Subfamily 'Helopodinae'. In his description of the third well-preserved Chinese sauropod (*Mamenchisaurus*), Young (1954): 499–501 recognized resemblances to the neck of *Omeisaurus* and to the caudal centra of titanosaurs, and the chevrons of diplodocids. Later, Young (1958: 25) and Young & Zhao (1972: 19–21) positioned *Omeisaurus* and *Euhelopus* in the broad-toothed family group Bothrosauropodidae, but placed the newly described genus *Mamenchisaurus* with titanosaurs in the opposing, peg-toothed family group Homalosauropodidae (family groups from Huene, 1956 after Janensch, 1929a). More recently, He *et al.* (1988: 131–2) united these three genera in the Family Mamenchisauridae on the basis of an extremely long neck, high cervical count, elongate cervical ribs, and low cervical neural spines that are anteroposteriorly elongate and have a flat dorsal border. McIntosh (1990), however, did not classify all Chinese genera together. He included *Shunosaurus* and *Omeisaurus* in the Subfamily Shunosaurinae on the basis of their shared possession of forked chevrons in the mid-caudal region, but allied *Euhelopus* and *Mamenchisaurus* with camarasaurids and diplodocids, respectively. In the first cladistic analysis of Sauropoda, Russell & Zheng (1994: 2090) hinted at a grouping of Chinese long-necked sauropods, noting that "links between the Chinese genera [*Omeisaurus* and *Mamenchisaurus*] and *Euhelopus* may be closer than suggested by this analysis."

No doubt, then, that there exists a precedent for a close relationship between some or all of the four well-known Chinese sauropods. Upchurch (1995, 1998), however, has been the first to support this hypothesis numerically, and it is his description of the supporting evidence that allows its evaluation. An attempt has been made to assess the strength of 'Euhelopodidae' on two fronts: evaluation of trees generated under different character assumptions and with pruned terminal taxa, as well as reassessment of the character distributions themselves. Both underscore that 'Euhelopodidae' is much more weakly supported than are other nodes on Upchurch's (1998) cladogram.

A final measure may be employed to determine support for 'Euhelopodidae' that does not involve manipulation of Upchurch's dataset, unlike the other measures. As developed by Templeton (1983), a simple nonparametric test can be used to determine whether a given dataset supports two alternate topologies. For example, a Templeton test could be used to determine whether a molecular dataset will accommodate a topology for the same taxa produced by morphological data. The procedure was described in detail by Larson (1994) and will be summarized here. After characters from one matrix that have different numbers of changes in the two specified topologies (e.g. molecular and morphological) have been identified, they can be given an integer value indicating which topology they favour. For example, a character changing twice on topology A and three times on topology B is scored 1; a character changing three times on topology A and twice on topology B is scored –1. These scores can be ranked and summed to obtain a value for the test statistic (T_s) that can be compared to values for the Wilcoxon rank sum probability. If the test is significant, the data matrix can only support one of the topologies, and the other can be rejected with at some level of confidence. If not, however, the data cannot reject either hypothesis. A Templeton test was used to determine whether Upchurch's (1998) data could reject a topology that resolves a paraphyletic 'Euhelopodidae' (Fig. 12). Twenty-two characters were identified as having different numbers of changes on the two topologies. Of these, 14 favoured the most parsimonious tree and 8 favoured a paraphyletic 'Euhelopodidae'. A test statistic (T_s) of 88 was calculated, which for 22 observations corresponds to a two-tailed probability, $P > 0.10$ (Rohlf & Sokal, 1981: table 30). Upchurch's data cannot reject the hypothesis that 'Euhelopodidae' is paraphyletic. A second topology, in which *Euhelopus* was resolved as sister-taxon of Titanosauria, was compared to the most parsimonious tree. This topology can be rejected by Upchurch's data with confidence ($P < 0.01$).

In summary, it is clear that as presently defined, 'Euhelopodidae' cannot be substantiated as a well-supported monophyletic group on several grounds. Not only is the character data reliant on specific cod-
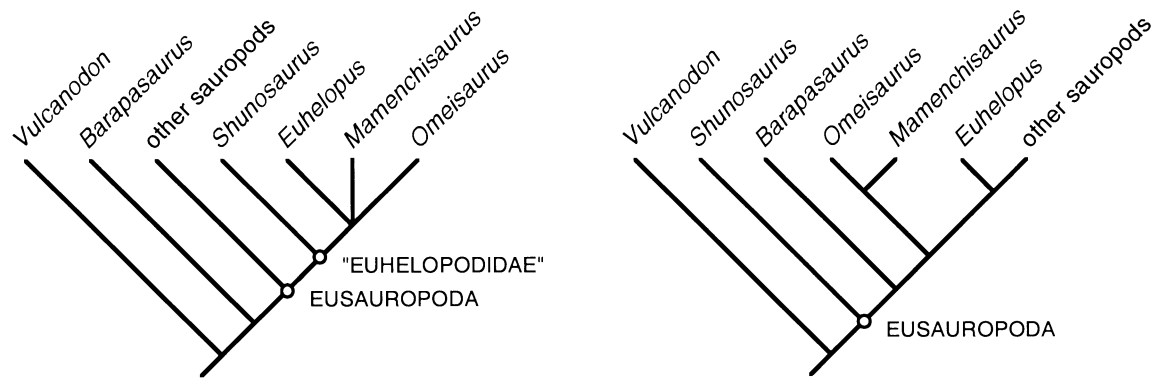
Figure 12. Topologies compared in Templeton test. Topology 1 is to equivalent the most parsimonious tree of Upchurch (1998); topology 2 is one in which 'Euhelopodidae' is decomposed into an array of genera in which *Shunosaurus* is the basalmost, *Euhelopus* is the most derived, and the *Omeisaurus–Mamenchisaurus* clade is intermediate. Twenty-two characters were found to have different numbers changes on the two topologies, 14 favoured topology 1 and eight favoured topology 2. The data matrix of Upchurch (1998) could not reject topology 2 with confidence ($T_s = 88$, $n = 22$, $P > 0.10$).

ing assumptions, their distributions are ambiguous or homoplastic upon reexamination. Further, it is shown that the original data support a suboptimal tree in which the group is paraphyletic.

THE LOWER-LEVEL RELATIONSHIPS OF SAUROPOD DINOSAURS

A generic-level phylogeny of Sauropoda is presented here. This analysis incorporates characters from previous phylogenetic analyses of sauropod dinosaurs (Calvo & Salgado, 1995; Upchurch, 1995, 1998; Salgado *et al*., 1997; Wilson & Sereno, 1998) as well as novel characters generated from research in museum collections. Details and implications of the analysis, resulting topology, and branch support are summarized below. The appendices contain a character-taxon matrix (Appendix 1), a list of characters and character states arranged anatomically (Appendix 2), a synapomorphy list (Appendix 3), and a list of autapomorphies for each terminal taxon (Appendix 4).

ANALYSIS

Twenty-seven terminal taxa were scored for 234 morphological characters and resolved by parsimony analysis (PAUP*; Swofford, 2000) into a series of sister-taxa. Polarity was determined by two outgroup taxa that were regarded as paraphyletic with respect to the ingroup taxon. Most characters were binary, although 18 were coded with multiple derived states. The choice of outgroup and terminal taxa, character coding strategies, and missing information are discussed below.

Outgroup relationships

The hierarchy of dinosaur relationships assumed in this study is illustrated in Figure 2 (based on Gauthier, 1986; Galton, 1990; Sereno *et al*., 1993; Sereno, 1999). Saurischia comprises two major groups: the predominantly carnivorous Theropoda and the herbivorous Sauropodomorpha, which includes Prosauropoda and Sauropoda. Prosauropod monophyly is based on the presence of a premaxillary beak, an inset first dentary tooth, a twisted first digit that is inset into the carpus, and an hourglass-shaped proximal articular surface of metatarsal II (Sereno, 1999). Sereno (1999) also recognized several prosauropod subclades that were supported by fewer characters. The analysis by Benton *et al*. (2000: fig. 20), however, found comparably weaker support for prosauropod monophyly and could not resolve relationships within the group. Recent work by Yates (2001) suggests that some prosauropod taxa form a monophyletic core, whereas others are more closely related to sauropods. Prosauropoda and Theropoda are considered successive outgroups to Sauropoda in this study. Because prosauropod interrelationships are not yet well established, scoring was based on several taxa: *Plateosaurus* (AMNH 6810; Huene, 1926; Galton, 1984, 1990), *Lufengosaurus* (Young, 1941, 1947), *Massospondylus* (Cooper, 1981; Gow, Kitching & Raath, 1990; Gow, 1990), and *Riojasaurus* (Bonaparte & Pumares, 1995). These four taxa are agreed to form a monophyletic Prosauropoda in the three analyses listed above. Scoring for Theropoda was based on *Eoraptor* (PVSJ 512) and *Herrerasaurus* (PVSJ 407), the basalmost members of the clade (Novas, 1993; Sereno & Novas, 1993; Sereno *et al*., 1993; Sereno, 1993, 1999).

Terminal taxa

Twenty-seven terminal taxa were chosen for phylogenetic analysis on the basis of completeness, morphological disparity, temporal disparity, and potential informativeness. All are monophyletic lower-level taxa (either genera or species) with node-based definitions (de Quieroz & Gauthier, 1990, 1992). The age, occurrence, and original reference for each are summarized in Table 7. Autapomorphies supporting the monophyly of each terminal taxon are tabulated in Appendix 4.

Scoring was based on personal observations for all terminal taxa but *Vulcanodon*, *Shunosaurus*, *Omeisaurus*, and *Neuquensaurus*, which were scored from published illustrations, photographs, and descriptions. The remains used to score certain genera deserve additional comment. Scoring of *Haplocanthosaurus* was based on *H. priscus* and *H. delfsi*. Neither the referred partial skeleton reported by Bilbey *et al*. (2000) nor the partial braincase and anterior cervical vertebrae described by Gilmore (1907) were incorporated into this analysis. The former has not yet received a detailed description, and the latter has not been convincingly referred to the genus (McIntosh, 1990: 378). *Rayososaurus* scoring was based on the specimen described by Calvo & Salgado (1995) as 'Rebbachisaurus' tessonei. Wilson & Sereno (1998: 18) listed characters present in the holotype *Rebbachisaurus garasbae* (Lavocat, 1954) that are lacking in 'R.' tessonei, including accessory infradiapophyseal and infrazygapophyseal laminae. Although Calvo (1999: 21) maintained that 'the condition of the two laminae cannot be determined' in 'R.' tessonei, published illustrations of dorsal vertebrae (Calvo & Salgado, 1995: figs 8, 9) and personal observation confirm that they are absent. In addition to differences in the absolute size of the animals, the fact that dorsal vertebrae – one of the two elements in common between these two specimens – can be readily distinguished forecasts more telling differences in other parts of the skeleton. For these reasons, the generic-level separation of the African and South American specimens is recommended here.

Alamosaurus scoring was based on the holotype and remains referred by Gilmore (1946) and Lehman & Coulson (2002). Remains referred to *Alamosaurus* by Kues, Lehman & Rigby (1980) and Sullivan & Lucas (2000) were not considered in this analysis because neither preserve skeletal elements that can be compared to the holotype. As Sullivan & Lucas (2000: 400) note, "... *Alamosaurus* is a form genus, to which we provisionally refer all Late Cretaceous sauropod material from the San Juan Basin." The well-preserved, associated skeleton of 'Titanosaurus' colberti was included in this analysis as the only representative of its genus (ISI R335; Jain & Bandyopadhyay, 1997). Although some have included cranial and other referred remains in their scoring of the Indian 'Titanosaurus' (e.g. Curry Rogers & Forster, 2001: fig. 4), the genus is likely invalid and only the associated 'T.' colberti skeleton is diagnostic (Wilson & Upchurch, in press).

Characters

A total of 234 characters has been coded from all regions of the skeleton. Character scoring is summarized in Appendix 1, characters are listed in Appendix 2. These data comprise 76 (32%) cranial characters, 72 (31%) axial characters, 85 (36%) appendicular characters, and one dermal armour character. The character data employed here were generated from collections research or culled from prior surveys of sauropod anatomy and relationships, including among others, Bonaparte (1986a, 1999), Gauthier (1986), McIntosh (1990), Calvo & Salgado (1995), Upchurch (1995, 1998), Salgado *et al*. (1997), Wilson & Sereno (1998), and Wilson (1999a, b).

Most characters code a single derived state (binary), although 18 code more than one derived state (multistate). Of these, 14 had two derived states and the remainder had three, four, or five derived states (see 'Multistate coding assumptions', below, for coding strategies). Question marks ('?') that appear in a data matrix can be interpreted as representing characters for which information is incomplete, inapplicable, or polymorphic. Incomplete and inapplicable data were scored differently in this analysis. The third type of missing data – polymorphic – did not appear in the matrix. Incomplete scoring implies that the taxon could be scored for any character state, whereas inapplicable scoring suggests that that a taxon could be scored for no character state (Platnick, Griswold & Coddington, 1991). Coding of inapplicable states as '?' can be problematic, as intervening taxa scored as missing are transparent to parsimony programs and allow the influence of distantly related, scorable taxa to 'leak through' (Maddison, 1993). In this analysis, taxa that could be scored for no character state (inapplicable) were scored as '9', whereas those that could be scored for any character state (missing) were scored as '?'. Strong & Lipscomb (1999: 367) have termed this strategy 'absence coding'.

Multistate coding assumptions

Eighteen characters were coded with multiple derived states. Transformations were assumed to be ordered for five of them (8, 37, 64, 66, 198) and unordered in the remaining 13 (36, 65, 68, 70, 72, 80, 91, 108, 116, 118, 134, 152, 181). The rationale for the coding of these multistate characters is summarized here.

Table 7. Geological age, geographical range, and original reference for 27 sauropod terminal taxa analysed

Taxon	Age (stage)	Continent (country)	Reference
Vulcanodon karibaensis	Early Jurassic (Hettangian)	Africa (Zimbabwe)	Raath (1972)
Barapasaurus tagorei	Early Jurassic	Asia (India)	Jain *et al.* (1975)
Shunosaurus lii	Middle Jurassic (Bathonian–Callovian)	Asia (China)	Dong *et al.* (1983)
Patagosaurus fariasi	Middle Jurassic (Callovian)	South America (Argentina)	Bonaparte (1979)
Mamenchisaurus	Late Jurassic	Asia (China)	Young (1954)
Omeisaurus	Late Jurassic	Asia (China)	Young (1939)
Apatosaurus	Late Jurassic (Kimmeridgian–Tithonian)	North America (USA)	Marsh (1877)
Barosaurus lentus	Late Jurassic (Kimmeridgian–Tithonian)	North America (USA)	Marsh (1890)
Brachiosaurus	Late Jurassic (Kimmeridgian–Tithonian)	North America Africa (USA, Tanzania)	Riggs (1903)
Camarasaurus	Late Jurassic (Kimmeridgian–Tithonian)	North America (USA)	Cope (1877)
Dicraeosaurus	Late Jurassic (Kimmeridgian)	Africa (Tanzania)	Janensch (1914)
Diplodocus	Late Jurassic (Kimmeridgian–Tithonian)	North America (USA)	Marsh (1878)
Haplocanthosaurus	Late Jurassic (Kimmeridgian–Tithonian)	North America (USA)	Hatcher (1903)
Amargasaurus cazaui	Early Cretaceous (Hauterivian)	South America (Argentina)	Salgado & Bonaparte (1991)
Euhelopus zdanskyi	Early Cretaceous	Asia (China)	Wiman (1929)
Jobaria tiguidensis	Early Cretaceous 'Neocomian'	Africa (Niger)	Sereno *et al.* (1999)
Malawisaurus dixeyi	Early Cretaceous	Africa (Malawi)	Haughton (1928)
Nigersaurus taqueti	Early Cretaceous (Aptian–Albian)	Africa (Niger)	Sereno *et al.* (1999)
Rayososaurus	Early Cretaceous (Albian–Cenomanian)	South America (Argentina)	Bonaparte (1996)
Rebbachisaurus garasbae	Late Cretaceous (Cenomanian)	Africa (Morocco)	Lavocat (1954)
Alamosaurus sanjuanensis	Late Cretaceous (Maastrichtian)	North America (USA)	Gilmore (1922)
Nemegtosaurus mongoliensis	Late Cretaceous (Maastrichtian)	Asia (Mongolia)	Nowinski (1971)
Neuquensaurus	Late Cretaceous (Campanian–Maastrichtian)	South America (Argentina)	Powell (1986)
Opisthocoelicaudia skarzynskii	Late Cretaceous (Maastrichtian)	Asia (Mongolia)	Borsuk-Bialynicka (1977)
Rapetosaurus krausei	Late Cretaceous (Maastrichtian)	Madagascar	Curry Rogers & Forster (2001)
Saltasaurus	Late Cretaceous (Campanian–Maastrichtian)	South America (Argentina)	Bonaparte & Powell (1980)
'Titanosaurus' colberti	Late Cretaceous (Maastrichtian)	Asia (India)	Jain & Bandyopadhyay (1997)

Three multistate characters (8, 37, 66) that code migrational or positional change of a structure were fully ordered. These characters assume a 'migrational' rather than a 'discontinuous' model for positional change of anatomical elements. Thus, retraction of the nares 'to the level of the orbit' (character 8, state 1) is an intermediate state between nares 'retracted above orbit' (state 2) and 'terminal' nares (state 0). Characters describing the position of the external naris (8), pterygoid flange (37), and posterior extreme of the tooth row (66) were assumed to have ordered transformations between states.

Two characters (64, 198) describe variation in the size or relative size of elements and were partially ordered as 'easy loss' characters. 'Easy loss' characters assume ordered changes on the way up (gains), but losses can occur at any stage and are unordered (Maddison & Maddison, 1992). Changes in the relative lengths of the major axes of the femoral midshaft cross-section (198), were ordered as an 'easy loss' character (Table 4). Similarly, character 64, which codes reduction in the size of the coronoid, was considered an 'easy loss' character, only the polarity of change was reversed because the character codes for size reduction.

Four multistate characters code for change in vertebral (80, 91, 108) or phalangeal (181) counts. Ordering these states implies a developmental model in which vertebrae and phalanges are added or lost incrementally, whereas assumption of unordered change implies that changes can occur directly between any two states. Current embryological data from living organisms do not support either model of character transformation. Vertebral and phalangeal count characters were coded as unordered, alternate codings did not affect the basic topology.

Nine of the multistate characters (36, 65, 68, 70, 72, 116, 118, 134, 152) cannot reasonably be interpreted as transformational and thus do not lend themselves to an assumption of ordered change. For example, characters that code the shape of centrum articular face (116, 118, 134) may have four states, such as flat, procoelous, biconvex, or opisthocoelous. There is no justification for ordering these states linearly, and little rationale for forming an ordered network. Although 'flat' and 'biconvex' may intuitively represent the most disparate centrum morphologies, there is no basis for considering transformations between amphicoelous and biconvex states more costly than those between opisthocoelous and biconvex or opisthocoelous and procoelous states.

Missing information
The percentage and rank incompleteness of each terminal taxon and for each anatomical region are summarized in Table 8. Missing data range from 0% (*Camarasaurus*) to 88% (*Rebbachisaurus*). *Brachiosaurus*, *Apatosaurus*, *Diplodocus*, and *Shunosaurus* had less than 10% missing data, whereas *Vulcanodon*, *Barosaurus*, and *Nemegtosaurus* had values of 70% or more. The total missing data in this 27×234 matrix is 44%, nearly the same value calculated for Upchurch's (1998) 26×205 analysis of Sauropoda. Not surprisingly, cranial data were the most incompletely scored among sauropods (57% incomplete), whereas axial data were the most completely scored (33% incomplete), and appendicular data were intermediate (41% incomplete).

Taxa with large amounts of missing information dramatically increase the number of most parsimonious trees in an analysis, thereby diminishing the resolution of consensus trees (Huelsenbeck, 1991; Wilkinson, 1995). As Wilkinson (1995) has noted, however, gross anatomical completeness is not an index for taxonomic informativeness – a fragmentary taxon can be informative phylogenetically, just as a more complete specimen may be relatively uninformative. No terminal taxon could be excluded from the analysis on the basis of Wilkinson's (1995) rules for safe taxonomic reduction, which remove from the analysis taxa that can have no effect on the relationships of the ingroup – i.e. those taxa that are redundant with more complete taxa. All taxa included in this analysis are phylogenetically informative.

TOPOLOGY

Twenty-seven taxa were scored for 234 characters in MacClade (Maddison & Maddison, 1992) and analysed in PAUP* (Swofford, 2000). The high number of terminal taxa precluded exact treebuilding methods, so an heuristic search was performed. To avoid local optima, stepwise addition and branch swapping were employed. Branches were added in a random sequence (100 replicates), and branch swapping was performed using the tree bisection-reconnection algorithm. Because 'easy loss' characters (64 and 198) are asymmetric stepmatrices (Table 5), a rooted tree was computed by PAUP after an ancestral state ('0') was specified (Swofford, 1993: 24–27).

Nine equally parsimonious trees (430 steps) supporting 26 internal nodes were obtained. These nine trees specify only three ingroup topologies; additional topologies record combinations in which the specified outgroups are either monophyletic or paraphyletic with respect to ingroup. These variant outgroup topologies are the result of computing rooted trees, which is mandated by use of 'easy loss' characters. When characters 64 and 198 are specified as 'ordered' rather than 'easy loss' characters, three trees (430 steps) are produced that vary only in ingroup relationships

Table 8. Missing data in sauropod terminal taxa. The percentage of missing data and rank for each terminal taxon relative to others (most complete ranked highest) for cranial, axial, appendicular, and all characters combined (total)

Taxon	Cranial		Axial		Appendicular		Total	
	%	rank	%	rank	%	rank	%	rank
Vulcanodon	100	19	81	26	35	14	70	24
Barapasaurus	100	19	29	15	33	11	53	15
Shunosaurus	8	4	4	4	6	4	6	2
Patagosaurus	78	17	44	20	43	17	55	16
Mamenchisaurus	71	15	21	10	44	18	46	13
Omeisaurus	21	8	10	6	7	6	12	7
Apatosaurus	24	9	1	2	2	3	9	5
Barosaurus	100	19	29	15	33	11	76	26
Brachiosaurus	0	1	11	8	6	4	6	2
Camarasaurus	0	1	1	2	0	1	0	1
Dicraeosaurus	33	11	10	6	28	9	24	8
Diplodocus	1	3	0	1	15	8	6	2
Haplocanthosaurus	100	19	14	9	66	22	61	20
Amargasaurus	64	14	61	23	69	23	65	21
Euhelopus	55	13	51	21	31	10	45	12
Jobaria	17	6	7	5	9	7	11	6
Malawisaurus	80	18	31	17	58	21	57	17
Nigersaurus	28	10	79	25	94	26	68	23
Rayososaurus	46	12	31	17	40	15	39	9
Rebbachisaurus	100	19	76	24	86	25	88	27
Alamosaurus	100	19	24	13	56	20	60	19
Nemegtosaurus	9	5	100	27	100	27	71	25
Neuquensaurus	100	19	39	19	34	13	57	17
Opisthocoelicaudia	100	19	21	10	1	2	39	9
Rapetosaurus	20	7	56	22	52	19	43	11
Saltasaurus	75	16	22	12	42	16	47	14
'T.' colberti	100	19	25	14	67	24	65	21

(Fig. 13A). The three equally parsimonious trees record the alternate hypotheses of relationship amongst the rebbachisaurid genera *Rebbachisaurus*, *Rayososaurus*, and *Nigersaurus*; all other nodes are invariant.

Seven genera are outgroups to Neosauropoda, a node-based clade that includes the two stem-groups Diplodocoidea and Macronaria. Diplodocoidea comprises *Haplocanthosaurus* and three clades – Rebbachisauridae, Dicraeosauridae, and Diplodocidae. Macronaria includes *Camarasaurus*, *Brachiosaurus*, *Euhelopus*, and Titanosauria. Titanosauria in turn unites *Malawisaurus*, Nemegtosauridae *(= Nemegtosaurus + Rapetosaurus)*, *'T.' colberti*, and Saltasauridae (= Opisthocoelicaudiinae + Saltasaurinae). The synapomorphies supporting this topology are listed in Appendix 3. The distribution of several synapomorphies were optimized differently under delayed (DELTRAN) and accelerated (ACCTRAN) transformation strategies. Those attributable to missing information (i.e. topologically adjacent taxa could not be scored)

are reported in Table 9; those due to character conflict are reported in Table 10.

Below, the stability of the resultant topology is determined by identifying nodes preserved in suboptimal trees, those preserved in trees generated with problematic taxa removed, as well as by calculation of decay indices. The topology is then compared to those of previous analyses, and unresolved areas are identified and discussed.

Suboptimal trees
Trees of up to five additional steps (435 steps) were generated, and strict, Adams, and semistrict consensus measures indicated those nodes that were the most stable (Table 11). There are 54 trees one step longer than the most parsimonious tree. All but nine nodes are recovered in a strict consensus of those trees; Adams and 50% majority-rule consensus trees recover all but five and two nodes, respectively. These

Figure 13. Phylogenetic relationships of Sauropoda proposed in this analysis (matrix in Appendix 1). A, most parsimonious tree. B, 50% majority-rule consensus of 1443 trees five steps longer than the most parsimonious tree produced by a pruned matrix. Percentages indicate frequency of preservation of nodes among trees.

results identify the weakest nodes on the tree, which involve the relationships of: (1) basal sauropods – *Omeisaurus*, *Patagosaurus*, and *Mamenchisaurus* – relative to more derived sauropods; (2) basal neosauropods – *Jobaria*, *Haplocanthosaurus*, and Neosauropoda; and (3) *Nemegtosaurus* and '*T.*' *colberti* relative to other titanosaurs. According to the Adams consensus, collapse of several nodes in the strict consensus tree are due to rearrangements involving four taxa, *Patagosaurus*, *Rebbachisaurus*, *Haplocanthosaurus*, and *Nemegtosaurus*. The 50% majority-rule consensus tree is identical to the most parsimonious tree, save the loss of the *Nemegtosaurus*–*Rapetosaurus* clade.

Table 9. Ambiguous character optimizations attributable to missing data, based on two optimization strategies in PAUP* (Swofford, 2000). Delayed transformations (DELTRAN) favour parallelism over reversals, whereas accelerated transformations (ACCTRAN) favour reversals over parallelisms. Abbreviations: mdd = more derived diplodocoids; mds = more derived sauropods; mdt = more derived titanosaurs. Italicization indicates characters that have ambiguous changes in other parts of the cladogram that are due to character conflict (**Table 10**). Characters are listed in approximate order of their appearance in the cladogram under delayed transformation

No.	DELTRAN	ACCTRAN
2, 3, 7, 8, 10–11, 20, 28–30, 32–33, 35, 37, 40–41, 54–55, 61, 63, 65–*68*, *69*–71, 80, 82, 87, 92, 115, 143–*144*, *164*, 174, 181, 183, 186, 200, 206	Eusauropoda	Sauropoda
97, 228	*Barapasaurus* + mds	Sauropoda
207, 213	*Barapasaurus* + mds	Eusauropoda
21	Omeisauridae + mds	Sauropoda
154, 184	*Jobaria* + mds	*Patagosaurus* + mds
58	*Jobaria* + mds	Neosauropoda
1, 2, 5, 22, 46, 53, 65–66, 70, 74, 137	Rebbachisauridae + mdd	Diplodocoidea
42, 79	Dicraeosauridae + mdd	Diplodocoidea
111	Dicraeosauridae + mdd	Rebbachisauridae + mdd
6, 13, 37, 138	Diplodocidae	Diplodocoidea
8, 31, 34	Diplodocidae	Dicraeosauridae + mdd
142	Titanosauriformes	Macronaria
143	Titanosauria	Titanosauriformes
106, 118, 132, 146, 158, 167	Titanosauria	Somphospondyli
110	'T.' colberti + mdt	Somphospondyli
126	'T.' colberti + mdt	Nemegtosauridae + mdt
44, 100	Nemegtosauridae + mdt	Somphospondyli
151, 192	Nemegtosauridae + mdt	Titanosauria
21, 29, 36, 52	Nemegtosauridae	Somphospondyli
35, 38	Nemegtosauridae	Titanosauria
1, 11, 57, 70	Nemegtosauridae	Nemegtosauridae + mdt
116, 213	Saltasauridae	Somphospondyli
137	Saltasauridae	Titanosauriformes
214	Saltasauridae	Titanosauria
198	Saltasauridae	Nemegtosauridae + mdt
156–157, 171, 201	Saltasauridae	'T.' colberti + mdt
173–174, 181–183	Opisthocoelicaudiinae	Somphospondyli
114, 182	Opisthocoelicaudiinae	Titanosauriformes
115	Opisthocoelicaudiinae	Nemegtosauridae + mdt
113	Saltasaurinae	Somphospondyli
88	*Mamenchisaurus*	Omeisauridae
220	*Omeisaurus*	Omeisauridae
57	*Nigersaurus*	Rebbachisauridae
106	*Rebbachisaurus*	Rebbachisauridae
75	*Diplodocus*	Diplodocidae
202	*Diplodocus*	Diplodocinae
36, 97	*Dicraeosaurus*	Dicraeosauridae
64	*Brachiosaurus*	Titanosauriformes
80	*Euhelopus*	Somphospondyli
138	*Opisthocoelicaudia*	Titanosauriformes
215, 229	*Opisthocoelicaudia*	Titanosauria
68	*Rapetosaurus*	Titanosauria
88, 125	*Saltasaurus*	Saltasaurinae

Table 10. Ambiguous character optimizations attributable to character conflict, based on two optimization strategies in PAUP* (Swofford, 2000). Abbreviations: mdd, more derived diplodocoids; mds, more derived sauropods; mdt, more derived titanosaurs. The dash (−) indicates character reversal, numbers inside parentheses identify direction of change between character states where these vary. Italicization indicates characters with ambiguities due to missing information as well (**Table 9**). Characters are listed in approximate order of their appearance in the cladogram under delayed transformation

No.	DELTRAN	ACCTRAN
91	Theropoda (1 > 0), Omeisauridae + mds (1 > 3), Diplodocidae (3 > 5), *Amargasaurus* (3 > 5), *Haplocanthosaurus* (3 > 2), *Opisthocoelicaudia* (3 > 4), *Shunosaurus* (1 > 2)	Prosauropoda (1 > 0), Sauropoda (0 > 2), *Barapasaurus* + mds (2 > 3), Diplodocoidea (3 > 2) Rebbachisauridae + mdd (2 > 5), *Dicraeosaurus* (5 > 3), Somphospondyli (3 > 2), Titanosauria (2 > 4)
34	Sauropoda (9 > 0), *Barapasaurus* + mds (0 > 1)	Omeisauridae + mds (9 > 1), Diplodocidae (1 > 0)
110	Omeisauridae + mds (9 > 1), *Barapasaurus* (9 > 0)	*Barapasaurus* + mds (9 > 0), *Patagosaurus* + mds (0 > 1)
84	Omeisauridae, *Shunosaurus*	Sauropoda, −*Jobaria* + mds
212	*Jobaria* + mds, *Mamenchisaurus*	*Barapasaurus* + mds, −*Omeisaurus*
203	*Jobaria* + mds, *Mamenchisaurus*	Omeisauridae + mds, −*Omeisaurus*
147	*Jobaria* + mds, *Shunosaurus*	Sauropoda, −Omeisauridae
9	*Jobaria* + mds, −Diplodocoidea	Macronaria, *Jobaria*
60	Macronaria, *Diplodocus*	Sauropoda, −Rebbachisauridae
73	Macronaria, Dicraeosauridae + mdd	Neosauropoda, −Rebbachisauridae
98	Diplodocidae, *Rebbachisaurus*, *Brachiosaurus*, *Euhelopus*, *Opisthocoelicaudia*, *Jobaria*, *Saltasaurus*	*Jobaria* + mds, −Dicraeosauridae, −*Haplocanthosaurus*, −*Camarasaurus*, −*Alamosaurus*, −Titanosauria, Saltasauria
93, 107	Dicraeosauridae, *Rebbachisaurus*	Rebbachisauridae + mdd, −Diplodocidae
68	Dicraeosauridae + mdd (0 > 2), *Nigersaurus* (0 > 1)	Diplodocoidea (9 > 1), Dicraeosauridae + mdd (1 > 2)
116	Diplodocidae, *Dicraeosaurus*	Dicraeosauridae + mdd, −*Amargasaurus*
144	Titanosauria *(1 > 9)*, *Camarasaurus (1 > 0)*	Macronaria (1 > 0), Titanosauriformes (1 > 9)
164	Saltasauridae, *Rapetosaurus*	−Nemegtosauridae + mdt, *'T.' colberti*
136	Saltasauridae, Rebbachisauridae + mdd	*Patagosaurus* + mds, −*Camarasaurus*
69	−Nemegtosauridae, −*Brachiosaurus*, −Rebbachisauridae + mdd	−Neosauropoda, *Camarasaurus*, *Euhelopus*
202	Saltasaurinae, *Rapetosaurus*	Titanosauria, −Opisthocoelicaudiinae
209	*Mamenchisaurus*, *Barapasaurus*	*Barapasaurus* + mds, −*Jobaria* + mds,
103	*Barapasaurus*, *Patagosaurus*	*Barapasaurus* + mds, −Omeisauridae + mds
152	*Brachiosaurus*, *Camarasaurus*	*Jobaria* + mds, −Diplodocoidea, −Somphospondyli
62	*Brachiosaurus*, *Camarasaurus*	Macronaria, −Somphospondyli
50	*Brachiosaurus*, *Saltasaurus*	Titanosauriformes, −Nemegtosauridae
48	*Nemegtosaurus*, *Saltasaurus*	Somphospondyli, −*Rapetosaurus*

Addition of two evolutionary steps (432 steps) yields 385 trees. Fourteen nodes dissolve in a strict consensus of these trees, involving taxa adjacent to those nodes identified above. An Adams consensus recovers many more nodes of these nodes, and the 50% majority-rule cladogram preserves all but three nodes – Rebbachisauridae, *Nemegtosaurus* + *Rapetosaurus*, and *'T.' colberti* Saltasauridae. One fewer node is preserved in a strict consensus of 1850 trees three steps outside the minimum treelength. Although not preserved in the strict consensus, Rebbachisauridae is recovered by the Adams consensus tree. The 50% majority-rule consensus tree does not preserve the node uniting *Haplocanthosaurus* and other diplodocoids.

Three additional nodes were lost in strict consensus of the 7252 trees four steps longer than the most parsimonious tree. Only eight nodes remain in the strict consensus, which are identified as well supported. These include Sauropoda, Eusauropoda, *Barapasaurus* and more derived sauropods, Diplodocidae plus Dicraeosauridae and all inclusive nodes, and Somphospondyli. The 50% majority-rule consensus cladogram is identical to that for trees three steps longer than the most parsimonious tree. Five additional evolutionary steps produced 24 330 trees that shared only five nodes in common: Sauropoda, Eusauropoda, *Barapasaurus* plus more derived sauropods, Diplodocidae, and Diplodocinae. The 50% majority-rule consensus cladogram retains all but five nodes present in the most parsimonious tree.

Table 11. Nodes that collapse in suboptimal trees generated from the original dataset, as well as the dataset without *Rebbachisaurus* and *Nemegtosaurus*. Suboptimal trees of up to five steps longer than the most parsimonious tree (mpt) were generated and summarized in strict, Adams, and 50% majority-rule (50%) consensus cladograms. Collapsed nodes are reported below for each. There were 26 and 24 recoverable nodes in the original ('ALL') and reduced ('PRUNED') datasets, respectively

	Treelength	Trees	Strict	Adams	50%
	430 (mpt)	3	1	1	1
A	431 (mpt + 1)	54	9	5	2
L	432 (mpt + 2)	385	14	8	3
L	433 (mpt + 3)	1850	15	8	4
	434 (mpt + 4)	7252	18	11	4
	435 (mpt + 5)	24 330	21	–	5
P	424 (mpt)	1	–	–	–
R	424 (mpt + 1)	8	4	3	0
U	425 (mpt + 2)	38	9	6	0
N	426 (mpt + 3)	151	11	7	0
E	427 (mpt + 4)	487	14	9	1
D	428 (mpt + 5)	1443	16	10	2

Taxon removal

Two problematic areas appear in suboptimal trees: one within Titanosauria associated with *Nemegtosaurus*, another within Rebbachisauridae associated with *Rebbachisaurus*. These two problematic, poorly represented taxa (missing data > 70%) were removed, and the pruned dataset was reanalysed. Perhaps not surprisingly, the pruned dataset produced fewer optimal and suboptimal trees than did the original (Table 11). The most parsimonious solution agrees with the tree produced by the original dataset (Fig. 13B). A strict consensus of the eight trees one step longer than the most parsimonious tree retains all but four nodes. Polytomies are positioned at the base of Eusauropoda (*Patagosaurus, Barapasaurus*), the base of Diplodocoidea (*Haplocanthosaurus*), and within Titanosauria ('*Titanosaurus*' *colberti*). The Adams consensus tree is essentially the same, only *Patagosaurus* is resolved as sister-taxon to *Omeisaurus* and *Mamenchisaurus*. No nodes were lost in the 50% majority-rule consensus for suboptimal trees allowing one, two, or three additional steps. The first node is lost in the 50% majority-rule consensus of the 487 trees four steps longer than the most parsimonious tree. Strict consensus of these trees retains 10 nodes, whereas Adams consensus retains 15. Polytomies include several basal taxa more derived than *Shunosaurus*, a cluster of basal neosauropod taxa, as well as all somphospondyls. There are 1443 trees five steps longer than the most parsimonious tree. These share

Table 12. Decay indices for the 24 nodes preserved in the topology presented in Figure 13A, as calculated by Autodecay v. 4.0 (Eriksson, 1998)

Clade	Decay index	Rank
Sauropoda	20	1
Eusauropoda	12	2
Barapasaurus + more derived sauropods	8	3
Patagosaurus + more derived sauropods	1	18
Omeisaurus + *Mamenchisaurus*	2	13
Omeisaurus + more derived sauropods	1	18
Jobaria + more derived sauropods	4	10
Neosauropoda	1	18
Macronaria	2	13
Titanosauriformes	5	6
Somphospondyli	5	6
Titanosauria	4	10
Rapetosaurus + more derived titanosaurs	4	10
'*T.*' *colberti* + more derived titanosaus	1	18
Saltasaurinae	1	18
Opisthocoelicaudiinae	1	18
Saltasaurinae	2	13
Diplodocoidea	1	18
Rebbachisauridae + more derived diplodocoids	2	13
Dicraeosauridae + Diplodocidae	5	6
Rebbachisauridae	2	13
Dicraeosauridae	5	6
Diplodocidae	7	4
Diplodocinae	7	4

eight nodes in common: Sauropoda, Eusauropoda, *Jobaria* + Neosauropoda, Somphospondyli, and Dicraeosauridae + Diplodocidae and all inclusive nodes. All but two nodes are recovered in the 50% majority-rule consensus tree, implying that the relationship of *Haplocanthosaurus* among neosauropods and that of *Patagosaurus* among basal eusauropods are the most weakly supported.

Decay indices

Robustness of nodes, as determined by Autodecay v. 4.0 (Eriksson, 1998), is summarized in Table 12. Naturally, these results match those generated by evaluating suboptimal trees. The three basalmost nodes – Sauropoda, Eusauropoda, and the clade uniting *Barapasaurus* and more derived sauropods – have the highest decay values (20, 12, and 8, respectively). The paucity of taxa and length of geological time separating them may in part explain the stability of these nodes. The monophyly of Diplodocidae, Diplodocinae, Dicraeosauridae, Dicraeosauridae + Diplodocidae, Titanosauriformes, and Somphospondyli are well-

supported with values of 5 or more. Other neosauropod clades, such as Titanosauria, Nemegtosauridae + more derived titanosaurs, and *Jobaria* + Neosauropoda have moderately high decay indices of 4. Twelve nodes had decay indices of 1 or 2, suggesting that these nodes are the most likely to be affected by changes in taxa or character distribution. These weakly supported nodes are localized in three areas: near the base of the tree (Omeisauridae, *Patagosaurus*/ *Omeisaurus* plus more derived sauropods), at the base of Neosauropoda (Neosauropoda, Diplodocoidea, Rebbachisauridae, Macronaria), and Saltasauridae ('*T.*' *colberti* + Saltasauridae, Saltasauridae, Opisthocoelicaudiinae). Each of these problematic areas is associated with taxa that have high levels of missing data and lack cranial remains.

COMPARISONS WITH PREVIOUS ANALYSES

A comparison of the topology presented here with those of Salgado *et al.* (1997), Wilson & Sereno (1998), Upchurch (1998), Sanz *et al.* (1999), and Curry Rogers & Forster (2001) reveals many nodes in common as well as several important differences. In some cases, topological differences are the result of incomplete anatomy (e.g. *Haplocanthosaurus*). Other differences, however, result from conflicting character distributions and disparate character scorings.

Salgado et al. *(1997)*

The topology of the analysis presented here (Fig. 13A) agrees with most aspects of Salgado *et al.* (1997). Among the taxa common to both analyses, a single topological difference exists, which involves the relative positions of *Opisthocoelicaudia* and *Alamosaurus*. Whereas these genera are resolved as sister-taxa (Opisthocoelicaudiinae) by this analysis, Salgado *et al.* (1997) list four synapomorphies that nest *Alamosaurus* closer than *Opisthocoelicaudia* to saltasaurines (*Saltasaurus*, *Neuquensaurus*). The distributions of these four features are discussed below.

The presence of a short ischium (character 36), was scored as derived in *Alamosaurus* and saltasaurines, but primitive (i.e. 'long') in *Opisthocoelicaudia* by Salgado *et al.* (1997: 27). They distinguished these states by the relative lengths of the shaft of the ischium and its iliac peduncle. Because the pelvis is partially co-ossified in *Opisthocoelicaudia*, however, the suture lines between the ischium, pubis, and ilium are difficult to identify (Borsuk-Bialynicka, 1977: 37). Careful examination of stereo photographs and illustrations of the pelvis (Borsuk-Bialynicka, 1977: pl. 3, fig. 6 & fig. 12) indicates that *Opisthocoelicaudia* should be scored as derived (i.e. 'short') for ischium length, both by the Salgado *et al.* (1997) metric and by

the metric employed here (Appendix 2, character 193: length of ischial shaft relative to that of the pubis).

A biconvex first caudal centrum (character 32) was also listed as shared by *Alamosaurus* and saltasaurines. This state is derived relative to the primitive shape of the first caudal centrum, which was defined as "amphiplatan–slightly platycoelous, moderately procoelous–strongly procoelous" (Salgado *et al.*, 1997: 31). The first caudal vertebra of *Opisthocoelicaudia* is opisthocoelous and was scored as unknown ('?'), which I interpret as 'inapplicable' rather than 'missing'. By virtue of this coding strategy, Salgado *et al.* resolved biconvex first caudal centrum as an ambiguous synapomorphy of *Alamosaurus* and saltasaurids. The coding strategy employed here (Appendix 2, character 116), on the other hand, identifies procoelous, opisthocoelous, and biconvex character states. Presence of a biconvex first caudal centrum has a homoplastic distribution that can be resolved as either (1) a synapomorphy of Opisthocoelicaudiinae and Saltasaurinae that was reversed in *Opisthocoelicaudia* or (2) a synapomorphy of Saltasaurinae that appeared independently in *Alamosaurus* (Table 10).

Salgado *et al.* (1997: 27) list dorsoventrally compressed posterior caudal vertebrae (character 34) as a third feature linking *Alamosaurus* and saltasaurines to the exclusion of *Opisthocoelicaudia*. In this analysis, however, only the saltasaurines *Neuquensaurus* and *Saltasaurus* were scored with the derived condition, in which centrum breadth exceeds twice centrum depth. Salgado *et al.* (1997: 27) list a fourth feature uniting *Alamosaurus* and saltasaurines, but this character is difficult to evaluate from the brief description given. Presence of a pronounced lateral ridge on the base of mid-caudal neural arches (character 35) could not be identified in those taxa scored as derived by the authors.

This analysis suggests that *Alamosaurus* and *Opisthocoelicaudia* form the clade Opisthocoelicaudiinae, which is the sister-taxon to Saltasaurinae (Fig. 13). Opisthocoelicaudiine monophyly is supported by derived characteristics of the tail and forelimb, several of which are ambiguous because they could not be scored in other titanosaurs (Table 9). Thus, they may obtain a broader distribution as more complete remains of phylogenetically adjacent taxa are discovered and described. Conflicting characters in *Opisthocoelicaudia* (e.g. opisthocoelous caudal centra) are autapomorphies, consistent with the interpretation of the tail of *Opisthocoelicaudia* as highly modified (Appendix 4).

Wilson & Sereno (1998)

Although many of the characters identified by Wilson & Sereno (1998) were employed in the analysis presented here, inclusion of additional genera resulted in

a slightly different topology. Specifically, *Haplocanthosaurus* was resolved as a basal diplodocoid rather than a basal macronarian. Wilson & Sereno (1998) cited three features nesting *Haplocanthosaurus* as the basal macronarian: chevrons with unbridged haemal canals, dorsal neural spines with pendant triangular processes, and coplanar ischia. These three features were scored identically in this analysis, but their distribution was broadened by the addition of rebbachisaurids and *Jobaria*. Consequently, short cervical ribs (character 140), shared by *Haplocanthosaurus* and diplodocoids, was resolved as a unambiguous synapomorphy. However, the position of *Haplocanthosaurus* is not strongly supported here. As noted above, the node uniting *Haplocanthosaurus* and other diplodocoids is among the first to breakdown in strict consensus of suboptimal trees. Although several taxa are more poorly represented, *Haplocanthosaurus* lacks cranial (100% missing) and appendicular remains (66% missing). Because synapomorphies from these regions of the skeleton are important in diagnosing neosauropod subgroups (see 'Data' below), neither features potentially allying *Haplocanthosaurus* with neosauropod subgroups, nor those barring it from others can be assessed at present.

Upchurch (1998, 1999)

Many of the topological differences between Upchurch (1995) and Wilson & Sereno (1998) were resolved in Upchurch's subsequent (1998) analysis. Still, two important differences remain – the relationships of Chinese sauropods to other sauropods and the affinities of *Nemegtosaurus*. The character data provided by the present analysis demonstrate convincing support for the constituency of Upchurch's 'Euhelopodidae' as a series of distantly related taxa, a topology that is supported in strict consensus of trees five steps longer than the most parsimonious tree. *Shunosaurus* is regarded here as the most primitive eusauropod, separated by two nodes from Omeisauridae. The latter is diagnosed largely on the basis of an elongate neck. *Euhelopus*, the fourth (and namesake) 'euhelopodid' is here resolved as the sister-taxon of Titanosauria, well distanced phylogenetically from any of the other Chinese taxa. Enforcing a 'euhelopodid' topological constraint in PAUP* results in trees 33 steps longer than the most parsimonious tree; other aspects of the topology are unaffected. This result holds regardless of choice for arrangements within or resolution of the 'euhelopodid' constraint tree.

The second topological difference concerns the relationships of *Nemegtosaurus* among neosauropods. Traditionally, *Nemegtosaurus* has been allied with *Dicraeosaurus*, as originally proposed by Nowinski (1971: 58) and accepted by Kurzanov & Bannikov

(1983: 91). Berman & McIntosh (1978: 32–34) formally included *Dicraeosaurus* and *Nemegtosaurus* in Diplodocidae, but they did not specify relationships within the family (contra Salgado & Calvo, 1992). McIntosh (1990: 393) likewise placed *Nemegtosaurus* in Diplodocidae and specified a close relationship to *Dicraeosaurus* on the basis of its "slender peg-teeth confined to the front of the jaws". McIntosh also recognized several differences in the shape of the snout, the length and orientation of the basipterygoid processes, and other features. Salgado & Calvo (1992: 346) interpreted these and other differences as conflicting with this assignment, noting that "*Nemegtosaurus* and *Quaesitosaurus*, with their short, downwardly projected basipterygoid processes . . . are clearly not dicraeosaurids".

In the first cladistic analyses to test these hypotheses, Upchurch (1995, 1998, 1999) interpreted *Nemegtosaurus* as a basal diplodocoid. Upchurch (1999: 118) listed seven characters in support of this view: (1) premaxilla narrow transversely and elongate anteroposteriorly; (2) subnarial foramen elongated along the premaxilla–maxilla suture; (3) posterior margin of the external naris posterior to anterior end of prefrontal; (4) vomerine (i.e. anteromedial) processes of the maxillae not visible laterally; (5) loss of the intercoronoid; (6) mandible subrectangular in dorsal view; and (7) teeth restricted to the anterior end of the jaws. My scoring of these same characters, based on study of the original material (Wilson, unpublished), suggests that only features (1) and (3) obtain a distribution that supports the diplodocoid affinities of *Nemegtosaurus*. The first, abbreviate premaxilla (1) is likely correlated with narrow tooth crowns. Because sauropod premaxillae carry only four alveoli that span the length of the element, narrow-crowned taxa (i.e. diplodocids, *Dicraeosaurus*, *Nemegtosaurus*) necessarily have shorter premaxillae than do broad-crowned taxa. In addition, *Nemegtosaurus* and derived diplodocoids (i.e. diplodocids) have nares that are retracted to a greater extent than those of other sauropods. In both, the external naris is positioned between, rather than anterior to, the prefrontals (3). However, *Nemegtosaurus* does not share with diplodocids the reduction or loss of the internarial bar, which it retains as a broad structure of unknown length and curvature (Wilson, pers. observ.). As described below, other characters listed by Upchurch (1999) are not special similarities of *Nemegtosaurus* and diplodocoids.

An elongate subnarial foramen (2) is not present in either diplodocoids or *Nemegtosaurus*. In *Diplodocus* (and presumably other diplodocoids), the structure Upchurch (1999: fig. 7C) identified as the subnarial foramen appears elongate because it is composed of two semicircular openings, the subnarial foramen and the anterior maxillary foramen (Wilson & Sereno,

1998: fig. 6B). In *Nemegtosaurus*, on the other hand, the opening identified as the subnarial foramen by Upchurch (1999: fig. 7B) passes into the maxilla rather than between it and the premaxilla (Nowinski, 1971: 59) and opens into an enclosed palatal shelf that appears to have been formed by coalescence of the dorsal and anteromedial processes of the maxilla (Wilson, pers. observ.). Nowinski (1971: fig. 1) labels this structure the 'intermaxillary foramen', but it is here considered the anterior maxillary foramen because of topological similarities with that opening in *Camarasaurus* (Madsen, McIntosh & Berman, 1995) and *Brachiosaurus* (pers. observ.). The subnarial foramen is either reduced or absent in *Nemegtosaurus*. *Quaesitosaurus* shares with *Nemegtosaurus* the presence of an enclosed anterior maxillary foramen and a reduced or absent subnarial foramen.

Lack of lateral exposure of the vomerine (i.e. anteromedial) processes of the maxilla (4) is here considered a primitive trait.

Loss of the intercoronoid (5) is an ambiguous feature that can be interpreted either as an autapomorphy for *Diplodocus* or as a diplodocine synapomorphy. Although no intercoronoid has been preserved in any of the several available skulls of *Diplodocus*, the condition in other diplodocoids is unknown. Other sauropods retain a free intercoronoid that overlaps all but the anteriormost four alveoli (e.g. *Brachiosaurus*; Janensch 1935–36: fig. 44). *Nemegtosaurus* represents a separate condition, in which the modified intercoronoid is a narrow, strap-like element whose posterior margin can be identified near the summit of the coronoid eminence and whose anterior end is fused to the dentary. The intercoronoid does not appear to cover any alveoli in *Nemegtosaurus*. This element is preserved on both available jaw rami of *Nemegtosaurus*, as it is in *Quaesitosaurus* (pers. observ.).

The mandibles are rectangular (6) in the diplodocoids *Diplodocus* (McIntosh & Berman, 1975: fig. 5C), *Dicraeosaurus* (Janensch, 1935–36: fig. 113), and *Nigersaurus* (Sereno *et al.*, 1999: fig. 2C). In contrast, available photographs of the mandibles of *Nemegtosaurus* (Nowinski, 1971: pl. 14) show no sharp angle between the jaw rami and the symphyseal portions of the mandible. Instead, the transition between these two portions of the jaw follows a gentle curve, as in nondiplodocoid sauropods.

Restriction of the teeth anterior to the antorbital fenestra (7) characterizes *Diplodocus* and *Nigersaurus* among diplodocoids; the condition in dicraeosaurids is unknown. This characteristic is not restricted to diplodocoids, however, because it is present in the macronarian *Brachiosaurus* (Wilson & Sereno, 1998: fig. 8A). *Nemegtosaurus* cannot be scored, because the anterior margin of the antorbital fenestra is not

preserved. The only other titanosaur skull known displays the primitive condition due to an anteroposteriorly elongate antorbital fenestra (*Rapetosaurus*; Curry Rogers & Forster, 2001).

In summary, only two of the features presented by Upchurch (1999) support the diplodocoid affinities of *Nemegtosaurus*. These features are outweighed by a host of synapomorphies that nest *Nemegtosaurus* within Titanosauria (see Appendix 3).

Sanz et al. *(1999)*

In their description of the well preserved remains of the Upper Cretaceous Spanish titanosaur *Lirainosaurus*, Sanz *et al.* presented an analysis of seven titanosaur genera. Because only two of those genera were included in the present analysis (*Opisthocoelicaudia* and *Saltasaurus*), our results are in agreement. Sanz *et al.* (1999: 252) coined the name 'Eutitanosauria' for the node-based group including "the most recent common ancestor of *Saltasaurus*, *Argyrosaurus*, *Lirainosaurus*, plus the Peirópolis titanosaur and all its descendants." The implications for 'Eutitanosauria' will not be discussed here because only one of the reference taxa appear in this analysis.

Curry Rogers & Forster (2001)

A second analysis of titanosaur relationships appeared in the description of *Rapetosaurus*, the first titanosaur known from well-preserved and nearly complete cranial and postcranial remains (Curry Rogers & Forster, 2001). Their analysis included 16 sauropod genera that were scored for 228 characters culled from analyses of Wilson (1999b) and Upchurch (1998, 1999). Both *Rapetosaurus* and *Nemegtosaurus* nested within Titanosauria, largely on the strength of the postcranial skeleton of the former. Only one uniquely derived cranial feature was listed as characterizing the titanosaur skull: presence of a 90° angle between the symphysis and jaw ramus (Upchurch, 1999: 108). All other cranial synapomorphies of *Rapetosaurus* and *Nemegtosaurus* were homoplastic, either because they are present in diplodocoids or represent reversals of the primitive sauropod condition. This analysis supports the Curry Rogers & Forster (2001) hypothesis that *Rapetosaurus* and *Nemegtosaurus* are titanosaurs with several new, uniquely derived cranial synapomorphies (Appendix 3). Whereas these new characters strongly support placement of *Nemegtosaurus* and *Rapetosaurus* within Titanosauria, they do not resolve their relationship to other titanosaurs, because most lack cranial remains. Those characters that could be scored for *Malawisaurus*, however, indicate that *Rapetosaurus* and *Nemegtosaurus* are derived.

The topology of Curry Rogers & Forster (2001) agrees for the most part with that presented here, save for two differences. Whereas this analysis resolves *Malawisaurus* as the basalmost titanosaur and *Alamosaurus* as the sister-taxon of *Opisthocoelicaudia*, Curry Rogers & Forster (2001) regarded *Malawisaurus* and *Rapetosaurus* as closely related and found no evidence for Opisthocoelicaudiinae (*Alamosaurus* plus *Opisthocoelicaudia*). Curry Rogers & Forster (2001) report low decay indices (1) for the node uniting *Malawisaurus* and *Rapetosaurus*; they did not discuss support within other clades. This analysis exhibits similarly low decay indices for Opisthocoelicaudiinae, but relatively high values (4; Table 12) for the clade joining *Rapetosaurus* '*T.*' *colberti*, and saltasaurids to the exclusion of *Malawisaurus*. Further comparisons of these analyses awaits a more detailed description of the anatomy and relationships of *Rapetosaurus* (Curry Rogers & Forster, in prep.).

IMPLICATIONS

Sauropoda incertae sedis
Several sauropod genera were not included in the phylogenetic analysis because they are represented by very incomplete material – most of them could be scored for less than 25% of the features coded in this analysis. Instead, synapomorphies derived from analysis of more complete genera (Appendix 3) were used to allocate 57 fragmentary taxa to the most exclusive clade possible. In cases where a fragmentary taxon shared synapomorphies with two sauropod subgroups, that genus was assigned to the clade uniting the two subgroups. All fragmentary taxa, their provenance, their most exclusive taxonomic assignment, and synapomorphies supporting this placement are recorded in Table 13.

Of the 57 fragmentary taxa listed in Table 13, nearly half (27) were allocated to Macronaria. Nearly all of these macronarians are Cretaceous in age, and the majority can be referred to Titanosauria. Comparably few genera (7) could be referred to Diplodocoidea, nearly all of which are from the Late Jurassic. The remainder (22) were referred to one of several basal sauropod clades. Most of these nonneosauropod genera are Jurassic in age, although three are Triassic.

The affinities and distributions of these fragmentary taxa point to three areas of future research in sauropod evolution. First, these distributions reveal an under-appreciated diversity of Cretaceous sauropods, the majority of which are titanosaurs. Titanosaurs are paradoxical because they were taxonomically diverse, morphologically distinct, and geographically widespread, yet their anatomy is incompletely known. Establishing the interrelationships of these biogeographically important sauropods will an important aspect of future systematic studies.

Second, the presence of numerous non-neosauropod genera in the Middle and Late Jurassic holds promise for understanding early neosauropod evolution. Although relationships within Neosauropoda are well-supported, its origin from non-neosauropod taxa is not. Resolution of the phylogenetic affinities of fragmentary Middle and Late Jurassic forms may have important effects on character polarity within Neosauropoda and on the temporal distributions of its principal lineages, all of which have first appearances in the Late Jurassic.

Third, the paucity of Late Triassic (1) and Early Jurassic (3) sauropods underscores a sampling bias that has hampered understanding of sauropod origins and early evolution. The morphological gap between sauropods and nonsauropods can be explained by the 15–25 million-year ghost lineage separating the first appearance of reasonably complete sauropods in the Early Jurassic (*Vulcanodon* – Raath, 1972) and their predicted divergence from Prosauropoda in the Late Triassic. This morphological gap can only be bridged by transitional Triassic-Jurassic forms, which are currently known from isolated fragments. Of these, *Gongxianosaurus* (He *et al.*, 1998) may be the most important. Only briefly described, this outstanding specimen preserves a premaxilla, teeth, a series of dorsal centra, portions of the tail, an articulated pectoral girdle and forelimb lacking the manus, and a complete, articulated hindlimb. Despite a strikingly sauropod-like snout, dentition, and long bones (Table 13), the pes of *Gongxianosaurus* is primitive in nearly all respects. In addition to maintaining a relatively long metatarsus (as in *Vulcanodon*), which may be correlated with a relatively short metatarsal V, it retains distal tarsals 3 and 4, a high phalangeal count (2-3-4-5-?), and short, flat unguals. If the assessment of *Gongxianosaurus* as the most plesiomorphic sauropod is correct, it indicates that early evolution of the sauropod appendicular skeleton was characterized by modification of proximal elements prior to distal elements. However, further speculation must await full description of this important specimen.

Additional information on the early evolution of sauropod locomotor evolution may be sought in the sauropod footprint record, which preserves several important Late Triassic (Lockley *et al.*, 2001) and Early Jurassic (Ishigaki, 1988; Dalla Vecchia, 1994; Gierlinski, 1997) ichnotaxa. These tracks indicate that a digitigrade manus, a plantigrade pes, and manus-pes heteropody evolved by the Late Triassic, earlier in sauropod history than implied by cladistic analysis.

Problematic areas

The phylogenetic analysis and exploration of suboptimal trees highlights several as yet unresolved areas in sauropod systematics (Fig. 13, Table 13). Although the position of *Omeisaurus* appears stable in both this analysis and that of Wilson & Sereno (1998), the positions of the Middle Jurassic taxa *Patagosaurus* and *Mamenchisaurus* could not be resolved relative to it. Both the latter taxa were incompletely scored (55% and 46%, respectively), which may account for this lack of resolution.

Basal saltasaurids represent another problematic area identified in this analysis. The positions of *'T.' colberti* and *Nemegtosaurus* were only weakly resolved relative to Saltasauridae. The uncertainty of relationships at this node is most likely due to the lack of complete skeletons – skull morphology is only rarely preserved and both vertebral counts and foot morphology are completely unknown. A related problem stems from the nonoverlap of the preserved anatomy of titanosaurs. Several of the more incompletely known titanosaurs are known from skeletal remains that

Table 13. Age, provenance, and taxonomic assignment of 57 fragmentary sauropods. Character numbers refer to features supporting higher-level (Appendix 3) and generic (Appendix 4) assignments. Age abbreviations: EJ = Early Jurassic; EK = Early Cretaceous; LJ = Late Jurassic; LK = Late Cretaceous; LTr = Late Triassic; MJ = Middle Jurassic. Area abbreviations: AF = Africa; AS = Asia; AU = Australia; EU = Europe; I = Indo-Pakistan; MA = Madagascar; NA = North America; SA = South America. Clade abbreviations: mdd = more derived diplodocoids; mds = more derived sauropods; mdt = more derived titanosaurs *Indicates referral based on dentary only

Taxon	Age	Area	Clade	Characters
Aegyptosaurus baharijensis	LK	AF	Nemegtosauridae + mdt	3
Aeolosaurus rionegrinus	LK	SA	Nemegtosauridae + mdt	3
Agustinia ligabuei	EK	SA	Titanosauria	11
Ampelosaurus atacis	LK	EU	Saltasauridae	4, 7–8, 11–12
Amphicoelias altus	LJ	NA	Dicraeosauridae + mdd	3, 7–8, 10, 12, 15
Amygdalodon patagonicus	MJ	SA	*Patagosaurus* + mds	6
Andesaurus delgadoi	EK	SA	Titanosauria	9
*Antarctosaurus wichmannianus**	LK	SA	*Nigersaurus*	1, 3–4
Antarctosaurus septentrionalis	LK	I	Nemegtosauridae	43
Argentinosaurus huinculensis	EK	SA	Macronaria	5
Argyrosaurus superbus	LK	SA	Nemegtosauridae + mdt	3
Asiatosaurus mongoliensis	EK	AS	Eusauropoda	23–27
Atlasaurus imelakei	MJ	AF	*Jobaria* + mds	9, 10
Austrosaurus mckillopi	LK	AU	Titanosauriformes	1, 8
'Barosaurus' africanus	LJ	AF	Diplodocinae	3–7
Bellusaurus sui	MJ	AS	*Patagosaurus* + mds	3–4
Bothriospondylus madagascariensis	LJ	EU	*Brachiosaurus*	17, 21, 23, 25
Campylodon ameghinoi	LK	SA	Neosauropoda	5
Cedarosaurus weiskopfae	EK	NA	*Brachiosaurus*	21, 23
Cetiosauriscus stewarti	MJ	EU	Eusauropoda	34–35
Cetiosaurus oxoniensis	MJ	EU	Neosauropoda	6
Chubutisaurus insignis	EK	SA	Titanosauria	3
Datousaurus bashanensis	MJ	AS	Eusauropoda	2, 4, 10, 24–25, 27
Dinheirosaurus lourinhanensis	LJ	EU	Dicraeosauridae + mdd	10
Dystrophaeus viaemalae	MJ-LJ	NA	*Jobaria* + mds	9
Epachthosaurus sciuttoi	EK	SA	Titanosauria	2
Gondwanatitan faustoi	LK	SA	Nemegtosauridae + mdt	3
Gongxianosaurus shibeiensis	EJ	AS	Sauropoda	3, 9, 14
Isanosaurus attavipachi	LTr	AS	Eusauropoda	29, 41
Janenschia robusta	LJ	AF	Titanosauria	8
Jianshangosaurus lixianensis	EK	AS	Somphospondyli	4
Klamelisaurus gobiensis	MJ	AS	*Patagosaurus* + mds	6
Kotasaurus yamanpalliensis	EJ	I	*Barapasaurus* + mds	2, 5, 10, 12
Lapparentosaurus madagascariensis	MJ	MA	*Jobaria* + mds	9–13
Lirainosaurus astibiae	LK	EU	Saltasaurinae	3

Table 13. *Continued*

Taxon	Age	Area	Clade	Characters
Losillasaurus giganteus	LJ-EK	EU	Dicraeosauridae + mdd	10, 13
Magyarosaurus dacus	LK	EU	Nemegtosauridae + mdt	3
Mongolosaurus haplodon	EK	AS	Neosauropoda	5
Paralititan stromeri	LK	AF	Titanosauria	3, 4
Pelligrinisaurus powelli	LK	SA	Saltasauridae	1
Phuwiangosaurus sirindhornae	EK	AS	Titanosauria	6, 9
Pleurocoelus nanus	EK	NA	Titanosauriformes	8
Quaesitosaurus orientalis	LK	AS	*Nemegtosaurus*	1–6, 9–16
Rhoetosaurus brownei	MJ	AU	Sauropoda	3, 12, 14
Rocasaurus muniozi	LK	SA	Saltasaurinae	2, 3
Sauroposeidon proteles	EK	NA	*Brachiosaurus*	9
Seismosaurus halli	LJ	NA	Diplodocinae	3–7
Sonorosaurus thompsoni	EK	NA	*Jobaria* + mds	9
Supersaurus vivianae	LJ	NA	Diplodocinae	6
Tangvayosaurus hoffeti	EK	AS	Titanosauriformes	8
Teheulchesaurus benitezii	MJ-LJ	SA	*Patagosaurus* + mds	3
Tendaguria tanzaniensis	LJ	AF	*Patagosaurus* + mds	3
Tienshanosaurus chitaiensis	EK	AS	*Patagosaurus* + mds	3, 4, 6,
'Titanosaurus' araukanicus	LK	SA	Saltasauridae	2, 3, 8
Venenosaurus dicrocei	EK	NA	*Brachiosaurus*	21, 23
Volkheimeria chubutensis	MJ	SA	Eusauropoda	29
Unnamed (Barrett, 1999)	EJ	AS	Eusauropoda	23, 27

have little to no comparison to other forms, which hampers discovery of features to differentiate them phylogenetically. Given the abundance of innovations in the preserved portions of their skeletons, it is probable that discovery of more complete remains will clarify saltasaurid relationships.

A third problematic area surrounds the origin of neosauropods. Conflicting evidence from *Jobaria* and the basal diplodocoids *Haplocanthosaurus*, *Rayososaurus*, and *Rebbachisaurus* results in a trichotomy at the base of Neosauropoda in suboptimal trees. Although *Jobaria* is nearly complete, critical postcranial information is still lacking for the basal members of the diplodocoid radiation. Discovery of well-preserved primitive diplodocoids should result in resolution of character polarity at the base of Neosauropoda that will settle the positions of *Jobaria* and *Haplocanthosaurus*.

Data
The relative import of cranial, axial, and appendicular data supporting the interrelationships of various sauropod clades can be compared by sorting characters by anatomical region and tallying the types of synapomorphies that characterize various groups (Table 14). Because of the prevalence of missing data in the analysis, some of the differences in the relative cladewise

support of different anatomical regions will be artifactual. Based on the relative frequencies of missing data in each terminal taxon (Table 8), these effects are expected to be minimal.

Macronaria and Diplodocoidea are comparably sized sister-taxa that comprise Neosauropoda. These sister-taxa have identical lineage durations that begin with the origin of Neosauropoda in the Middle or Late Jurassic and end at the Cretaceous–Tertiary boundary. During this interval, which lasted less than 100 Myr, 365 synapomorphies and autapomorphies are recovered by this analysis; 149 within Diplodocoidea and 216 within Macronaria. Despite similar amounts of missing data, the relationships in the two clades are supported by anatomical data from distinct anatomical regions. In diplodocoids, cranial and axial features constitute 85% of the total support for the topology, whereas appendicular synapomorphies provide only minimal support. Macronarians, in contrast, have much more balanced support. They are characterized by fewer cranial synapomorphies and a surprisingly high proportion of appendicular synapomorphies. Changes in the axial column were common in both lineages. The discrepancy in support for the two major neosauropod lineages suggests that the divergence and subsequent diversification of each may have been shaped by innovations focused in different regions of the skeleton. Interestingly, Late Cretaceous

Table 14. Data support in the two neosauropod lineages Macronaria and Diplodocoidea. The relative proportions of cranial, axial, and appendicular characters supporting the interrelationships of these clades are compared below. Percent character support was calculated by tallying the characters supporting each node (Appendix 3) and genus (Appendix 4) within each lineage. Missing data scores were based on Table 8. Total missing data were higher in Diplodocoidea (48%) than Macronaria (44%)

	Macronaria	Diplodocoidea
Number of taxa	11	9
Cranial		
% missing data	58	55
% character support	30	39.5
Axial		
% missing data	35	33
% character support	37	45.5
Appendicular		
% missing data	41	55
% character support	33	15

survivors of each clade represent the morphological extremes in each case – diplodocoids survive in the form of shovel-snouted, slender-necked rebbachisaurids; macronarians persist as stocky, wide-gauged saltasaurines.

CONCLUSIONS

The cladistic analysis presented here resolves a hierarchy of relationships that is supported by a series of cranial, axial, and appendicular synapomorphies. The early evolution of Sauropoda is chronicled by a paraphyletic series of basal forms that are sequential outgroups to Neosauropoda. Basal sauropods are characterized by relatively low cladogenesis; most branches lead to singleton taxa. Omeisauridae (*Omeisaurus, Mamenchisaurus*), a remnant of Upchurch's 'Euhelopodidae', is the only non-neosauropod clade recognized. Poor sampling during this stratigraphic interval may account for this pattern. Although early sauropods record the evolution of several important features, they so closely resemble later sauropods that the evolution of graviportality, herbivory, and neck elongation is still poorly understood.

Neosauropoda is composed of two lineages, Macronaria and Diplodocoidea. Macronarians are characterized by a substantial number of appendicular synapomorphies that may be involved in the acquisition of a novel 'wide-gauge' locomotory style in titanosaurs. Although several nodes within Titanosauria were strongly supported by characters recorded in this analysis, future discoveries and analyses will be required to accommodate the score of fragmentary

titanosaurs already recorded from around the globe. Diplodocoids, in contrast, are known from comparably fewer taxa whose relationships are based on predominantly cranial and axial features. Diplodocoids underwent a radical change in skull shape that involved a reorientation of the skull relative to the axial column, a drastic reduction in the number and size of teeth, and retraction of the external nares to a position between the orbits. Diplodocoid axial features include a highly modified set of vertebral laminae and the acquisition of an elongate, 'whiplash' tail.

This hypothesis of descent, with its attendant patterns of spatiotemporal distribution and skeletal modification, provides a starting point for analysis the evolution of herbivory, neck elongation, and locomotory specializations within Sauropoda.

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APPENDIX 1

CHARACTER–TAXON MATRIX

	0 1 0	0 2 0	0 3 0	0 4 0	0 5 0
Prosauropoda	0000000000	0000000000	0000000000	0009900000	0000000000
Theropoda	0000000000	0000000000	0000000000	0009900000	0000000000
Vulcanodon	??????????	??????0???	??????????	??????????	??????????
Barapasaurus	??????????	??????????	??????????	??????????	??????????
Omeisaurus	1110001101	1?000?0101	1000010111	?11?0?1??1	1100?0?0?0
Shunosaurus	0110001101	1000000001	??00000111	0110001001	100000000?
Patagosaurus	1?100?11??	??????0???	??????????	??????????	?1?????????
Mamenchisaurus	??????????	??????????	??????????	??110?????	??????????
Apatosaurus	0011111201	1?111?0101	11?1010111	11100020?1	?000010000
Barosaurus	??????????	??????????	??????????	??????????	??????????
Brachiosaurus	1111001111	1100010101	1000010111	1111001011	1100000001
Camarasaurus	1111001111	1100010101	1001010111	0011011011	1100000000
Dicraeosaurus	00?11?????	0??00?0111	1111011111	?????1?0??	1000111010
Diplodocus	0011111201	1111110101	1101010111	1110002011	1000010000
Haplocanthosaurus	??????????	??????0???	??????????	??????????	????????0?
Amargasaurus	??????????	1??0010111	1?11011111?	??????????	??00111011
Euhelopus	11100?11??	1????10???	??????????	?1100??0?1	11???????
Jobaria	1111001111	1100010101	1000010111	01110?10?1	1?000??000
Malawisaurus	11?????1??	1?????????	??????????	??????????	??????????
Nigersaurus	00110?1100	???0011900	1??9199991	?1110?????	??0001?00?
Rayososaurus	?????????0	1??0011900	1109199911	0?110??0??	??10010101
Rebbachisaurus	??????????	??????????	??????????	??????????	??????????
Alamosaurus	??????????	??????????	??????????	??????????	??????????
Nemegtosaurus	01?19011?1	0100010101	0101010101	0111121111	1?11000100
Neuquensaurus	??????????	??????????	??????????	??????????	??????????
Opisthocoelicaudia	??????????	??????????	??????????	??????????	??????????
Rapetosaurus	0011?111?1	0?000?0001	0101010101	0?1112111?	??11?0100?
Saltasaurus	??????????	???00??101	?00101????	??????????	??01000101
'T.' colberti	??????????	??????????	??????????	??????????	??????????

	0 6 0	0 7 0	0 8 0	0 9 0	1 0 0
Prosauropoda	0000000000	0000000900	0000000001	1090000009	1000000000
Theropoda	0000000000	0000000900	0000000000	1090000009	0000000000
Vulcanodon	??????????	??????????	???????0??	??9???????	??????????
Barapasaurus	??????????	?????????1	?0?????0??	019??01009	?101011011
Omeisaurus	?00110000?	1???111011	111?000104	0111010?09	3101?11011
Shunosaurus	000110000?	101?111011	120?000003	1191001009	210000?000
Patagosaurus	?????0????	????1?1011	1???0001??	011?001009	?101011101?
Mamenchisaurus	????10000?	10111?1?11	1100011?4	01?1010110	31010?1?1?
Apatosaurus	0011??????	????221202	121??0114	0110101111	5101111111
Barosaurus	??????????	??????????	??????01??	011?111?11	?101????11
Brachiosaurus	1001100111	1112111001	1210001103	0110011009	3101011111
Camarasaurus	1001100111	1111111011	1210000102	0110101010	3101011011
Dicraeosaurus	1011110???	????221202	121?000112	0110101011	3111110011
Diplodocus	1011110101	101?221202	1211100114	0110111111	5101111111
Haplocanthosaurus	??????????	??????????	??????01?3	0110001009	2101011011

Appendix 1 *Continued*

	060	070	080	090	100
Amargasaurus	?011??????	??????????	??????0013	019?101010	5111????1?
Euhelopus	????10011?	????1?1011	12101011?4	1111011011	2101011111?
Jobaria	?001000???	????111011	1000001?3	0110001009	3101011111
Malawisaurus	????100???	????1?1??1	1210?011??	1100011?09	?10101?01?
Nigersaurus	?011109100	????221102	12010101??	0110001?09	??????????
Rayososaurus	1011??????	??????1??2	12???101??	0110001009	?1?10???11
Rebbachisaurus	??????????	??????????	???????1??	???????09	?11??11111
Alamosaurus	??????????	??????????	??????11??	1100001?09	?101011010
Nemegtosaurus	010110111?	?01?111?02	121000????	??????????	??????????
Neuquensaurus	??????????	??????????	??????11??	010?001?09	?101????1?
Opisthocoelicaudia	??????????	??????????	???????1??	???????010	4101011110
Rapetosaurus	110100111?	????111102	12100011??	110?011?09	?10101?010
Saltasaurus	???1??????	??????????	??????11??	0110001109	?10101?110
'T.' colberti	??????????	??????????	???????1??	1100001009	?101011010

	110	120	130	140	150
Prosauropoda	0000000009	0000000000	0000000000	0000009900	0009000000
Theropoda	0000000009	0000000000	0000000000	0000009900	0009000001
Vulcanodon	???????1??	??0??0?00?	??????1000	01????????	????00??10
Barapasaurus	1010000110	0?0??0?00?	??????1000	00000099??	?01?00?011
Omeisaurus	1000000211	01?0100000	0000001000	0?000??10	0?11000011
Shunosaurus	00000?0109	0000100000	0000001000	0?0009990?	0011101010
Patagosaurus	?010000200?	0???????00?	??????1???	0?000??1?	00??00??11
Mamenchisaurus	10?00002??	???0110100	0000001000	0?000??10	001100?01?
Apatosaurus	100000021?	1100110000	1111011111	0000011111	0011001011
Barosaurus	1000000???	??0110111	1111011111	1110011???	?01?00?01?
Brachiosaurus	1100100211	010?100000	0011001000	00000??10	11??10??11
Camarasaurus	1100100211	0100100000	0011011000	0000009910	0?10101011
Dicraeosaurus	100000121?	1?0?110000	1011011100	0000011?11	001?00??11
Diplodocus	1000000211	1100110111	1111011111	1110011111	0011001011
Haplocanthosaurus	1100000211	010?100000	0011001000	0000????11	00??10??10
Amargasaurus	?0000?12??	1????0????	??????????	??0???????	?0??????1?
Euhelopus	11011?03??	01????????	??????????	???????10	11??????11
Jobaria	1100000211	0100100000	0011001000	00000??10	001?001011
Malawisaurus	1101110???	????1??10?	0011101000	01000??10	1?0911??1?
Nigersaurus	??????????	??????????	??????????	???????11	00??????1
Rayososaurus	10000?1???	??00100000	0011011000	0000011?1?	????1???11
Rebbachisaurus	1000011???	??????????	??????????	??????????	????????11
Alamosaurus	1101110???	???1231100	0011011000	01010?????	??09111111
Nemegtosaurus	??????????	??????????	??????????	??????????	??????????
Neuquensaurus	1?0111031?	0?1??3010?	0011?11000	0101110???	???????11
Opisthocoelicaudia	110111031?	0??1221200	0011011000	01020100??	1109111111
Rapetosaurus	110111103??	???????1??	0??????00	???1????1?	????????11
Saltasaurus	1101110312	011????10?	0011111000	0101110?1?	????11?011
'T.' colberti	100?110312	0??????10?	0011011000	01010???1?	?10911?010

Appendix 1 *Continued*

	1 6 0	1 7 0	1 8 0	1 9 0	2 0 0
Prosauropoda	0000000000	0100090000	0000000100	0000000000	0000000000
Theropoda	0000000000	0110090000	0000000000	0000000000	0000000000
Vulcanodon	?????????1	010?111010	01????0???	????1???00	010101010?
Barapasaurus	0000000?01	0101111010	0?????????	???0110001	0101011101
Omeisaurus	000?000001	0101101010	0101000000	111?110001	010101?100
Shunosaurus	0000000001	0101101010	0101000001	1010110001	010?011101
Patagosaurus	0?0?000?01	0111111010	0?????????	????110001	0101011101
Mamenchisaurus	????????01	0101111010	01????????	????110??	??01011101
Apatosaurus	0011000001	0101101010	0111110000	1111110011	0100011101
Barosaurus	???????0??	??????????	??????????	????????11	??????????
Brachiosaurus	0101000001	0101111010	0211111111	1011110101	1101111111
Camarasaurus	0101000001	0101111010	0111111100	1111110001	1101111101
Dicraeosaurus	0001000?01	0101111011	?1????????	???1110011	0100011101
Diplodocus	0001000001	0101111010	01????????	???1110011	0100011101
Haplocanthosaurus	0001000???	??????????	??????????	???1110001	0101111101
Amargasaurus	?0?1????01	0101101010	01????????	????1100??	?????1110?
Euhelopus	0010000?11	0101??????	??????????	???1110101	0101111111
Jobaria	0101000001	0101111010	0101110000	1111110001	0101111101
Malawisaurus	????000111	0101100010	0???1??111	??????????	??111?111?
Nigersaurus	020?0?????	??????????	??????????	??????????	??????????
Rayososaurus	020?000101	0001111010	01????????	????11??01	010111110?
Rebbachisaurus	0201?????1	?0????????	??????????	??????????	??011?????
Alamosaurus	101111?111	1110110011	1?99111111	299???????	?01111?????
Nemegtosaurus	??????????	??????????	??????????	??????????	??????????
Neuquensaurus	1010111111	1110110111	1?????????	????111101	?011111211
Opisthocoelicaudia	0011111111	1110110111	1199111111	2991111?01	1011111211
Rapetosaurus	10??100111	01101?0011	0?????1?1?	???1110101	1011111?11
Saltasaurus	1010111111	1110110111	1?????????	???1111101	1011111211
'T.' colberti	1010????11	0111111101??	??????????	???1111101	10111?????

	2 1 0	2 2 0	2 3 0	
Prosauropoda	0000000000	0000000000	0000000000	0000
Theropoda	0000000000	0000000099	0000000000	0000
Vulcanodon	??000?0000	1000010?10	0100100?01	1000
Barapasaurus	000101111?	1?10???010	???????1??	11?0
Omeisaurus	0?01011??0	1010011111	1111111111	1110
Shunosaurus	00?101?100	10?0011110	1110111?11	1110
Patagosaurus	000001????	??????1010	11????????	???0
Mamenchisaurus	001101?110	1110?11???	??1?11?1??	1??0
Apatosaurus	0011011101	1110111111	1111?1111?	1110
Barosaurus	??????????	??????????	??????????	???0
Brachiosaurus	0011011111	1110011110	111?11?1??	11?0
Camarasaurus	0011011101	1110011110	1111111111	1110
Dicraeosaurus	0011011101	1110??1111	11?11????1	1??0
Diplodocus	011101?101	1110011111	1111111?1	1110
Haplocanthosaurus	00????????	??????????	??????????	???0
Amargasaurus	00????????	??????????	??????????	???0
Euhelopus	001101?101	11?00?1110	1111?1??11	11?0

Appendix 1 *Continued*

	2 1 0	2 2 0	2 3 0	
Jobaria	0011011101	1110011110	11111?????	???0
Malawisaurus	????11110?	??????1???	??????????	1??1
Nigersaurus	??????????	??????????	??????????	????
Rayososaurus	00?10??1?1	???0??1000	1111??????	???0
Rebbachisaurus	??????????	??????????	??????????	???0
Alamosaurus	??????????	??????????	??????????	???0
Nemegtosaurus	??????????	??????????	??????????	????
Neuquensaurus	111111?101	1101??1110	?????1????	???1
Opisthocoelicaudia	1011111101	1101111110	1111111101	1110
Rapetosaurus	01????????	??????????	??????????	???1
Saltasaurus	111111110?	??????????	??????????	???1
'T.' colberti	??????????	??????????	??????????	????

APPENDIX 2

CHARACTERS ORDERED BY ANATOMICAL REGION

The cladistic codings for the 234 characters (76 cranial, 72 axial, 85 appendicular, 1 dermal) used in this analysis are listed below in anatomical order. For the 18 multistate characters, transformations were fully ordered for five (8, 37, 64, 66, 198) and unordered in the remaining 13 (36, 65, 68, 70, 72, 80, 91, 108, 116, 118, 134, 152, 181).

1. Posterolateral processes of premaxilla and lateral processes of maxilla, shape: without midline contact (0); with midline contact forming marked narial depression, subnarial foramen not visible laterally (1).
2. Premaxillary anterior margin, shape: without step (0); with marked step, anterior portion of skull sharply demarcated (1).
3. Maxillary border of external naris, length: short, making up much less than one-fourth narial perimeter (0); long, making up more than one-third narial perimeter (1).
4. Preantorbital fenestra: absent (0); present (1).
5. Subnarial foramen and anterior maxillary foramen, position: well distanced from one another (0); separated by narrow bony isthmus (1).
6. Antorbital fenestra, maximum diameter: much shorter than (0) or subequal to (1) orbital maximum diameter.
7. Antorbital fossa: present (0); absent (1).
8. External nares, position: terminal (0); retracted to level of orbit (1); retracted to a position between orbits (2).
9. External nares, maximum diameter: shorter (0) or longer (1) than orbital maximum diameter.
10. Orbital ventral margin, anteroposterior length: broad, with subcircular orbital margin (0); reduced, with acute orbital margin (1).
11. Lacrimal, anterior process: present (0); absent (1).
12. Jugal–ectopterygoid contact: present (0); absent (1).
13. Jugal, contribution to antorbital fenestra: very reduced or absent (0); large, bordering approximately one-third its perimeter (1).
14. Prefrontal, posterior process size: small, not projecting far posterior of frontal–nasal suture (0); elongate, approaching parietal (1).
15. Prefrontal, posterior process shape: flat (0); hooked (1).
16. Postorbital, ventral process shape: transversely narrow (0); broader transversely than anteroposteriorly (1).
17. Postorbital, posterior process: present (0); absent (1).
18. Frontal contribution to supratemporal fossa: present (0); absent (1).
19. Frontals, midline contact (symphysis): sutured (0) or fused (1) in adult individuals.
20. Frontal, anteroposterior length: approximately twice (0) or less than (1) minimum transverse breadth.
21. Parietal occipital process, dorsoventral height: short, less than the diameter of the foramen magnum (0); deep, nearly twice the diameter of the foramen magnum (1).
22. Parietal, contribution to post-temporal fenestra: present (0); absent (1).
23. Postparietal foramen: absent (0); present (1).
24. Parietal, distance separating supratemporal fenestrae: less than (0) or twice (1) the long axis of supratemporal fenestra.
25. Supratemporal fenestra: present (0); absent (1).

26. Supratemporal fenestra, long axis orientation: anteroposterior (0); transverse (1).
27. Supratemporal fenestra, maximum diameter: much longer than (0) or subequal to (1) that of foramen magnum.
28. Supratemporal region, anteroposterior length: temporal bar longer (0) or shorter (1) anteroposteriorly than transversely.
29. Supratemporal fossa, lateral exposure: not visible laterally, obscured by temporal bar (0); visible laterally, temporal bar shifted ventrally (1).
30. Laterotemporal fenestra, anterior extension: posterior to orbit (0); ventral to orbit (1).
31. Squamosal–quadratojugal contact: present (0); absent (1).
32. Quadratojugal, anterior process length: short, anterior process shorter than dorsal process (0); long, anterior process more than twice as long as dorsal process (1).
33. Quadrate fossa: absent (0); present (1).
34. Quadrate fossa, depth: shallow (0); deeply invaginated (1).
35. Quadrate fossa, orientation: posterior (0); posterolateral (1).
36. Palatobasal contact, shape: pterygoid with small facet (0), dorsomedially orientated hook (1), or rocker-like surface (2) for basipterygoid articulation.
37. Pterygoid, transverse flange (i.e. ectopterygoid process) position: posterior of orbit (0); between orbit and antorbital fenestra (1); anterior to antorbital fenestra (2).
38. Pterygoid, quadrate flange size: large, palatobasal and quadrate articulations well separated (0); small, palatobasal and quadrate articulations approach (1).
39. Pterygoid, palatine ramus shape: straight, at level of dorsal margin of quadrate ramus (0); stepped, raised above level of quadrate ramus (1).
40. Palatine, lateral ramus shape: plate-shaped (long maxillary contact) (0); rod-shaped (narrow maxillary contact) (1).
41. Epipterygoid: present (0); absent (1).
42. Vomer, anterior articulation: maxilla (0); premaxilla (1).
43. Supraoccipital, height: twice (0) subequal to or less than (1) height of foramen magnum.
44. Paroccipital process, ventral nonarticular process: absent (0); present (1).
45. Crista prootica, size: rudimentary (0); expanded laterally into 'dorsolateral process' (1).
46. Basipterygoid processes, length: short, approximately twice (0) or elongate, at least four times (1) basal diameter.
47. Basipterygoid processes, angle of divergence: approximately 45° (0); less than 30° (1).
48. Basal tubera, anteroposterior depth: approximately half dorsoventral height (0); sheet-like, 20% dorsoventral height (1).
49. Basal tubera, breadth: much broader than (0) or narrower than (1) occipital condyle.
50. Basioccipital depression between foramen magnum and basal tubera: absent (0); present (1).
51. Basisphenoid/basipterygoid recess: present (0); absent (1).
52. Basisphenoid–quadrate contact: absent (0); present (1).
53. Basipterygoid processes, orientation: perpendicular to (0) or angled approximately 45° to (1) skull roof.
54. Occipital region of skull, shape: anteroposteriorly deep, paroccipital processes oriented posterolaterally (0); flat, paroccipital processes oriented transversely (1).
55. Dentary, depth of anterior end of ramus: slightly less than that of dentary at midlength (0); 150% minimum depth (1).
56. Dentary, anteroventral margin shape: gently rounded (0); sharply projecting triangular process or 'chin' (1).
57. Dentary symphysis, orientation: angled 15° or more anteriorly to (0) or perpendicular to (1) axis of jaw ramus.
58. External mandibular fenestra: present (0); absent (1).
59. Surangular depth: less than twice (0) or more than two and one-half times (1) maximum depth of the angular.
60. Surangular ridge separating adductor and articular fossae: absent (0); present (1).
61. Adductor fossa, medial wall depth: shallow (0); deep, prearticular expanded dorsoventrally (1).
62. Splenial posterior process, position: overlapping angular (0); separating anterior portions of prearticular and angular (1).
63. Splenial posterodorsal process: present, approaching margin of adductor chamber (0); absent (1).
64. Coronoid, size: extending to dorsal margin of jaw (0); reduced, not extending dorsal to splenial (1); absent (2).
65. Tooth rows, shape of anterior portions: narrowly arched, anterior portion of tooth rows V-shaped (0); broadly arched, anterior portion of tooth rows U-shaped (1); rectangular, tooth-bearing portion of jaw perpendicular to jaw rami (2).
66. Tooth rows, length: extending to orbit (0); restricted anterior to orbit (1); restricted anterior to subnarial foramen (2).

67. Crown-to-crown occlusion: absent (0); present (1).
68. Occlusal pattern: interlocking, V-shaped facets (0); high-angled planar facets (1); low-angled planar facets (2).
69. Tooth crowns, orientation: aligned along jaw axis, crowns do not overlap (0); aligned slightly anterolingually, tooth crowns overlap (1).
70. Tooth crowns, cross-sectional shape at mid-crown: elliptical (0); D-shaped (1); cylindrical (2).
71. Enamel surface texture: smooth (0); wrinkled (1).
72. Marginal tooth denticles: present (0); absent on posterior edge (1); absent on both anterior and posterior edges (2).
73. Dentary teeth, number: greater than 20 (0); 17 or fewer (1).
74. Replacement teeth per alveolus, number: two or fewer (0); more than four (1).
75. Teeth, orientation: perpendicular (0) or oriented anteriorly relative (1) to jaw margin.
76. Teeth, longitudinal grooves on lingual aspect: absent (0); present (1).
77. Presacral bone texture: solid (0); spongy, with large, open internal cells, 'camellate' (Britt, 1993, 1997) (1).
78. Presacral centra, pneumatopores (pleurocoels): absent (0); present (1).
79. Atlantal intercentrum, occipital facet shape: rectangular in lateral view, length of dorsal aspect subequal to that of ventral aspect (0); expanded anteroventrally in lateral view, anteroposterior length of dorsal aspect shorter than that of ventral aspect (1).
80. Cervical vertebrae, number: 9 or fewer (0); 10 (1); 12 (2); 13 (3); 15 or greater (4).
81. Cervical neural arch lamination: well developed, with well defined laminae and coels (0); rudimentary; diapophyseal laminae only feebly developed if present (1).
82. Cervical centra, articular face morphology: amphicoelous (0); opisthocoelous (1).
83. Cervical pneumatopores (pleurocoels), shape: simple, undivided (0); complex, divided by bony septa (1).
84. Anterior cervical centra, height:width ratio: less than 1 (0); approximately 1.25 (1).
85. Anterior cervical neural spines, shape: single (0); bifid (1).
86. Mid-cervical centra, anteroposterior length/height of posterior face: 2.5–3.0 (0); > 4 (1).
87. Mid-cervical neural arches, height: less than that of posterior centrum face (0); greater than that of posterior centrum face (1).
88. Middle and posterior cervical neural arches, centroprezygapophyseal lamina (cprl), shape: single (0); divided (1). Wilson [1999a: 650, 651] errone-

ously lists this as characterizing dorsal neural arches.)
89. Posterior cervical and anterior dorsal neural spines, shape: single (0); bifid (1).
90. Posterior cervical and anterior dorsal bifid neural spines, median tubercle: absent (0); present (1).
91. Dorsal vertebrae, number: 15 (0); 14 (1); 13 (2); 12 (3); 11 (4); 10 or fewer (5).
92. Dorsal neural spines, breadth: narrower (0) or much broader (1) transversely than anteroposteriorly.
93. Dorsal neural spines, length: approximately twice (0) or approximately four times (1) centrum length.
94. Anterior dorsal centra, articular face shape: amphicoelous (0); opisthocoelous (1).
95. Middle and posterior dorsal neural arches, centropostzygapophyseal lamina (cpol), shape: single (0); divided (1).
96. Middle and posterior dorsal neural arches, anterior centroparapophyseal lamina (acpl): absent (0); present (1).
97. Middle and posterior dorsal neural arches, prezygoparapophyseal lamina (prpl): absent (0); present (1).
98. Middle and posterior dorsal neural arches, posterior centroparapophyseal lamina (pcpl): absent (0); present (1).
99. Middle and posterior dorsal neural arches, spinodiapophyseal lamina (spdl): absent (0); present (1).
100. Middle and posterior dorsal neural arches spinopostzygapophyseal lamina (spol) shape: single (0); divided (1).
101. Middle and posterior dorsal neural arches, spinodiapophyseal lamina (spdl) and spinopostzygapophyseal lamina (spol) contact: absent (0); present (1).
102. Middle and posterior dorsal neural spines, shape: tapering or not flaring distally (0); flared distally, with pendant, triangular lateral processes (1).
103. Middle and posterior dorsal neural arches, 'infradiapophyseal' pneumatopore between acdl and pcdl: absent (0); present (1).
104. Middle and posterior dorsal neural spines, orientation: vertical (0); posterior, neural spine summit approaches level of diapophyses (1).
105. Posterior dorsal centra, articular face shape: amphicoelous (0); opisthocoelous (1).
106. Posterior dorsal neural arches, hyposphene–hypantrum articulations: present (0); absent (1).
107. Posterior dorsal neural spines, shape: rectangular through most of length (0); 'petal' shaped,

expanding transversely through 75% of its length and then tapering (1).

108. Sacral vertebrae, number: 3 or fewer (0); 4 (1); 5 (2); 6 (3).
109. Sacrum, sacricostal yoke: absent (0); present (1).
110. Sacral vertebrae contributing to acetabulum: numbers 1–3 (0); numbers 2–4 (1).
111. Sacral neural spines, length: approximately twice (0) or four times (1) length of centrum.
112. Sacral ribs, dorsoventral length: low, not projecting beyond dorsal margin of ilium (0); high extending beyond dorsal margin of ilium (1).
113. Caudal bone texture: solid (0); spongy, with large internal cells (1).
114. Caudal vertebrae, number: more than 45 (0); 35 or fewer (1).
115. Caudal transverse processes: persist through caudal 20 or more posteriorly (0); disappear by caudal 15 (1); disappear by caudal 10 (2).
116. First caudal centrum, articular face shape: flat (0); procoelous (1); opisthocoelous (2); biconvex (3).
117. First caudal neural arch, coel on lateral aspect of neural spine: absent (0); present (1).
118. Anterior caudal centra (excluding the first), articular face shape: amphiplatyan or platycoelous (0); procoelous (1); opisthocoelous (2).
119. Anterior caudal centra, pneumatopores (pleurocoels): absent (0); present (1).
120. Anterior caudal centra, length: approximately the same (0) or doubling (1) over the first 20 vertebrae.
121. Anterior caudal neural arches, spinoprezygapophyseal lamina (sprl): absent (0); present and extending onto lateral aspect of neural spine (1).
122. Anterior caudal neural arches, spinoprezygapophyseal lamina (sprl)-spinopostzygapophyseal lamina (spol) contact: absent (0); present, forming a prominent lamina on lateral aspect of neural spine (1).
123. Anterior caudal neural arches, prespinal lamina (prsl): absent (0); present (1).
124. Anterior caudal neural arches, postspinal lamina (posl): absent (0); present (1).
125. Anterior caudal neural arches, postspinal fossa: absent (0); present (1).
126. Anterior caudal neural spines, transverse breadth: approximately 50% of (0) or greater than (1) anteroposterior length.
127. Anterior caudal transverse processes, proximal depth: shallow, on centrum only (0); deep, extending from centrum to neural arch (1).
128. Anterior caudal transverse processes, shape: triangular, tapering distally (0); 'wing-like', not tapering distally (1).
129. Anterior caudal transverse processes, diapophyseal laminae (acdl, pcdl, prdl, podl): absent (0); present (1).
130. Anterior caudal transverse processes, anterior centrodiapophyseal lamina (acdl), shape: single (0); divided (1).
131. Anterior and middle caudal centra, shape: cylindrical (0); quadrangular, flat ventrally and laterally (1).
132. Anterior and middle caudal centra, ventral longitudinal hollow: absent (0); present (1).
133. Middle caudal neural spines, orientation: angled posterodorsally (0); vertical (1).
134. Middle and posterior caudal centra, anterior articular face shape: flat (0); procoelous (cone shaped) (1); opisthocoelous (2).
135. Posterior caudal centra, shape: cylindrical (0); dorsoventrally flattened, breadth at least twice height (1).
136. Distalmost caudal centra, articular face shape: platycoelous (0); biconvex (1).
137. Distalmost biconvex caudal centra, length-to-height ratio: less than 4 (0); greater than 5 (1).
138. Distalmost biconvex caudal centra, number: 10 or fewer (0); more than 30 (1).
139. Cervical rib, tuberculum–capitulum angle: greater than 90° (0); less than 90°, rib ventrolateral to centrum (1).
140. Cervical ribs, length: much longer than centrum, overlapping as many as three subsequent vertebrae (0); shorter than centrum, little or no overlap (1).
141. Dorsal ribs, proximal pneumatocoels: absent (0); present (1).
142. Anterior dorsal ribs, cross-sectional shape: subcircular (0); plank-like, anteroposterior breadth more than three times mediolateral breadth (1).
143. 'Forked' chevrons with anterior and posterior projections: absent (0); present (1).
144. 'Forked' chevrons, distribution: distal tail only (0); throughout middle and posterior caudal vertebrae (1).
145. Chevrons, 'crus' bridging dorsal margin of haemal canal: present (0); absent (1).
146. Chevron haemal canal, depth: short, approximately 25% (0) or long, approximately 50% (1) chevron length.
147. Chevrons: persisting throughout at least 80% of tail (0); disappearing by caudal 30 (1).
148. Posterior chevrons, distal contact: fused (0); unfused (open) (1).
149. Posture: bipedal (0); columnar, obligately quadrupedal posture (1).
150. Scapular acromion process, size: narrow (0); broad, width more than 150% minimum width of blade (1).

151. Scapular blade, orientation: perpendicular to (0) or forming a 45° angle with (1) coracoid articulation.
152. Scapular blade, shape: acromial edge not expanded (0); rounded expansion on acromial side (1); racquet-shaped (2).
153. Scapular glenoid, orientation: relatively flat or laterally facing (0); strongly bevelled medially (1).
154. Scapular blade, cross-sectional shape at base: flat or rectangular (0); D-shaped (1).
155. Coracoid, proximodistal length: less than (0) or approximately twice (1) length of scapular articulation.
156. Coracoid, anteroventral margin shape: rounded (0); rectangular (1).
157. Coracoid, infraglenoid lip: absent (0); present (1).
158. Sternal plate, shape: oval (0); crescentic (1).
159. Humeral proximolateral corner, shape: rounded (0); square (1).
160. Humeral deltopectoral attachment, development: prominent (0); reduced to a low crest or ridge (1).
161. Humeral deltopectoral crest, shape: relatively narrow throughout length (0); markedly expanded distally (1).
162. Humeral midshaft cross-section, shape: circular (0); elliptical, with long axis orientated transversely (1).
163. Humeral distal condyles, articular surface shape: restricted to distal portion of humerus (0); exposed on anterior portion of humeral shaft (1).
164. Humeral distal condyle, shape: divided (0); flat (1).
165. Ulnar proximal condyle, shape: subtriangular (0); triradiate, with deep radial fossa (1).
166. Ulnar proximal condylar processes, relative lengths: subequal (0); unequal, anterior arm longer (1).
167. Ulnar olecranon process, development: prominent, projecting above proximal articulation (0); rudimentary, level with proximal articulation (1).
168. Ulna, length-to-proximal breadth ratio: gracile (0); stout (1).
169. Radial distal condyle, shape: round (0); subrectangular, flattened posteriorly and articulating in front of ulna (1).
170. Radius, distal breadth: slightly larger than (0) or approximately twice (1) midshaft breadth.
171. Radius, distal condyle orientation: perpendicular to (0) or bevelled approximately 20° proximolaterally (1) relative to long axis of shaft.
172. Humerus-to-femur ratio: less than 0.60 (0); 0.60 or more (1).

173. Carpal bones, number: 3 or more (0); 2 or fewer (1).
174. Carpal bones, shape: round (0); block-shaped, with flattened proximal and distal surfaces (1).
175. Metacarpus, shape: spreading (0); bound, with subparallel shafts and articular surfaces that extend half their length (1).
176. Metacarpals, shape of proximal surface in articulation: gently curving, forming a 90° arc (0); U-shaped, subtending a 270° arc (1).
177. Longest metacarpal-to-radius ratio: close to 0.3 (0); 0.45 or more (1).
178. Metacarpal I, length: shorter than (0) or longer than (1) metacarpal IV.
179. Metacarpal I, distal condyle shape: divided (0); undivided (1).
180. Metacarpal I distal condyle, transverse axis orientation: bevelled approximately 20° proximodistally (0) or perpendicular (1) with respect to axis of shaft.
181. Manual digits II and III, phalangeal number: 2-3-4-3-2 or more (0); reduced, 2-2-2-2-2 or less (1); absent or unossified (2).
182. Manual phalanx I.1, shape: rectangular (0); wedge-shaped (1).
183. Manual nonungual phalanges, shape: longer proximodistally than broad transversely (0); broader transversely than long proximodistally (1).
184. Pelvis, anterior breadth: narrow, ilia longer anteroposteriorly than distance separating preacetabular processes (0); broad, distance between preacetabular processes exceeds anteroposterior length of ilia (1).
185. Ilium, ischial peduncle size: large, prominent (0); low, rounded (1).
186. Iliac blade dorsal margin, shape: flat (0); semicircular (1).
187. Iliac preacetabular process, orientation: anterolateral to (0) or perpendicular to (1) body axis.
188. Iliac preacetabular process, shape: pointed, arching ventrally (0); semicircular, with posteroventral excursion of cartilage cap (1).
189. Pubis, ambiens process development: small, confluent with (0) or prominent, projecting anteriorly from (1) anterior margin of pubis.
190. Pubic apron, shape: flat (straight symphysis) (0); canted anteromedially (gentle S-shaped symphysis) (1).
191. Puboischial contact, length: approximately one-third (0) or one-half (1) total length of pubis.
192. Ischial blade, length: much shorter than (0) or equal to or longer than (1) pubic blade.
193. Ischial blade, shape: emarginate distal to pubic peduncle (0); no emargination distal to pubic peduncle (1).

194. Ischial distal shaft, shape: triangular, depth of ischial shaft increases medially (0); bladelike, medial and lateral depths subequal (1).

195. Ischial distal shafts, cross-sectional shape: V-shaped, forming an angle of nearly 50° with each other (0); flat, nearly coplanar (1).

196. Femoral fourth trochanter, development: prominent (0); reduced to crest or ridge (1).

197. Femoral lesser trochanter: present (0); absent (1).

198. Femoral midshaft, transverse diameter: subequal to (0), 125–150%, or (1) at least 185% (2) anteroposterior diameter.

199. Femoral shaft, lateral margin shape: straight (0); proximal one-third deflected medially (1).

200. Femoral distal condyles, relative transverse breadth: subequal (0); tibial much broader than fibular (1).

201. Femoral distal condyles, orientation: perpendicular or slightly bevelled dorsolaterally (0) or bevelled dorsomedially approximately 10° (1) relative to femoral shaft.

202. Femoral distal condyles, articular surface shape: restricted to distal portion of femur (0); expanded onto anterior portion of femoral shaft (1).

203. Tibial proximal condyle, shape: narrow, long axis anteroposterior (0); expanded transversely, condyle subcircular (1).

204. Tibial cnemial crest, orientation: projecting anteriorly (0) or laterally (1).

205. Tibia, distal breadth: approximately 125% (0) or more than twice (1) midshaft breadth.

206. Tibial distal posteroventral process, size: broad transversely, covering posterior fossa of astragalus (0); shortened transversely, posterior fossa of astragalus visible posteriorly (1).

207. Fibula, proximal tibial scar, development: not well-marked (0); well-marked and deepening anteriorly (1).

208. Fibula, lateral trochanter: absent (0); present (1).

209. Fibular distal condyle, size: subequal to shaft (0); expanded transversely, more than twice midshaft breadth (1).

210. Astragalus, shape: rectangular (0); wedge-shaped, with reduced anteromedial corner (1).

211. Astragalus, foramina at base of ascending process: present (0); absent (1).

212. Astragalus, ascending process length: limited to anterior two-thirds of astragalus (0); extending to posterior margin of astragalus (1).

213. Astragalus, posterior fossa shape: undivided (0); divided by vertical crest (1).

214. Astragalus, transverse length: 50% more than (0) or subequal to (1) proximodistal height.

215. Calcaneum: present (0); absent or unossified (1).

216. Distal tarsals 3 and 4: present (0); absent or unossified (1).

217. Metatarsus, posture: bound (0); spreading (1).

218. Metatarsal I proximal condyle, transverse axis orientation: perpendicular to (0) or angled ventromedially approximately 15° to (1) axis of shaft.

219. Metatarsal I distal condyle, transverse axis orientation: perpendicular to (0) or angled dorsomedially to (1) axis of shaft.

220. Metatarsal I distal condyle, posterolateral projection: absent (0); present (1).

221. Metatarsal I, minimum shaft width: less than (0) or greater than (1) that of metatarsals II–IV.

222. Metatarsal I and V proximal condyle, size: smaller than (0) or subequal to (1) those of metatarsals II and IV.

223. Metatarsal III length: more than 30% (0) or less than 25% (1) that of tibia.

224. Metatarsals III and IV, minimum transverse shaft diameters: subequal to (0) or less than 65% (1) that of metatarsals I or II (1).

225. Metatarsal V, length: shorter than (0) or at least 70% (1) length of metatarsal IV.

226. Pedal nonungual phalanges, shape: longer proximodistally than broad transversely (0); broader transversely than long proximodistally (1).

227. Pedal digits II–IV, penultimate phalanges, development: subequal in size to more proximal phalanges (0); rudimentary or absent (1).

228. Pedal unguals, orientation: aligned with (0) or deflected lateral to (1) digit axis.

229. Pedal digit I ungual, length relative to pedal digit II ungual: subequal (0); 25% larger than that of digit II (1).

230. Pedal digit I ungual, length: shorter (0) or longer (1) than metatarsal I.

231. Pedal ungual I, shape: broader transversely than dorsoventrally (0); sickle-shaped, much deeper dorsoventrally than broad transversely (1).

232. Pedal ungual II–III, shape: broader transversely than dorsoventrally (0); sickle-shaped, much deeper dorsoventrally than broad transversely (1).

233. Pedal digit IV ungual, development: subequal in size to unguals of pedal digits II and III (0); rudimentary or absent (1).

234. Osteoderms: absent (0); present (1).

APPENDIX 3

SYNAPOMORPHIES

The shared derived characters supporting various sauropod subgroups are listed below from the most inclusive node (Sauropoda) to the least inclusive node

(Diplodocinae). Characters were optimized as delayed transformations (DELTRAN); ambiguous synapomorphies are listed in Tables 9 and 10. Character numbers are indicated in square brackets.

Where two authors are listed after a named node, the first name identifies the author who is credited with coining the name, and the second indicates the first author to employ it. By the Principle of Coordination (ICZN Article 36), an author creates names at all hierarchical levels within the family group when s/he creates one of them. For example, Marsh (1884) is credited with naming the Superfamily Diplodocoidea because he coined Diplodocidae, but the superfamily was first applied more than a century later by Upchurch (1995). I have chosen to identify both authors where appropriate. Authors are credited with identifying diagnostic sauropod features, irrespective of whether the feature was coded cladistically or whether all taxa included in the clade existed at the time of their writing.

Sauropoda (Marsh, 1878)

1. Sacral vertebrae number four or more (one caudosacral vertebra added; Wilson & Sereno, 1998) (Jain *et al*., 1975; Upchurch, 1995). [108]
2. Anterior caudal transverse processes deep, extending from centrum to neural arch (Upchurch, 1998). [127]
3. Columnar, obligately quadrupedal posture (Marsh, 1878). [149]
4. Humeral deltopectoral attachment reduced to a low crest or ridge (Raath, 1972; McIntosh, 1990). [160]
5. Ulnar proximal condyle triradiate, with deep radial fossa (Wilson & Sereno, 1998). [165]
6. Ulnar proximal condylar processes unequal in length, anterior arm longer. [166]
7. Ulnar olecranon process reduced or absent (Wilson & Sereno, 1998). [167]
8. Radial distal condyle subrectangular with flat posterior margin for ulna (Wilson & Sereno, 1998). [169]
9. Humerus-to-femur ratio 0.70 or more (Marsh, 1878, 1882; Romer, 1956; Gauthier, 1986; Upchurch, 1995, 1998). [172]
10. Ilium with low ischial peduncle (Jain *et al*., 1975; McIntosh, 1990). [185]
11. Ischial blade equal to or longer than pubic blade (Wilson & Sereno, 1998). [192]
12. Ischial distal shaft bladelike (Wilson & Sereno, 1998). [194]
13. Femoral fourth trochanter reduced to crest or ridge (Marsh, 1878; Riggs, 1904; Raath, 1972; Gauthier, 1986; McIntosh, 1990). [196]
14. Femoral midshaft elliptical in cross-section,

transverse diameter at least 150% anteroposterior diameter (Raath, 1972; Gauthier, 1986; McIntosh, 1990). [198]
15. Astragalar fossa and foramina at base of ascending process absent (Wilson & Sereno, 1998). [211]
16. Distal tarsals 3 and 4 absent or unossified (Marsh, 1882; Raath, 1972; Gauthier, 1986). [216]
17. Metatarsal I distal condyle angled dorsomedially relative to axis of shaft. [219]
18. Metatarsal I and V with proximal condyle subequal to those of metatarsal II and IV (Wilson & Sereno, 1998). [222]
19. Metatarsal V at least 70% length of metatarsal IV (Cruickshank, 1975; Van Heerden, 1978; Gauthier, 1986). [225]
20. Pedal digit I ungual longer than metatarsal I (Wilson & Sereno, 1998). [230]
21. Pedal ungual I deep and narrow (sickle-shaped) (Wilson & Sereno, 1998). [231]

Eusauropoda (Upchurch, 1995)

1. Snout with stepped anterior margin (Wilson & Sereno, 1998). [2]
2. Maxillary border of external naris long (Wilson & Sereno, 1998). [3]
3. Antorbital fossa absent (Wilson & Sereno, 1998). [7]
4. External nares retracted to level of orbit (Gauthier, 1986; McIntosh, 1990; Upchurch, 1995). [8]
5. Orbital ventral margin reduced, with acute orbital margin and laterotemporal fenestra extending under orbit (Gauthier, 1986; McIntosh, 1990; Upchurch, 1995). [10]
6. Lacrimal anterior process absent. [11]
7. Frontal anteroposterior length much less than minimum transverse breadth (Gauthier, 1986). [20]
8. Temporal bar shorter anteroposteriorly than transversely (Wilson & Sereno, 1998). [28]
9. Supratemporal fossa visible laterally, temporal bar shifted ventrally (Wilson & Sereno, 1998). [29]
10. Laterotemporal fenestra extends ventral to orbit (Gauthier, 1986; Upchurch, 1998). [30]
11. Quadratojugal anterior process more than twice as long as dorsal process (Wilson & Sereno, 1998). [32]
12. Quadrate fossa present (Wilson & Sereno, 1998). [33]
13. Quadrate fossa posteriorly oriented. [35]
14. Pterygoid flange positioned below orbit or more anteriorly (Upchurch, 1998). [37]
15. Lateral ramus of palatine rod-shaped (narrow

maxillary contact) (Wilson & Sereno, 1998). [40]

16. Epipterygoid absent. [41]

17. Occipital region of skull flat, paroccipital processes oriented transversely. [54]

18. Anterior dentary ramus 150% minimum depth (Wilson & Sereno, 1998). [55]

19. Adductor fossa deep medially, prearticular expanded dorsoventrally. [61]

20. Splenial posterodorsal process absent. [63]

21. Tooth rows broadly arched, anterior portion of tooth rows U-shaped (Wilson & Sereno, 1998). [65]

22. Tooth rows restricted anterior to orbit (Upchurch, 1998). [66]

23. Crown-to-crown occlusion (Wilson & Sereno, 1998). [67]

24. Interlocking, V-shaped wear facets (Wilson & Sereno, 1998). [68]

25. Overlapping tooth crowns (Wilson & Sereno, 1998). [69]

26. Spatulate (D-shaped) tooth crowns (Wilson & Sereno, 1998). [70]

27. Wrinkled enamel surface texture (Wilson & Sereno, 1998). [71]

28. Cervical vertebrae 13 or more in number (Upchurch, 1995). [80]

29. Opisthocoelous cervical centra (Marsh, 1881). [82]

30. Mid-cervical neural arches taller than height of posterior centrum face (Bonaparte, 1986a). [87]

31. Dorsal neural spines broader transversely than anteroposteriorly (Bonaparte, 1986a). [92]

32. Caudal transverse processes disappear by caudal 15. [115]

33. Forked chevrons with anterior and posterior projections. [143]

34. Forked chevrons present in middle and posterior caudal vertebrae. [144]

35. Humeral distal condyles flat. [164]

36. Carpal bones block-shaped (Wilson & Sereno, 1998). [174]

37. Manual phalangeal formula reduced to 2-2-2-2-2 or less (II-ungual, III-3 and ungual absent or unossified) (Wilson & Sereno, 1998). [181]

38. Manual nonungual phalanges broader than long (Wilson & Sereno, 1998). [183]

39. Iliac blade dorsal margin semicircular (McIntosh, 1990). [186]

40. Pubic apron canted anteromedially, S-shaped medial aspect (Wilson & Sereno, 1998). [190]

41. Femoral lesser trochanter absent (Upchurch, 1998). [197]

42. Femoral distal condyles asymmetrical, tibial condyle much broader than fibular. [200]

43. Tibial cnemial crest projecting laterally (Wilson & Sereno, 1998). [204]

44. Tibial distal posteroventral process reduced, astragalar fossa visible in posterior view (Wilson & Sereno, 1998). [206]

45. Fibular lateral trochanter present (Wilson & Sereno, 1998). [208]

46. Metatarsus with spreading configuration (Marsh, 1878; Janensch, 1922; Lapparent & Lavocat, 1955; Cooper, 1984; McIntosh, 1990). [217]

47. Metatarsal I minimum shaft width greater than those of metatarsals II–IV (Wilson & Sereno, 1998). [221]

48. Metatarsal III length less than 25% tibia (Wilson & Sereno, 1998). [223]

49. Pedal nonungual phalanges broader than long (Wilson & Sereno, 1998). [226]

50. Pedal digits II–IV, penultimate phalanges rudimentary or absent (Wilson & Sereno, 1998). [227]

51. Pedal digit I ungual 25% larger than that of digit II (Wilson & Sereno, 1998). [229]

52. Pedal ungual II–III sickle-shaped, much deeper dorsoventrally than broad transversely (Wilson & Sereno, 1998). [232]

53. Pedal digit IV ungual rudimentary or absent (Wilson & Sereno, 1998). [233]

Barapasaurus + (Patagosaurus + ((Omeisauridae) + (Jobaria + Neosauropoda)))

1. Well developed cervical neural arch lamination. [81]

2. Opisthocoelous anterior dorsal centra (Wilson & Sereno, 1998). [94]

3. Middle and posterior dorsal neural arches with anterior centroparapophyseal lamina (acpl) (Wilson, 1999a). [96]

4. Middle and posterior dorsal neural arches with prezygoparapophyseal lamina (prpl) (Wilson, 1999a). [97]

5. Middle and posterior dorsal neural arches with spinodiapophyseal lamina (spdl) (Wilson, 1999a). [99]

6. Middle and posterior dorsal neural arches with divided spinopostzygapophyseal lamina (spol) (Wilson, 1999a). [100]

7. Middle and posterior dorsal neural arches with spinodiapophyseal lamina (spdl) contacting spinopostzygapophyseal lamina (spol) (Wilson & Sereno, 1998). [101]

8. Sacricostal yoke (Wilson & Sereno, 1998). [109]

9. Scapular acromion process broad, width more than 150% minimum width of blade (Wilson & Sereno, 1998). [150]

10. Fibula with broad, triangular tibial scar that

deepens anteriorly (Wilson & Sereno, 1998). [207]

11. Astragalar posterior fossa divided by vertical crest (Wilson & Sereno, 1998). [213]
12. Pedal unguals deflected laterally (Wilson & Sereno, 1998). [228]

Patagosaurus + *((Omeisauridae) + (*Jobaria + *Neosauropoda))*

1. Narial depression. [1]
2. Vomer contacts premaxilla. [42]
3. Presacral pneumatopores (pleurocoels) (Marsh, 1878; Calvo & Salgado, 1995). [78]
4. Cervical pneumatopores (pleurocoels) divided (Wilson & Sereno, 1998). [83]
5. Five or more sacral vertebrae (at least one dorsosacral added; Wilson & Sereno, 1998) (McIntosh, 1990; Upchurch, 1995). [108]
6. Cervical rib positioned ventrolateral to centrum (Wilson & Sereno, 1998). [139]

*Omeisauridae + (*Jobaria + *Neosauropoda)*

1. Frontal excluded from supratemporal fossa (Wilson & Sereno, 1998). [18]
2. Parietal occipital process deep, nearly twice diameter of foramen magnum. [21]
3. Supratemporal fenestra, long axis oriented transversely (Wilson & Sereno, 1998). [26]
4. Quadrate fossa deep. [34]
5. Coronoid reduced posteriorly. [64]
6. Dorsal vertebral number 12 or fewer (Wilson & Sereno, 1998). [91]
7. Sacral vertebrae 1–3 contributing to acetabulum. [110]
8. Manual phalanx I.1 wedge-shaped. [182]
9. Metatarsal I proximal condyle angled relative to axis of shaft. [218]
10. Metatarsals III and IV less than 65% breadth of metatarsals I or II (Wilson & Sereno, 1998). [224]

Omeisauridae (= Omeisaurus + Mamenchisaurus) (new taxon)

1. Marginal tooth denticles absent on posterior edge of crown. [72]
2. Fifteen or more cervical vertebrae (Upchurch, 1995, 1998). [80]
3. Anterior cervical centra height/width approximately 1.25 (Upchurch, 1998). [84]
4. Mid-cervical centra elongate, more than four times longer than the height of their posterior face (Upchurch, 1995, 1998). [86]
5. Mid-cervical neural arches low, shorter than posterior centrum face (He *et al*., 1988). [87]

Jobaria + *Neosauropoda*

1. Preantorbital fenestra (Wilson & Sereno, 1998). [4]
2. Jugal–ectopterygoid contact absent (Wilson & Sereno, 1998). [12]
3. Postorbital ventral process broader transversely than anteroposteriorly (Wilson & Sereno, 1998). [16]
4. Dorsal neural spines with triangular lateral processes (Upchurch, 1995). [102]
5. Anterior caudal neural arches with prespinal lamina (prsl). [123]
6. Anterior caudal neural arches with postspinal lamina (posl). [124]
7. Chevrons disappear by caudal 30. [147]
8. Scapular base with D-shaped cross-section. [154]
9. Metacarpus bound, with long proximal intermetacarpal articular surfaces (Wilson & Sereno, 1998). [175]
10. Metacarpals, proximal end subtriangular, composite proximal articular surface U-shaped (McIntosh, 1990; Upchurch, 1995). [176]
11. Anterior pelvis broad, distance between preacetabular processes exceeds anteroposterior length of ilia (Wilson & Sereno, 1998). [184]
12. Ischial distal shafts flat, nearly coplanar (Gauthier, 1986; Wilson & Sereno, 1998). [195]
13. Tibial proximal condyle subcircular (Wilson & Sereno, 1998). [203]
14. Astragalus with reduced anteromedial corner (Wilson & Sereno, 1998). [210]
15. Astragalar ascending process extending to posterior margin of astragalus (Wilson & Sereno, 1998). [212]

Neosauropoda (Bonaparte, 1986b)

1. Supratemporal fenestrae separated by twice longest diameter of supratemporal fenestra. [24]
2. Pterygoid palatine ramus with stepped dorsal margin. [39]
3. Basisphenoid/basipterygoid recess. [51]
4. External mandibular fenestra closed (McIntosh, 1990; Upchurch, 1995). [58]
5. Marginal tooth denticles absent on both anterior and posterior margins of crown (McIntosh, 1990; Calvo & Salgado, 1995). [72]
6. Chevrons lack 'crus' bridging dorsal margin of haemal canal (Upchurch, 1995). [145]
7. Carpal bones number two or fewer (Wilson & Sereno, 1998). [173]

Macronaria (Wilson & Sereno, 1998)

1. External naris, maximum diameter greater than orbital maximum diameter (McIntosh,

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1990; Upchurch, 1995; Wilson & Sereno, 1998).
[9]

2. Coronoid process on lower jaw (surangular depth more than twice depth of the angular) (Wilson & Sereno, 1998). [59]

3. Surangular ridge separating adductor and articular fossae. [60]

4. Dentary teeth 17 or fewer (Wilson & Sereno, 1998). [73]

5. Posterior dorsal centra opisthocoelous (McIntosh, 1990; Salgado *et al.*, 1997). [105]

6. Longest metacarpal-to-radius ratio 0.45 or more (Salgado *et al.*, 1997). [177]

7. Metacarpal I longer than metacarpal IV (Wilson & Sereno, 1998). [178]

8. Puboischial contact one-half total length of pubis (Gauthier, 1986; Salgado *et al.*, 1997). [191]

Titanosauriformes (Salgado et al*., 1997)*

1. Spongy presacral bone texture (Wilson & Sereno, 1998). [77]

2. Mid-cervical centra elongate, length four times posterior centrum height [86]

3. Dorsal ribs with pneumatic cavities (Wilson & Sereno, 1998). [141]

4. Anterior dorsal ribs plank-like. [142]

5. Metacarpal I distal condyle undivided, phalangeal articular surface reduced (Wilson & Sereno, 1998). [179]

6. Metacarpal I distal condyle oriented perpendicular to axis of shaft. [180]

7. Iliac preacetabular process semicircular (Salgado *et al.*, 1997). [188]

8. Femoral shaft with lateral bulge, proximal one-third deflected medially (McIntosh, 1990; Salgado & Coria, 1993; Calvo & Salgado, 1995; Salgado *et al.*, 1997). [199]

Somphospondyli (Wilson & Sereno, 1998)

1. Reduced cervical neural arch lamination (Wilson & Sereno, 1998). [81]

2. Middle and posterior dorsal neural spines oriented posteriorly (McIntosh, 1990; Wilson & Sereno, 1998). [104]

3. Six sacral vertebrae (one dorsosacral added, Huene, 1929; Wilson & Sereno, 1998). [108]

4. Scapular glenoid strongly bevelled medially (Wilson & Sereno, 1998). [153]

5. Scapular base flat in cross-section (reversal). [154]

6. Humerus with well developed proximomedial corner. [159]

Titanosauria (Bonaparte & Coria, 1993)

1. Cervical pneumatopores (pleurocoels) undivided (reversal). [83]

2. Posterior dorsal neural arches lack hyposphene–hypantrum articulations (Powell, 1986). [106]

3. Anterior caudal centra procoelous (McIntosh, 1990). [118]

4. Anterior and middle caudal centra with ventral longitudinal hollow. [132]

5. Absence of forked chevrons (reversal). [143]

6. Deep haemal canal. [146]

7. Crescentic sternal plates (Huene, 1929; Powell, 1986). [158]

8. Ulnar olecranon process prominent (reversal). [167]

9. Ischial blade platelike, no emargination distal to pubic peduncle. [193]

10. Distal tibia expanded transversely to twice midshaft breadth. [205]

11. Osteoderms. [234]

Nemegtosauridae + ('T.' colberti *+ Saltasauridae)*

1. Paroccipital process with nonarticular ventral process. [44]

2. Middle and posterior dorsal neural arches with divided spinopostzygapophyseal lamina. [100]

3. Middle and posterior caudal vertebrae procoelous. [134]

4. Scapular blade forming a 45° angle with coracoid articulation. [151]

5. Coracoid proximodistally elongate, approximately twice length of scapular articulation. [155]

6. Humeral distal condyles exposed on anterior aspect of shaft. [163]

7. Radius distal breadth approximately twice midshaft breadth. [170]

8. Ischial blade shorter than pubic blade (reversal). [192]

'T.' colberti *+ Saltasauridae*

1. Mid-cervical centra not elongate (reversal). [86]

2. Sacral vertebrae 2–4 contributing to acetabulum. [110]

3. Anterior caudal neural spines transversely broad [126]

4. Stout ulna. [168]

5. Iliac blade orientated perpendicular to body axis (McIntosh, 1990; Salgado & Coria, 1993). [187]

Saltasauridae (Powell, 1992)

1. Biconvex first caudal centrum (Marsh, 1898). [116]

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2. Biconvex distal caudal centra (Huene, 1929; Wilson *et al.*, 1999). [136]
3. Distalmost biconvex caudal centra short (Wilson *et al.*, 1999). [137]
4. Coracoid with rectangular anteroventral margin (Huene, 1929; Powell, 1986). [156]
5. Coracoid with infraglenoid lip. [157]
6. Humeral deltopectoral crest markedly expanded distally. [161]
7. Humeral distal condyles divided (reversal). [164]
8. Distal radius bevelled dorsolaterally. [171]
9. Femoral midshaft transverse diameter at least 185% anteroposterior diameter (Wilson & Carrano, 1999). [198]
10. Femoral distal condyles bevelled dorsomedially (Wilson & Carrano, 1999). [201]
11. Astragalar posterior fossa undivided (reversal). [213]
12. Astragalus pyramidal. [214]

Opisthocoelicaudiinae (McIntosh, 1990)
1. Thirty-five or fewer caudal vertebrae. [114]
2. Caudal transverse processes disappear by caudal 10. [115]
3. First caudal neural arch with coel on lateral aspect of neural spine. [117]
4. Posterior caudal chevrons unfused (open) distally. [148]
5. Scapular base D-shaped. [154]
6. Carpus unossified (Upchurch, 1998). [173]
7. Manual phalanges unossified (Gimenez, 1992; Salgado & Coria, 1993). [181]
8. Loss of osteoderms (reversal). [234]

Saltasaurinae (Powell, 1992)
1. Cervical neural arch lamination well developed. [81]
2. Spongy caudal bone texture (Powell, 1986). [113]
3. Posterior caudal centra dorsoventrally flattened, breadth of posterior centrum at least twice height. [135]
4. Femoral distal condyles exposed on anterior portion of femoral shaft. [202]

Nemegtosauridae (= Nemegtosaurus + Rapetosaurus) (Upchurch, 1995)
1. Posterolateral processes of premaxilla and maxilla without midline contact (reversal). [1]
2. Lacrimal with anterior process (reversal). [11]
3. Parietal occipital process short, less than long diameter of foramen magnum (reversal). [21]
4. Parietal does not contribute to post-temporal foramen. [22]

5. Supratemporal fossa not visible laterally (reversal). [29]
6. Quadrate fossa oriented posterolaterally. [35]
7. Palatobasal contact 'rocker'-like, pterygoid with convex articular surface. [36]
8. Pterygoid with reduced quadrate flange, palatobasal and quadrate articulations approach. [38]
9. Supraoccipital less than height of foramen magnum. [43]
10. Basisphenoid–quadrate contact. [52]
11. Dentary symphysis orientated perpendicular to jaw ramus (Upchurch, 1999). [57]
12. Tooth crowns do not overlap (reversal). [69]
13. Tooth crowns cylindrical in cross-section. [70]

Diplodocoidea (Marsh, 1884; Upchurch, 1995)
1. Cervical ribs shorter than centrum (Berman & McIntosh, 1978). [140]

Rebbachisauridae + (Diplodocidae + Dicraeosauridae)
1. Posterolateral processes of premaxilla and lateral processes of maxilla without midline contact. [1]
2. Premaxillary anterior margin without step (reversal). [2]
3. Parietal excluded from margin of post-temporal fenestra. [22]
4. Elongate basipterygoid processes (Berman & McIntosh, 1978). [46]
5. Basipterygoid processes oriented anteriorly (Calvo & Salgado, 1995). [53]
6. Rectangular-shaped dentary ramus (Berman & McIntosh, 1978). [64]
7. Tooth rows restricted anterior to subnarial foramen. [66]
8. Tooth crowns do not overlap. [69]
9. Cylindrical tooth crowns (Marsh, 1884). [70]
10. More than four replacement teeth per alveolus (Hatcher, 1901). [74]
11. Loss of triangular neural spines (reversal). [102]
12. Anterior caudal neural spines broad. [126]
13. Biconvex distalmost caudal centra (Upchurch, 1998; Wilson *et al.*, 1999). [136]
14. Biconvex caudal centra elongate (Wilson *et al.*, 1999). [137]

Rebbachisauridae (Bonaparte, 1997)
1. Orbital ventral margin rounded (reversal). [10]
2. Postorbital lacks posterior process. [17]

3. Frontal elongate anteroposteriorly, approximately twice transverse breadth (reversal). [20]
4. Supratemporal fenestra reduced or absent. [25]
5. Teeth with longitudinal grooves on lingual aspect. [76]
6. 'Petal'-shaped posterior dorsal neural spines. [107]
7. Racquet-shaped scapular blade (Lavocat, 1954; Calvo & Salgado, 1995). [152]
8. Humerus with circular midshaft cross-section. [162]

Diplodocidae + Dicraeosauridae
1. Subnarial foramen and anterior maxillary foramen separated by narrow bony isthmus. [5]
2. Vomer articulates with maxilla (reversal). [42]
3. Dentary with sharply projecting triangular process or 'chin' (Wilson & Smith, 1996). [56]
4. Dentary teeth 17 or fewer. [73]
5. Low-angled planar wear facets (Calvo, 1994). [68]
6. Atlantal intercentrum expanded anteroventrally. [79]
7. Anterior cervical neural spines bifid (McIntosh, 1990). [85]
8. Posterior cervical and anterior dorsal neural spines bifid (McIntosh, 1990). [89]
9. Medial tubercle between bifid neural spines [90]
10. Anterior dorsal neural arches with divided centropostzygapophyseal lamina (cpol). [95]
11. Sacral neural spines approximately four times length of centrum. [111]
12. Anterior caudal neural arches with spinoprezygapophyseal lamina (sprl) on lateral aspect of neural spine (Wilson, 1999a). [121]
13. Anterior caudal vertebrae with 'wing-like' transverse processes (Berman & McIntosh, 1978). [128]
14. Chevrons with proximal 'crus' bridging dorsal margin of haemal canal. [145]
15. Pubis with prominent ambiens process (McIntosh, 1990). [189]
16. Triangular distal ischial shaft cross-section (reversal). [194]
17. V-shaped distal ischial distal shafts (reversal). [195]
18. Metatarsal I distal condyle with posterolateral projection (Berman & McIntosh, 1978; McIntosh, 1990). [220]

Diplodocidae (Marsh, 1884)
1. Antorbital fenestra subequal to orbital maximum diameter. [6]
2. External nares retracted above orbit, dorsally facing (Marsh, 1898). [8]

3. Jugal with large contribution to antorbital fenestra (Upchurch, 1998). [13]
4. Prefrontal elongate, approaching parietal. [15]
5. Squamosal–quadratojugal contact absent. [31]
6. Quadrate fossa shallow (reversal). [34]
7. Pterygoid flange positioned anterior to antorbital fenestra (Upchurch, 1998). [37]
8. Fifteen or more cervical vertebrae (Huene, 1929; Berman & McIntosh, 1978). [80]
9. Middle and posterior cervical neural arches with divided centroprezygapophyseal lamina (cprl). [88]
10. Ten or fewer dorsal vertebrae (Huene, 1929; Berman & McIntosh, 1978). [91]
11. Middle and posterior dorsal neural arches with posterior centroparapophyseal lamina (pcpl). [98]
12. Procoelous caudal centrum 1. [116]
13. Anterior caudal neural arches with spinoprezygapophyseal lamina (sprl)-spinoprezygapophyseal lamina (sprl) contact on lateral aspect of neural spine (Wilson, 1999a). [122]
14. Anterior caudal transverse processes with diapophyseal laminae (acdl, pcdl, prdl, podl) (Wilson, 1999a). [129]
15. Anterior caudal transverse processes with divided anterior centrodiapophyseal lamina (acdl). [130]
16. Thirty or more biconvex caudal centra (Wilson *et al*., 1999). [138]

Dicraeosauridae (Huene, 1927)
1. Frontals fused in adults (Salgado & Calvo, 1992). [19]
2. Postparietal foramen (Salgado & Calvo, 1992). [23]
3. Supratemporal fenestra smaller than foramen magnum (Salgado & Calvo, 1992). [27]
4. Crista prootica with enlarged 'dorsolateral process' (Salgado & Calvo, 1992). [45]
5. Basipterygoid processes with little distal divergence. [47]
6. Basal tubera narrower than occipital condyle. [49]
7. Dorsal neural spines approximately four times centrum length (McIntosh, 1990; Salgado & Calvo, 1992). [93]
8. 'Petal' shaped posterior dorsal neural spines. [107]

Diplodocinae (Marsh, 1884; Janensch, 1929b)
1. Elongate mid-cervical centra. [86]
2. Procoelous anterior caudal vertebrae. [118]

3. Anterior caudal centra with pneumatopores (pleurocoels). [119]
4. Caudal centrum length doubles over first 20 vertebrae. [120]
5. Anterior and middle caudal centra flat ventrally and laterally. [131]
6. Anterior and middle caudal centra with ventral longitudinal hollow (Marsh, 1895). [132]
7. Middle caudal neural spines vertical. [133]

APPENDIX 4

AUTAPOMORPHIES

The autapomorphies diagnosing each sauropod terminal taxon are listed below. Bracketed numbers (characters listed in Appendix 1) refer to homoplastic autapomorphies resolved the phylogenetic analysis. Other listed features are unique autapomorphies that were not included in the analysis.

Vulcanodon karibaensis *(Raath, 1972)*
1. Middle caudal centra with ventral hollow. [132]
2. Marked dorsoventral flattening of the unguals of pedal digits II and III (Wilson & Sereno, 1998).

Barapasaurus tagorei *(Jain* et al., *1975)*
1. Posterior dorsal vertebrae with slit-shaped neural canal (Jain *et al.*, 1979).
2. Middle and posterior dorsal neural arches with 'infradiapophyseal' pneumatopore opening into the neural canal (Jain *et al.*, 1979). [103]
3. Fibular distal condyle broad transversely. [209]

Shunosaurus lii *(Dong* et al., *1983)*
1. Strap-shaped pterygoid.
2. Marginal tooth denticles absent on both anterior and posterior margins of crown. [72]
3. Anterior portion of the axial neural spine prominent (Wilson & Sereno, 1998).
4. Anterior cervical centra height/width = 1.25 (Upchurch, 1998). [84]
5. Thirteen dorsal vertebrae. [91]
6. 'Postparapophyses' on posterior dorsal vertebrae (Wilson & Sereno, 1998).
7. Chevrons lack 'crus' bridging dorsal margin of haemal canal. [145]
8. Chevrons disappear by caudal 30. [147]
9. Terminal tail club composed of at least three enlarged, co-ossified caudal vertebrae with two dermal spines (Zhang, 1988).
10. Ulnar proximal condylar processes subequal in length. [166]

11. Metacarpal I distal condyle perpendicular to axis of shaft. [180]
12. Metatarsal I proximal condyle angled relative to axis of shaft. [218]

Patagosaurus fariasi *(Bonaparte, 1979)*
1. Cervical vertebrae with elongate centroprezygapophyseal laminae and 'hooded' infra-prezygapophyseal coels.
2. Anterior dorsal vertebrae with elongate centropostzygapophyseal and postzygodiapophyseal laminae.
3. Middle and posterior dorsal neural arches with 'infradiapophyseal' pneumatopore opening into the neural canal (Jain *et al.*, 1979; Bonaparte, 1986b). [103]
4. Transversely narrow third sacral vertebra.
5. Proximal humerus with median ridge on posterior aspect.
6. Humeral distal condyles exposed on anterior aspect of shaft. [163]
7. Tibial cnemial crest projects anteriorly (reversal). [204]

Mamenchisaurus *(Young, 1954)*
1. Presacral bone spongy. [77]
2. Middle and posterior dorsal neural arches with divided centroprezygopophyseal lamina (cprl). [88]
3. Accessory prezygodiapophyseal lamina in anterior dorsal vertebrae.
4. Posterior cervical and anterior dorsal neural spines bifid. [89]
5. Anterior caudal centra procoelous. [116, 118]
6. 'Forked' chevrons in mid-caudal region with anterior and posterior projections oriented less than 45 ° to each other.
7. Ulna with anterior arm of proximal condyle nearly one-half the length of shaft.
8. Femur with medially expanded tibial condyle.
9. Proximal half of femoral shaft broader than distal half.
10. Tibial proximal condyle subcircular. [203]
11. Fibular distal condyle broad transversely. [209]
12. Astragalar ascending process extending to posterior margin of astragalus. [212]

Omeisaurus *(Young, 1939)*
1. Maxillary ascending ramus with dorsoventrally expanded distal end (Wilson & Sereno, 1998).
2. Dentary teeth 17 or fewer. [73]
3. Distalmost caudal chevrons fused to anteriormost portion of ventral centrum.

4. Ulnar proximal condylar processes subequal in length. [166]
5. Femoral distal condyles subequal in breadth. [200]
6. Metatarsal I distal condyle with posterolateral projection. [220]

Apatosaurus *(Marsh, 1877)*
1. Basisphenoid/basipterygoid recess absent (reversal). [51]
2. Atlantal neural arch pierced by foramen.
3. Cervical ribs projecting well below and lateral of centrum (total height of cervical vertebrae exceeding length).
4. Posterior process of rib subequal in length to diapophysis and tuberculum.
5. Posterior process of cervical ribs has rounded lateral process distally.
6. Scapular glenoid bevelled medially. [153]
7. Ulnar proximal condylar processes subequal in length. [166]
8. Medial cotylus of astragalus without foramina.
9. Calcaneum absent. [215]
10. Stout metatarsal I.
11. Pronounced ligament scars on distolateral metatarsals II–IV.

Barosaurus lentus *(Marsh, 1890)*
1. Accessory spinodiapophyseal laminae in posterior dorsal neural arches.
2. Anterior caudal neural spines with lateral projection at intersection of spinoprezygapophyseal and spinopostzygapophyseal laminae.
3. Middle caudal vertebrae with distally rounded neural spines.

Brachiosaurus *(Riggs, 1903)*
1. Elongate, boot shaped snout.
2. Supratemporal fenestra not visible laterally.
3. Parietals broad transversely, supratemporal fenestra separated by twice their maximum length. [24]
4. Squamosal-quadratojugal contact absent. [31]
5. Basioccipital depression between foramen magnum and basal tubera. [50]
6. Splenial posterior process separating anterior portions of angular and prearticular. [62]
7. Coronoid absent. [64]
8. Tooth crowns do not overlap (reversal). [69]
9. Elongate cervical centra (L:W > 6).
10. Middle and posterior dorsal neural arches with posterior centroparapophyseal lamina (pcpl). [98]

11. Tall anterior dorsal neural spines.
12. Transverse process of first caudal vertebra with prominent ventral bulge.
13. Prominent prdl on anterior caudal vertebrae.
14. Base of scapula deep below acromion.
15. Scapular blade with rounded expansion on acromial side. [152]
16. Humerus longer than femur.
17. Proximal humerus strongly canted medially with lateral margin straight.
18. Proximal radius broad transversely (subequal to anteroposterior length).
19. Manual phalanx I.1 rectangular (reversal). [182]
20. Pubis with low anterior crest at level of obturator foramen.
21. Ischium with flat and abbreviate pubic peduncle.
22. Ischium with lateral tubercle.
23. Ischium with relatively small contribution to acetabulum.
24. Fibular shaft straight (no sigmoid curvature).
25. Fibula with broadly expanded distal condyle [209].

Camarasaurus *(Cope, 1877)*
1. Lacrimal with long axis directed anterodorsally (Wilson & Sereno, 1998).
2. Quadratojugal with short anterior ramus that does not extend anterior to the laterotemporal fenestra (Wilson & Sereno, 1998).
3. Quadratojugal anterior process shorter than dorsal process (reversal). [32]
4. Pterygoid with dorsomedially orientated basipterygoid hook. [36]
5. Conspicuous groove passing anteroventrally from the surangular foramen to the ventral margin of the dentary (Wilson & Sereno, 1998).
6. Splenial posterior process separating anterior portions of angular and prearticular. [62]
7. Twelve cervical vertebrae (reversal). [80]
8. Anterior cervical neural spines bifid. [85]
9. Posterior cervical and anterior dorsal neural spines bifid. [89]
10. Anterior caudal neural spines broad transversely. [126]
11. Forked chevrons restricted to distal tail (reversal). [144]
12. Scapular blade with rounded expansion on acromial side. [152]
13. Ischial blade directed posteriorly so that the long axis of its shaft passes though the pubic peduncle (Wilson & Sereno, 1998).
14. Fibula with proximodistally deep (one-half shaft length) tibial scar (Wilson & Sereno, 1998).

Dicraeosaurus *(Janensch, 1914)*

1. Premaxilla with anteroventrally orientated vascular grooves originating from an opening in the maxillary contact.
2. Lacrimal anterior process present (reversal). [11]
3. Pterygoid with dorsomedially oriented basipterygoid hook. [36]
4. Twelve cervical vertebrae (reversal). [80]
5. Middle and posterior dorsal neural arches lack prezygoparapophyseal lamina (prpl) (reversal). [97]
6. First caudal vertebra procoelous. [116]
7. Anterior caudal vertebrae with prespinal and postspinal laminae projecting above level of spine.
8. Middle to distal caudal neural spines extending well beyond posterior margin of centrum.
9. Humerus with pronounced proximolateral corner.
10. Ischium with lateral fossa at base of shaft, femoral head abbreviate.
11. Femur with large nutrient foramen opening anteriorly near midshaft.

Diplodocus *(Marsh, 1878)*

1. Preantorbital fenestra with sharply defined fossa.
2. Dorsal process of maxilla tongue-shaped (antorbital fenestra with concave dorsal margin).
3. Dorsal process of maxilla extending further posteriorly than does body of maxilla.
4. Vomer not contacting premaxilla.
5. Pterygoid medial to ectopterygoid on transverse palatal hook.
6. Intercoronoid not ossified.
7. Surangular ridge separating adductor and articular fossae present. [60]
8. Teeth orientated anteriorly relative to jaw ramus. [75]
9. Posterior cervical vertebrae with convex, transversely broad (three times anteroposterior length) prezygapophyses.
10. Posterior cervical neural arches with accessory spinal lamina running vertically just posterior to spinoprezygapophyseal lamina.
11. Posterior cervical and anterior dorsal vertebrae with ligament attachment scar on lateral aspect of postzygapophysis.
12. Anterior and mid-dorsal vertebrae with circular ligament attachment scars on the dorsal surfaces of diapophyses and on lateral aspect of distal neural spine.
13. Anterior caudal vertebrae with concavo–convex zygapophyseal articulation.

14. Femoral distal condyles expanded onto anterior portion of shaft. [202]

Haplocanthosaurus *(Hatcher, 1903)*

1. Thirteen dorsal vertebrae (reversal). [91]
2. Dorsal neural arches with elongate centropostzygapophyseal laminae (Wilson & Sereno, 1998).
3. Dorsal diapophyses projecting dorsolaterally at 45° and approaching the height of the neural spines (Wilson & Sereno, 1998).
4. Scapular acromion process narrow. [150]
5. Scapular blade with a dorsally and ventrally expanded distal end (Wilson & Sereno, 1998).

Amargasaurus cazaui *(Salgado & Bonaparte, 1991)*

1. Multiple foramina leading into endocranial cavity in a depression located between the supraoccipital and exoccipital.
2. Basioccipital depression between foramen magnum and basal tubera. [50]
3. Marked ventral excavation of paroccipital processes.
4. Basal tubera fused to one another (Salgado & Bonaparte, 1991).
5. Presacral pneumatophores (pleurocoels) absent (reversal). [78]
6. Extremely elongate cervical neural spines (Salgado & Bonaparte, 1991).
7. Ten or fewer dorsal vertebrae. [91]
8. First dorsal vertebra with fused diapophysis and parapophysis.
9. Ulnar proximal condylar processes subequal in length. [166]

Euhelopus zdanskyi *(Wiman, 1929)*

1. Preantorbital fenestra absent (reversal). [4]
2. Quadrate fossa shallow (reversal). [34]
3. Procumbent teeth with asymmetrical enamel (i.e. the anterior crown-root margin is closer to the apex of the crown) (Wilson & Sereno, 1998).
4. Well developed crown buttresses on lingual crown surface (Wilson & Sereno, 1998).
5. Presacral neural spines with divided coel above the 'prezygapophyseal–postzygapophyseal' lamina (Wilson & Sereno, 1998).
6. Fifteen or more cervical vertebrae. [80]
7. Anterior cervical centra height/width = 1.25 (Upchurch, 1998). [84]
8. Anterior cervical vertebrae with three costal spurs (on diapophysis, tuberculum, and capitulum.

9. Posterior cervical and anterior dorsal neural spines bifid. [89]
10. Median tubercle between bifid spines. [90]
11. Thirteen dorsal vertebrae (reversal). [91]
12. Middle and posterior dorsal neural arches with posterior centroparapophyseal lamina (prpl). [98]
13. Broadly expanded acromion process of scapula.
14. Puboischial contact only one-third length of pubis (reversal). [191]

Jobaria tiguidensis *(Sereno* et al., *1999)*
1. External nares larger than orbit. [9]
2. Dentary anterior depth slightly less than that of dentary at midlength (reversal). [55]
3. Cervical prezygapophyses with anterior prong located below articular facet (Sereno *et al*., 1999).
4. Cervical neural arches with pronounced coel between centropostzygapophyseal and intrapostzygapophyseal laminae (Sereno *et al*., 1999).
5. Cervical ribs with secondary anterior projection.
6. Dorsal prezygapophyses with ventral flange below prezygapophyses (Sereno *et al*., 1999).
7. Dorsal neural arches with well developed, paired coels below diapophysis (Sereno *et al*., 1999).
8. Middle and posterior dorsal neural arches with posterior centroparapophyseal lamina (pcpl). [98]
9. U-shaped first caudal chevron (Sereno *et al*., 1999).
10. Anterior caudal neural spines with circular depression at base of prespinal lamina (Sereno *et al*., 1999).
11. Middle caudal chevrons with pronounced ligamentous scar encircling distal end (Sereno *et al*., 1999).
12. Scapular blade with rounded expansion on acromial side. [152]

Malawisaurus dixeyi *(Haughton, 1928)*
1. Abbreviate premaxillary portion of snout, dentary arched ventrally.
2. Surangular notch and groove on dentary.
3. Posterior dorsal neural arches with enlarged coel between anterior centroparapophyseal lamina and posterior centrodiapophyseal lamina.
4. Posterior dorsal neural arches with pronounced pneumatization on posterior aspect of diapophysis and lateral aspect of neural spine.
5. Anterior caudal neural arches with postspinous fossa. [125]

6. Ulnar proximal condylar processes subequal (reversal). [166]

Nigersaurus taqueti *(Sereno* et al. *1999)*
1. Dentary tooth row extends laterally beyond mandibular ramus.
2. Dentary symphysis subcircular, Meckel's canal exposed ventrally on dentary.
3. Marked increase in number of dentary teeth.
4. Tooth row restricted to transverse portion of dentary.
5. Reduced enamel thickness on lingual aspect of crown.

Rayososaurus *(Bonaparte, 1996)*
6. Extremely reduced lateral temporal fenestra.
7. Supraoccipital height less than that of foramen magnum. [43]
8. Basal tubera sheet-like. [48]
9. Basioccipital depression between foramen magnum and basal tubera. [50]
10. Cervical neural arches with accessory lamina extending from the postzygodiapophyseal lamina anterodorsally (Calvo & Salgado, 1995).
11. Anterior caudal transverse processes composed of two lateral bars (Calvo & Salgado, 1995).
12. Sternal plates crescent-shaped. [158]
13. Metatarsal I proximal condyle oriented perpendicular axis of shaft (reversal). [218]
14. Metatarsal I distal condyle oriented perpendicular to axis of shaft (reversal). [219]

Rebbachisaurus garasbae *(Lavocat, 1954)*
1. Dorsal neural arches deep below zygapophyses.
2. Dorsal neural arches with accessory 'centrodiapophyseal' laminae uniting the anterior centrodiapophyseal and centropostzygapophyseal laminae.
3. Dorsal neural arches with accessory centroprezygapophyseal laminae below the prezygapophysis.
4. Dorsal neural arches with thin, platelike anterior centroparapophyseal, posterior centrodiapophyseal, and spinodiapophyseal laminae.
5. Dorsal neural spines elongate. [93]
6. Middle and posterior dorsal neural arches with posterior centroparapophyseal lamina (pcpl). [98]
7. Posterior dorsal neural arches lack hyposphene–hypantrum articulations. [106]
8. Dorsal neural spines with irregular coels located alongside prespinal and postspinal laminae.

9. Dorsal neural spines with accessory spinopostzygapophyseal laminae.

Alamosaurus sanjuanensis *(Gilmore (1922)*
1. Anterior and middle caudal vertebrae with several foramina opening at base of transverse process.
2. Posterior caudal vertebrae with notched ventral margins on anterior and posterior centrum faces.
3. Ulnar shaft not stout (reversal). [168]

Nemegtosaurus mongoliensis *(Nowinski, 1971)*
1. Symphyseal eminence on external aspect of premaxillae.
2. Premaxilla and maxilla with sinuous contact.
3. Anterior process of the maxilla dorsoventrally deep.
4. Tooth bearing portion of snout highly vascularized, delimited by transverse groove.
5. Palatal shelf on maxilla enclosed to form 'maxillary canal'.
6. Postorbital, prefrontal, and frontal with orbital ornamentation.
7. Prefrontal diverges laterally; skull roof broadest across prefrontals.
8. Postorbital with deep posterior process.
9. Squamosal excluded from supratemporal fenestra.
10. Ectopterygoid and palatine fused (or one element has been lost) (Nowinski, 1971).
11. Pterygoid with tongue-and-groove articulation with ectopterygoid–palatine.
12. Quadratojugal with sinous ventral margin.
13. Basal tubera sheet-like. [48]
14. Basisphenoid/basipterygoid recess absent (reversal). [51]
15. Intercoronoid partially fused to dentary.
16. Dentary with weak, anteroposteriorly narrow symphysis.
17. Dentary teeth smaller in diameter than premaxillary and maxillary teeth.

Neuquensaurus *(Powell, 1986)*
1. Anteriormost dorsal vertebrae lacking centroprezygapophyseal (cprl) and centropostzygapophyseal (cpol) laminae.
2. Fibula with strong lateral tuberosity and bent shaft (Powell, 1986).

Opisthocoelicaudia skarzynskii *(Borsuk-Bialynicka, 1977)*
1. Anterior dorsal neural spines bifid. [89]
2. Eleven dorsal vertebrae. [91]

3. Dorsal neural arches lacking postzygodiapophyseal lamina
4. Dorsal neural arches with enlarged coel between posterior centrodiapophyseal lamina (pcdl), spinodiapophyseal lamina (spdl), and centropostzygapophyseal lamina (cpol).
5. Middle and posterior dorsal neural arches with posterior centroparapophyseal lamina (pcpl). [98]
6. Opisthocoelous caudal centra (Borsuk-Bialynicka, 1977). [116, 118, 134]
7. Anterior caudal prezygapophyses and postzygapophyses connect above transverse process.
8. Anterior caudal chevrons 1–4 unfused distally.
9. Chevrons disappearing after caudal 19 (Borsuk-Bialynicka, 1977).
10. Scapular blade perpendicular to coracoid articulation (reversal). [151]
11. Scapulocoracoid strongly arched medially.
12. Femoral fourth trochanter positioned distal to midshaft.
13. Calcaneum absent. [215]
14. Pedal digit I ungual subequal in length to that of digit II (reversal). [229]

Rapetosaurus krausei *(Curry Rogers & Forster, 2001)*
1. Premaxilla without anterior step (reversal). [2]
2. Maxilla with posteriorly elongate jugal process, creating an anteroposteriorly elongate antorbital fenestra (Curry Rogers & Forster, 2001; considered two characters by those authors).
3. Antorbital fenestra diameter subequal to that of orbit. [6]
4. Frontal with median bulge (Curry Rogers & Forster, 2001).
5. Frontal contributes to supratemporal fossa (reversal). [18]
6. Basipterygoid process angle of divergence less than 30°. [47]
7. Dentary anterior depth slightly less than that of dentary at midlength (reversal). [55]
8. Dorsal neural arches with reduced zygapophyses that have weak facets and do not project beyond the vertebra.
9. Humeral distal condyle flat (reversal). [164]
10. Pubis twice length of ischium (Curry Rogers & Forster, 2001).
11. Femoral distal condyles expanded onto anterior aspect of shaft. [202]

Saltasaurus *(Bonaparte & Powell, 1980)*
1. Frontal with bulge near mid-orbit.
2. Basal tubera sheet-like. [48]

3. Basioccipital depression between foramen magnum and basal tubera. [50]
4. Cervical pneumatopores (pleurocoels) divided. [83]
5. Cervical prezygapophyses low and wide.
6. Cervical parapophyses broad anteroposteriorly and extending the length of centrum.
7. Cervical neural spines low.
8. Cervical ribs with tuberculum–capitulum angle less than 30°.
9. Middle and posterior cervical neural arches with divided centroprezygapophyseal lamina (cprl). [88]
10. Middle and posterior dorsal neural arches with posterior centroparapophyseal lamina (pcpl). [98]
11. Anterior caudal neural arches with postspinous fossa. [125]
12. Scapula with medial tuberosity on acromial side.
13. Interosseous ridge on radius.
14. Acetabulum facing ventrolaterally and broadening anteriorly.
15. Pubic peduncle of ilium broad transversely.
16. Pubis with small contribution to acetabulum.
17. Ventral ridge on pubis.
18. Femur with vertically oriented posterior crest on proximal half of shaft.

'Titanosaurus' colberti *(Jain & Bandyopadhyay, 1997)*
1. Cervical centra broader than long.
2. Anteroposteriorly elongate cervical parapophyses.
3. Cervical neural arches with prespinal and postspinal laminae (Wilson, 1999a).
4. Cervical neural arches with divided cpol.
5. Anteriormost dorsal vertebra with pronounced coel between prezygodiapophyseal (prdl), centroprezygapophyseal (cprl), and anterior centrodiapophyseal laminae (acdl).
6. Middle and posterior dorsal neural spines not flaring distally (reversal). [102]
7. Posterior dorsal neural arches with parapophyses positioned above level of prezygapophyses.
8. Anteroposteriorly compressed distal caudal chevron blades.
9. Scapular acromion process narrow (reversal). [150]