The phylogenetic relationships of sauropod dinosaurs

PAUL UPCHURCH

School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG

A data-matrix of 205 osteological characters for 26 sauropod taxa is subjected to cladistic analysis. Two most parsimonious trees are produced, differing only in the relationships between *Euhelopus, Omeisaurus* and *Mamenchisaurus*. The monophyly of the Euhelopodidae (including *Shunosaurus*) is supported by seven synapomorphies. The Cetiosauridae (*Patagosaurus, Cetiosaurus* and *Haplocanthosaurus*) is paraphyletic with respect to the Neosauropoda. The latter clade divides into two major radiations—the 'Brachiosauria' (*Camarasaurus,* brachiosaurids and titanosauroids), and the Diplodocoidea (nemegtosaurids, dicraeosaurids, diplodocids and *Rebbachisaurus*). Further evidence for the inclusion of *Opisthocoelicaudia* in the Titanosauroidea is presented. *Phuwiangosaurus,* a problematic sauropod from Thailand, may represent one of the most plesiomorphic titanosauroids. 'Peg'-like teeth have evolved at least twice within the Sauropoda. The postspinal lamina, on the neural spines of middle and caudal dorsal vertebrae, represents a neomorph rather than a fusion of pre-existing structures. Forked chevrons may have evolved convergently in the Euhelopodidae and the diplodocid-dicraeosaurid clade, or they may have been acquired early in sauropod evolution and subsequently lost in the 'Brachiosauria'. The strengths and weaknesses of the data-matrix and tree topologies are explored using bootstrapping, decay analysis and randomization tests. Several nodes are only poorly supported, but this seems to reflect the large proportion of missing data in the matrix ($\sim 46\%$), rather than an abnormally high level of homoplasy. The results of the randomization tests indicate that the data-matrix probably contains a strong phylogenetic 'signal'. The relationships of some forms, such as *Haplocanthosaurus,* are influenced by the inclusion or exclusion of certain taxa with unusual combinations of character states. Such a result suggests that there are dangers inherent in the view that 'higher' level sauropod phylogeny can be accurately reconstructed using only a small number of well-known taxa.

CONTENTS

INTRODUCTION

The phylogenetic relationships of sauropod dinosaurs have received relatively little attention. Such neglect has been caused, in part, by the frustratingly fragmentary preservation of most sauropod remains. Indeed, the absence of well preserved material is often cited as a major obstacle to the accurate reconstruction of sauropod evolutionary history (McIntosh, 1990a; Madsen, McIntosh & Berman, 1995). Furthermore, the large size of much sauropod material makes the collection of anatomical data both laborious and time-consuming. Nevertheless, several recent cladistic analyses (Yu, 1990; Wilson & Sereno, 1994; Calvo & Salgado, 1995; Upchurch, 1995) suggest that some phylogenetic 'signal' can be detected for the Sauropoda. These studies have contributed several important insights into sauropod phylogeny, but all suffer from the disadvantage that they provide detailed consideration of only a minority of the available characters. At present, the most complete published data-sets on the Sauropoda are the 49 characters listed by Calvo & Salgado (1995) and the 125 synapomorphies summarized by Upchurch (1995). Failure to utilize and/or present all available characters can impede replication of the results by other workers, and may increase the probability that tree topologies are 'incorrect'. The majority of work in this area has attempted to examine the 'higher' level phylogenetic relationships of sauropods by concentrating on a relatively small number (15 genera or fewer) of well-known taxa. Some of the less perfectly preserved sauropods, however, possess unusual combinations of character states. The inclusion or exclusion

of such taxa could have a profound effect on tree topology (Smith, 1994). Therefore, the main aims of the current work are: (i) construction of a sauropod data-matrix based on an increased number of taxa (26 genera) and a virtually exhaustive list of available characters; (ii) analysis of the data-matrix in order to produce a robust tree topology; (iii) testing of the tree topologies in order to assess the strengths and weaknesses of the relationships; (iv) re-assessment of sauropod phylogenetic relationships, systematic classification and morphological evolution in the light of the new results.

ABBREVIATIONS

Anatomy. Cd = caudal vertebra; Cv = cervical vertebra; D = dorsal vertebra; S = sacral vertebra.

Institutions. BPI = Bernard Price Institute, Johannesburg; BYU = Earth Sciences Museum, Brigham Young University, Provo; CMNH = Carnegie Museum of Natural History, Pittsburgh; FMNH = Field Museum of Natural History, Chicago; HMN = Humboldt Museum für Naturkunde, Berlin; IVPP = Institute for Vertebrate Paleontology and Paleoanthropology, Beijing; LCM = Leicester City Museum and Art Gallery, Leicester; MACN = Museo Argentino de Ciencias Naturales, Buenos Aires; MNHN = Museum National d'Histoire Naturelle, Paris; MUCPv = Museo de Ciencias Naturales, Universidad Nacional del Comahue, Argentina; PMU = Paleontological Museum, Uppsala; PVL = Instituto Miguel Lillo de la Universidad de Tucuman, Tucuman; SAM = South African Museum, Cape Town; SMNS = Staatliches Museum für Naturkunde, Stuttgart; USNM = United States National Museum of Natural History, Washington D.C.; ZDM = Zigong Dinosaur Museum, Zigong; Z.Pal. = Paleozoological Institute of the Polish Academy of Sciences, Warsaw.

Measurements (see 'Methods'). EI = elongation index; SI = slenderness index.

MATERIALS

The data-matrix (Appendix 1) consists of 205 osteological characters for 26 sauropod genera. The choice of taxa has been partly dictated by the completeness of their anatomy. In addition, taxa with 'unusual' combinations of character states (e.g. *Phuwiangosaurus*), and/or those which provide important stratigraphic and geographic representation, have also been favoured. Some of these genera have problematic taxonomics at the species level, necessitating some decision regarding which specimens will represent the genus in this analysis. These decisions, and the sources of data on the various genera, are summarized in Appendix 2.

METHODS

Many stages in cladistic analysis require the systematist to make assumptions or reach subjective decisions. For example, there are different ways of determining character state polarities, coding multistate characters, weighting character state

transformations, and so on. It is not surprising, therefore, that different workers often produce different cladograms from essentially similar data. The assumptions underlying the current analysis are presented below in an attempt to facilitate replication and revision of this study by other workers.

Multistate characters

Several of the characters used in this analysis possess three or more states. It is important to justify the decision to make such multistate characters 'ordered' or 'unordered', since this may have ramifications for the resulting tree topologies. Ordered characters are often perceived as involving more *a priori* assumptions about character evolution. Several authors, therefore, have suggested that multistate characters should be left unordered, and the tree topology should then be used to determine character state transformation series (Hauser, 1992; Smith, 1994). Alternatively, ordered multistate characters may have greater explanatory value (i.e. explanation of the similarity shared by derived states) and the use of such ordering is supported by 'Hennig's auxiliary principle' (Mickevich & Weller, 1990; Wilkinson, 1992a). In this analysis, the following strategy is used:

(i) Multistate characters are unordered unless one or more states can be identified as structurally intermediate (the 'method of intermediates' discussed by Wilkinson, 1992a).

(ii) Ordered multistate characters are coded using additive binary coding (Farris, Kluge & Eckardt, 1970). This method is operationally equivalent to the use of an ordered multistate character coded within a single column. Additive binary coding, however, has the advantage that it can increase the information content of the matrix when missing data is common. For example, the exact number of cervical vertebrae in *Cetiosaurus* is unknown, but it seems very probable that there were at least 12 cervicals. If only a single column is used to code for the character 'number of cervical vertebrae', *Cetiosaurus* would be given state '?'. Additive binary coding assigns state '1' for 'at least 12 cervical vertebrae present', and state '?' for the remaining columns which deal with higher numbers of vertebrae.

(iii) The effect of using ordered or unordered multistate characters is assessed (see 'Analyses and results', pp. 73–80).

Variable characters

'Variable' or 'continuous' characters have often played a significant role in cladistic analyses of dinosaur relationships. Exactly how continuous variation in a character should be subdivided into two or more discrete states is often problematic, although some 'rules of thumb' are available (Smith, 1994: 38–39). The simplest method for coping with variable characters is the use of ratios between two parameters. Such ratios are fraught with difficulties, including: (i) the denominator (e.g. a basic measurement such as skull or femur length) may itself show phylogenetically related variation; (ii) errors may be caused by ontogenetic variation, which cannot be accurately studied in groups known from small sample sizes; and (iii) potential over-weighting of some of the variation (e.g. sauropods possess numerous structures in the skull which are relatively small compared to overall body size). Ideally, variable

Pterosauria
Scleromochlus
Lagerpeton
Marasuchus
Pseudolagosuchus
Ornithischia
Eoraptor
Herrerasauridae
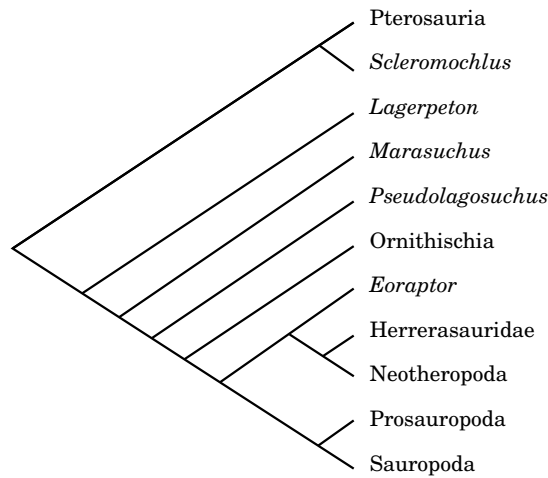Neotheropoda
Prosauropoda
Sauropoda

Figure 1. Cladogram showing the relationships between the Sauropoda and the outgroups, based on Novas (1996) and references therein.

characters should be examined using more advanced statistical techniques, such as Principal Components Analysis or some form of 'landmark' analysis (Chapman, 1990; Weishampel & Chapman, 1990). The application of such techniques to the Sauropoda, however, would represent a major project which lies outside the scope of the current study. In this analysis, therefore, simple ratios are employed because of their ease of use and their direct comparability with the characters used in the vast majority of studies on dinosaur relationships. Such ratios may be an inadequate way to represent continuous variation, but they can at least help to pin-point phylogenetically informative variation which can be scrutinized more rigorously in subsequent morphometric analyses.

Two standard ratios are defined here. The Elongation Index ('EI') is the length of a vertebral centrum divided by the width across its caudal face. The Slenderness Index ('SI') is the length of the tooth crown divided by its maximum mesiodistal width.

Character state polarity

Outgroup comparisons are used in order to polarise character state transformations. The 'rules' for outgroup comparison proposed by Maddison, Donoghue & Maddison (1984) produce the most globally parsimonious solutions and are employed here. Prosauropods, theropods, ornithischians, *Pseudolagosuchus*, *Marasuchus*, *Lagerpeton* and Pterosauria are taken as successively more distant outgroups to the Sauropoda (Fig. 1). The resulting character state polarities are represented in the analysis by the hypothetical taxon 'Ancestor', which is given the plesiomorphic state for each character.

Software

The software utilized in the cladistic analyses, and the post-analysis exploration of the data, includes: PAUP version 3.1.1 (Swofford, 1993), Autodecay (Erikson &

Wikström, 1996), reduced consensus and randomisation programs (the latter two are available at http:www.610.brs.ac.uk/research/markwilk/software/.htm.).

<div align="center">CHARACTER DESCRIPTION AND DISCUSSION</div>

<div align="center">*Format*</div>

This character description follows a logical anatomical order, starting with the cranium, and then working along the axial and appendicular skeletons. Each character is designated by 'C' plus a number (i.e. 'C33' refers to the character coded in the 33rd column of the data-matrix). The references cited with a particular character relate to sources of further information and/or illustrations; they do not necessarily provide a comprehensive list of those works which have mentioned or employed the character. 'Modified' indicates characters cited elsewhere which have had their definitions, state distributions and/or polarities altered.

In order to keep this section to a reasonable length, only those characters which are new, complex or particularly controversial, will be discussed in detail.

<div align="center">*External features of the skull (C1–C37)*</div>

C1. Rostral end of snout in dorsal view: is acute (0); is broad and rounded (1).

C2. Caudal rim of external naris: lies rostral to the rostral margin of the antorbital fenestra (0); lies caudal to the rostral margin of the antorbital fenestra (1) (McIntosh, 1990b; Upchurch, 1994a) (Fig. 2).

C3. Rostral rim of external naris: lies in front of the rostral margin of the antorbital fenestra (0); lies caudal to the rostral margin of the antorbital fenestra (1) (McIntosh, 1990b; Upchurch, 1994a) (Fig. 2).

C4. External nares; face laterally or rostrolaterally (0); face dorsally or rostrodorsally (1) (Upchurch, 1995).

C5. Greatest length of external naris divided by skull length: is 0.30 or less (0); is approximately 0.40 (1) (Upchurch, 1995).

C6. Subnarial foramen (on premaxilla-maxilla suture): faces laterally (0); faces dorsally (1).

C7. Subnarial foramen: is small and subcircular (0); is narrow and elongated along the line of the premaxilla-maxilla suture (1).

C8. Subnarial foramen: lies outside the fossa of the external naris (0); lies within the narial fossa (1).

C9. 'Lateral plate' on premaxillae, maxillae and dentaries: absent (0); present (1) (Upchurch, 1995: fig. 12).

C10. 'Muzzle'-like region on snout: absent (0); present (1). Here, a 'muzzle' is defined as a subhorizontal region on the main body of the premaxilla, which lies rostral to the base of the internarial bar. The presence of this feature greatly emphasizes the 'break of slope' between the main body and ascending process of the premaxilla in lateral view (Fig. 2). In the data-matrix, the various diplodocid taxa have been assigned state '?' because the ascending process of the premaxilla is greatly reduced and the entire snout has been strongly modified as a result of narial
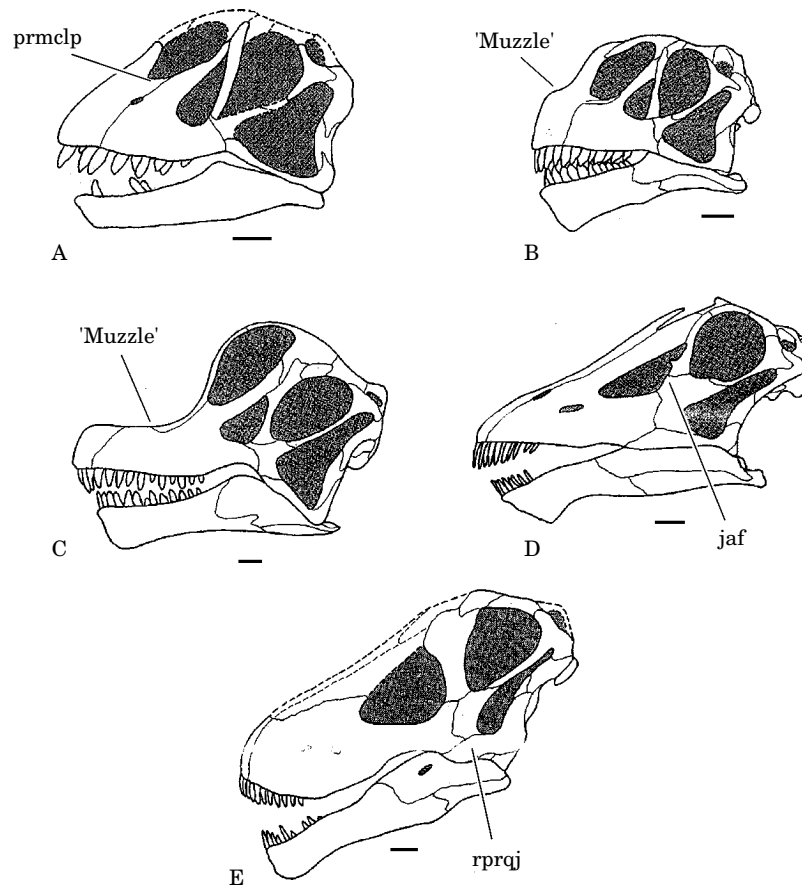
Figure 2. Sauropod skulls in left lateral view: A, *Euhelopus* (PMU R233a, after Mateer & McIntosh, 1985); B, *Camarasaurus* (CMNH 11338, after Gilmore, 1925); C, *Brachiosaurus* (HMN SII, after Janensch, 1935–36); D, *Diplodocus* (based on CMNH 11161); E, *Nemegtosaurus* (Z.Pal. MgD-1/9, after Nowinski, 1971). Abbreviations: jaf = jugal contribution to antorbital fenestra; prmclp = caudolateral process of the premaxilla; rprqj = rostral process of the quadratojugal. Scale bars = 50 mm.

retraction. *Omeisaurus* has been assigned state '0', although one specimen (ZDM T5703, see He, Li & Cai, 1988: fig. 14) does possess a muzzle-like region similar to that present in *Camarasaurus*.

C11. Ascending process of the premaxilla: is directed caudodorsally (0); is directed dorsally (1); internarial bar is lost (2) (Gauthier, 1986; Wilson & Sereno, 1994; Upchurch, 1995). This character is unordered.

C12. Premaxilla: is formed from a heavy main body and distinct ascending process (0); is formed from a transversely narrow main body which is greatly elongated rostrocaudally (1).

C13. Caudolateral process of the premaxilla: present (0); absent (1). The premaxillae of ornithischians, basal theropods, prosauropods and some sauropods, possess a caudally directed process at the caudolateral corner of the main body (Fig. 2). This process typically overlaps the rostral end of the maxilla, and in more 'advanced' ornithischians it becomes enlarged and intervenes between the maxilla
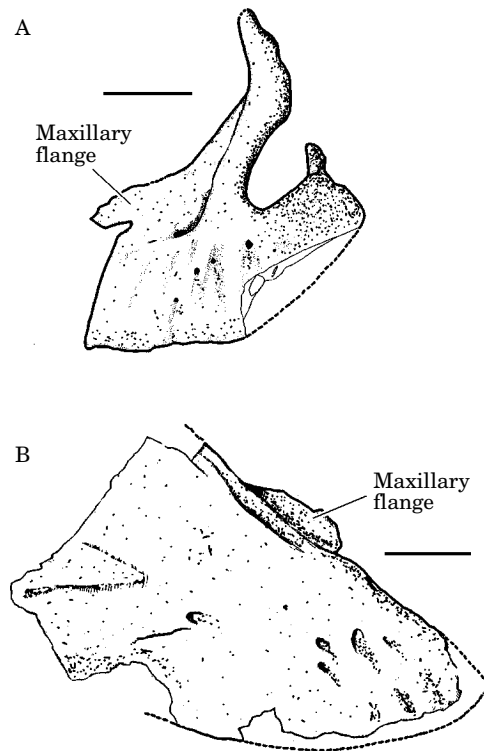
Figure 3. Sauropod maxillae in lateral view: A, left maxilla of *Patagosaurus* (MACN CH 934, after Bonaparte, 1986b); B, right maxilla of *Dicraeosaurus* (HMN dd 42, after Janensch, 1935–36). Scale bars = 50 mm.

and nasal (Sereno, 1986). The presence of this process represents a derived condition with respect to non-dinosaurian archosaurs, and can therefore be considered as a new cranial autapomorphy of the Dinosauria. This caudolateral premaxillary process is absent in at least some theropods (e.g. *Allosaurus*, Madsen, 1976) and the majority of sauropods. Within the Dinosauria, therefore, absence of this caudolateral process is considered to be a derived condition.

C14. Maxilla-lacrimal contact: is located above the mid-point of the antorbital fenestra (0); is located close to the caudal margin of the antorbital fenestra (1) (Gauthier, 1986).

C15. Flange-like structure attached to the base of the maxillary ascending process: absent (0); present (1). A thin flange or sheet of bone projects rostrally or rostromedially from the base of the sauropod maxillary ascending process (Fig. 3). In euhelopodids, brachiosaurids, and camarasaurids, these flanges are visible in lateral view and often form part of the back wall of the narial fossa. They are also present in diplodocoids, but are obscured in external view by the profoundly modified premaxillae.

C16. Maxillary flanges: do not contact each other on the midline (0); contact each other on the midline (1).

C17. 'Shelf'-like area lateral to the external naris, extending onto the rostral end of the maxilla: absent (0); present (1) (McIntosh, 1990b).

C18. Additional antorbital fenestra: absent (0); present (1) (Berman & McIntosh,

1978; Upchurch, 1995). A small canal passes through the base of the maxillary ascending process in *Brachiosaurus*, *Camarasaurus*, *Dicraeosaurus*, and *Nemegtosaurus*. A much larger oval opening is present in *Diplodocus*.

C19. Sheet of bone partially backing the rostral portion of the antorbital fossa: present (0); absent (1) (Sereno, 1989 [modified]; Galton, 1990 [modified]). The presence of a sheet of bone extending caudally from the maxillary ascending process has been considered to be a derived state in prosauropods (Sereno, 1989; Galton, 1990). This structure, however, is also present in the basal theropod *Eoraptor* (Sereno *et al.*, 1993), Ornithischia and *Scleromochlus*. In this analysis, therefore, the absence of the sheet of bone backing the antorbital fenestra is considered to represent a derived state.

C20. Jugal contribution to caudolateral margin of the antorbital fenestra: small or non-existent (0); large (1) (Berman & McIntosh, 1978) (Fig. 2).

C21. Rostral process of quadratojugal: is subequal in length to the dorsal process (0); is 2–3 times the length of the dorsal process (1).

C22. Maxilla-quadratojugal contact: absent (0); present (1) (Upchurch, 1995). The derived condition is present in *Apatosaurus*, *Diplodocus*, *Nemegtosaurus* and *Camarasaurus*, but is absent in *Omeisaurus*. The presence or absence of the derived state is more difficult to establish in other sauropod genera. *Shunosaurus* has been reconstructed with the derived state (McIntosh, 1990b: fig. 16.2). Examination of two skulls of this genus (ZDM T5401, T5402) suggests that the rostral end of the quadratojugal lies very close to the caudal end of the maxilla. The ventral part of the jugal, however, is not reduced and it seems likely that a small portion of this bone intervenes between the quadratojugal and maxilla. *Shunosaurus* has been provisionally assigned the plesiomorphic state in this analysis. The skull of *Euhelopus* has been reconstructed with the quadratojugal in contact with the maxilla (Mateer & McIntosh, 1985). Although the quadratojugal does possess a very long rostral process, it was not actually found in articulation with the maxilla. Whether the quadratojugal could have reached the caudal end of the maxilla depends on the estimated length of the skull, and it is possible that the contact did not occur. For the present, therefore, *Euhelopus* is assigned state '?'. *Brachiosaurus* has been reconstructed with a small gap between the maxilla and the rostral end of the quadratojugal (Janensch, 1935–36: Abb. 56). HMN S116 preserves the right quadratojugal, jugal and lacrimal in articulation. The jugal is approximately 'arrow-head'-shaped in lateral view, with a sharp rostral point and two caudal processes. The ventral caudal process is longer than the dorsal one and seems to articulate along the dorsomedial margin of the quadratojugal rostral process. Unfortunately, this specimen is damaged at its rostroventral corner, and an accurate assessment of the rostral extent of the quadratojugal cannot be made. Measurements based on disarticulated quadratojugals, combined with the reduced nature of the ventral part of the jugal, suggest that the latter was probably excluded from the ventral margin of the jaw by a maxilla-quadratojugal contact. *Brachiosaurus* is therefore assigned the derived state.

C23. Rostral process of quadratojugal: tapers to a slender rostral point (0); expands dorsoventrally at its rostral tip (1) (Fig. 2).

C24. Rostral process of quadratojugal: is straight or curves gently upwards towards its rostral tip (0); has a 'step'-like change of direction at mid-length, such that the rostral half of the process runs rostroventrally (1) (Fig. 2).

C25. Angle between the rostral and dorsal rami of the quadratojugal: is 90° or less (0); is approximately 130° or more (1).

C26. Rostral margin of infratemporal fenestra: lies caudal to the orbit (0); lies below the mid-point of the orbit, or further forwards (1) (Gauthier, 1986; Upchurch, 1995) (Fig. 2).

C27. Rostral margin of infratemporal fenestra: lies below the mid-point of the orbit, or more caudally (0); extends as far as, or beyond, the rostral margin of the orbit (1) (Upchurch, 1995).

C28. Caudal end of prefrontal in dorsal view: is rounded or subrectangular (0); is acute, subtriangular, and inset into the rostrolateral corner of the frontal (1) (Berman & McIntosh, 1978). In this analysis, diplodocids (*Apatosaurus* and *Diplodocus*) and euhelopodids (*Euhelopus*, *Omeisaurus* and *Shunosaurus*) are assigned the derived state. In diplodocids, the caudal half of the prefrontal 'cuts' deeply into the rostrolateral corner of the frontal, whereas in euhelopodids the prefrontal 'overlaps' this region of the frontal.

C29. Rostrocaudal length of frontals: is greater than their combined transverse width (0); is less than their combined transverse width (1) (Gauthier, 1986: Sereno, 1989).

C30. Midline contact between frontals: sutured but not fused (0); coalesced (1) (Salgado & Calvo, 1992).

C31. Excavation of the frontal and parietal around the margin of the supratemporal fenestra: present (0); absent (1) (Gauthier, 1986).

C32. Supratemporal fenestra: faces dorsally or dorsolaterally (0); faces laterally (1) (Salgado & Calvo, 1992).

C33. Rostrocaudal diameter of supratemporal fenestra: is more than 10% of occipital width (0); is less than 10% of occipital width (1) (Salgado & Calvo, 1992 [modified]). Powell (1992) states that the supratemporal fenestra is small and closed dorsally in *Saltasaurus*. The best preserved skull material of this genus (PVL 4017–161, 162), however, does not seem to possess complete supratemporal fenestrae. For the present, therefore, *Saltasaurus* is assigned state '?'.

C34. Postparietal fenestra: absent (0); present (1) (Salgado & Calvo, 1992).

C35. Squamosal-quadratojugal contact: present (0); absent (1) (Gauthier, 1986 [modified]; Upchurch, 1995).

C36. Proximal end of quadrate: is concealed in lateral view by the squamosal (0); is exposed in lateral view by a notch in the main body of the squamosal (1) (Berman & McIntosh, 1978). Lateral exposure of the proximal end of the quadrate is an autapomorphy of the Dinosauria (Novas, 1996). In some sauropods, the caudal part of the squamosal is developed into a slender process which is almost 'hook'-like in lateral view, producing the 'notch' described above.

C37. Dorsal margin of supratemporal fenestra: is formed by the parietal, postorbital and squamosal (0); is formed by the parietal and postorbital (i.e. the squamosal is excluded) (1) (Upchurch, 1995).

Braincase and occiput (C38–C45)

C38. Distal end of paroccipital process: is slightly expanded, with a straight distal margin (0); is not expanded, and has a rounded 'tongue'-like distal margin (1).

C39. Occipital condyle: is caudoventrally directed (0); is ventrally directed (1) (Berman & McIntosh, 1978; Salgado & Calvo, 1992). *Apatosaurus* appears to have

the derived condition, although the true orientation of the condyle may have been exaggerated by post-mortem distortion (Berman & McIntosh, 1978). Nowinski (1971: 67) describes the occipital condyle of *Nemegtosaurus* as being ". . . ventroanteriorly directed with respect to the horizontal plane of the skull". Figure 5a in Nowinski (1971), however, shows the occiput in 'posteroventral' view, with the occipital condyle directed towards the observer. It appears, therefore, that *Nemegtosaurus* actually possesses the plesiomorphic state (see also Salgado & Calvo, 1992). Similarly, Kurzanov & Bannikov (1983) suggest that the occipital condyle of *Quaesitosaurus* is directed downwards and forwards. Once again, however, the accompanying figures indicate that this genus possesses the plesiomorphic state (Kurzanov & Bannikov, 1983: fig. 2).

C40. 'Leaf'-like dorsolaterally directed process on the crista prootica (near the base of the basipterygoid process): absent (0); present (1) (Salgado & Calvo, 1992).

C41. Basipterygoid process: is directed ventrolaterally (0); is directed rostrolaterally (1) (Berman & McIntosh, 1978; McIntosh, 1990b; Upchurch, 1995).

C42. Length of basipterygoid process: is equal to, or less than, the distance from the occipital condyle to the basal tubera (0); is at least 1.5 times the distance from the occipital condyle to the basal tubera (1) (Janensch, 1935–36, Abb. 94; Salgado & Calvo, 1992; Upchurch, 1995).

C43. Angle between the basipterygoid processes: is approximately 45° (0); is approximately 20° (1) (Salgado & Calvo, 1992).

C44. Area between the bases of the basipterygoid processes: is shallowly concave (0); is deeply excavated into a long narrow pit extending caudally beneath the rostral part of the braincase (1) (Upchurch, 1995).

C45. Parasphenoid rostrum: is triangular in lateral view and possesses a groove along its dorsal midline (0); is a long, slender, strongly laterally compressed process which lacks the dorsal groove (1) (McIntosh, 1990b; Upchurch, 1995).

Palate (C46–C56)

C46. Maxillary process of the palatine: is either poorly developed or does not expand transversely at its rostral tip (0); expands transversely at its rostral tip (1) (Madsen *et al.*, 1995 [modified]).

C47. Ectopterygoid process of the pterygoid: lies below the caudal rim of the orbit (0); lies below the rostral rim of the orbit, or more rostrally (1) (Gauthier, 1986; Upchurch, 1994a).

C48. Ectopterygoid process of the pterygoid: lies below the lacrimal or more caudally (0); lies rostral to the lacrimal, under the antorbital fenestra (1) (Upchurch, 1994a).

C49. Ectopterygoid process of the pterygoid: is robust and projects below the level of the jaw margin (0); is reduced and does not project below the margin of the upper jaw (1) (Berman & McIntosh, 1978; Upchurch, 1994a).

C50. Rostral process of pterygoid: is formed from two sheets of bone which project vertically and laterally (or ventrolaterally) (0); is formed from a single sheet of bone which lies in the same plane as the 'main sheet' of the pterygoid (1).
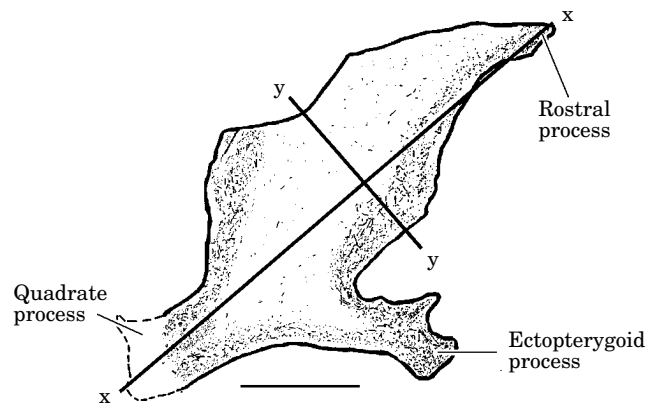
Figure 4. Right pterygoid of *Diplodocus* in lateral view (based on CMNH 3452, after McIntosh & Berman, 1975); x–x and y–y define the length of the pterygoid and the breadth across its 'main sheet' respectively. Scale bar = 50 mm.

C51. Breadth of 'main sheet' of pterygoid: is less than 20% of the total length of the pterygoid (0); is approximately 30% of the total length of the pterygoid (1) (McIntosh & Berman, 1975 [modified]). Figure 4 shows the length and breadth axes employed in this comparison.

C52. Basal articulation on pterygoid (for reception of the distal end of the basipterygoid process): is formed by a medially directed shelf of the pterygoid, which opens dorsally and caudally (0); is formed by a caudoventrally facing depression (1) (Upchurch, 1995).

C53. 'Hook' or 'finger'-like process on basal articulation, which curves around the distal end of the basipterygoid process: absent (0); present (1) (Madsen *et al.*, 1995).

C54. Lateral end of ectopterygoid: contacts the medial surface of the jugal (0); contacts the medial surface of the maxilla (1) (Madsen *et al.*, 1995).

C55. Excavation in caudal surface of quadrate: absent (0); present (1) (Kurzanov & Bannikov, 1983; Russell & Zheng, 1993; Calvo & Salgado, 1995; Upchurch, 1995).

C56. Long-axis of the quadrate shaft: is oriented approximately perpendicular to the long-axis of the skull (0); is directed caudodorsally (1) (Berman & McIntosh, 1978; Gauthier, 1986 [modified]; Upchurch, 1995).

Mandible (C57–C64)

C57. Rostral end of dentary: decreases in depth and robustness towards the symphysis (0); increases in depth and robustness towards the symphysis (1).

C58. Ventral margin of the dentary (in the transverse portion leading to the symphysis): is stout, rounded rostrocaudally, and does not project far below the rest of the dentary (0); is formed into a thin sharp transverse ridge (1).
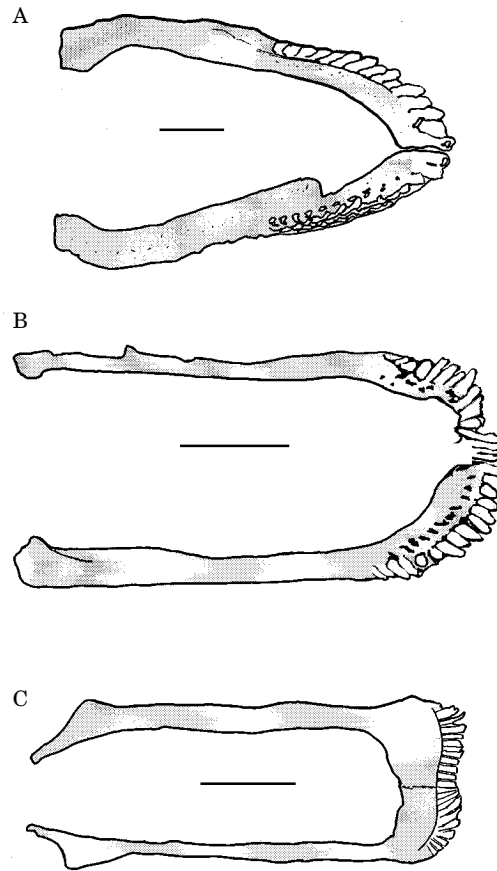
Figure 5. Dorsal profiles of sauropod mandibles: A, *Brachiosaurus* (HMN S66, after Janensch, 1935–36); B, *Nemegtosaurus* (Z.Pal. MgD-1/9, after Nowinski, 1971); C, *Diplodocus* (based on CMNH 11161). Scale bars = 100 mm.

C59. Shape of mandible in dorsal view: broadly rounded, 'U'-shaped (0); rectangular, with the most rostral portion of the dentary oriented perpendicular to the long-axis of the skull (1) (Russell & Zheng, 1993; Upchurch, 1995) (Fig. 5).

C60. Angle between the long-axis of the mandibular symphysis and the long-axis of the mandible: is approximately 45° (0); is approximately 90° (1) (Upchurch, 1995) (Fig. 6).

C61. Rostral end of splenial: terminates caudal to the mandibular symphysis (0); participates in the mandibular symphysis (1). The derived condition is present in larger specimens of *Camarasaurus*, but is apparently absent in smaller, presumably younger, individuals (Madsen *et al.*, 1995).

C62. Long diameter of external mandibular fenestra: is 10–15% of mandible length (0); is 5% of mandible length, or less (1) (Upchurch, 1994a, 1995).

C63. External mandibular fenestra: open (0); closed (1) (Russell & Zheng, 1993; Upchurch, 1995) (Fig. 6).

C64. Jaw articulation: is level with, or above, the mandibular tooth row (0); is below the mandibular tooth row (1) (Gauthier, 1986 [modified]).

Figure 6. Left mandible of *Diplodocus* in lateral view (based on CMNH 11161); x–x and y–y define the long-axis of the mandible and the long-axis of the mandibular symphysis respectively. Scale bar = 100 mm.

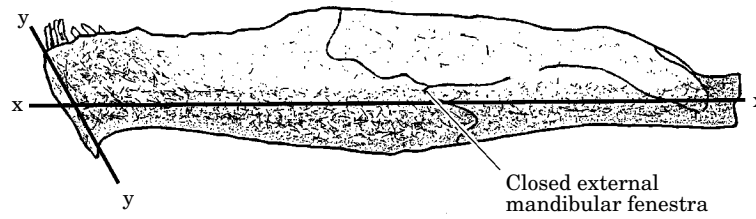### *Dentition (C65–C74)*

C65. Longest tooth crowns in upper jaw: are situated on the rostral or middle part of the maxilla (0); are situated on the premaxilla (1) (Gauthier, 1986; Upchurch, 1995). The derived state is also present in many juvenile prosauropods, such as *Massospondylus* (BP1-FN4376, Cooper, 1981) and *Mussaurus* (Bonaparte & Vince, 1979), whereas adult forms possess the plesiomorphic state.

C66. Denticles (serrations) on tooth crowns: present (0); absent (1) (McIntosh, 1990b; Upchurch, 1994a).

C67. Lingual surface of the tooth crown: is convex (0); is concave (1) (Upchurch, 1994a).

C68. Prominent grooves near the mesial and distal margins of the labial surface of each tooth crown: absent (0); present (1) (Upchurch, 1994a) (Fig. 7).

C69. SI values (see 'Abbreviations'): are less than 3.0 (0); are approximately 4.0 (1) (Fig. 7).

C70. SI values: are less than 4.0 (0) are 5.0 or more (1).

C71. Tooth crown shape: 'spatulate' (0); 'parallel-sided' (1). Here, 'spatulate' teeth are those which expand mesiodistally from the base, reaching maximum width at approximately 1/3 to 1/2 of crown height. 'Parallel-sided' crowns are those in which the mesial and distal margins are parallel over most of the length of the crown (Fig. 7).

C72. Long-axis of tooth crown: is oriented perpendicular to the jaw margin (0); slopes forwards (i.e. the teeth are 'procumbent') (1) (Gauthier, 1986).

C73. Position of most caudal tooth in tooth row: below the orbit (0); below the antorbital fenestra or more rostrally (1) (Gauthier, 1986; Upchurch, 1994a) (Fig. 2).

C74. Position of most caudal tooth in tooth row: below antorbital fenestra or more caudally (0); rostral to the antorbital fenestra (1) (Upchurch, 1994a) (Fig. 2).

Cervical vertebrae and ribs (C75–C94)

C75–C79. Number of cervicals (see 'note' which follows 'C79'):
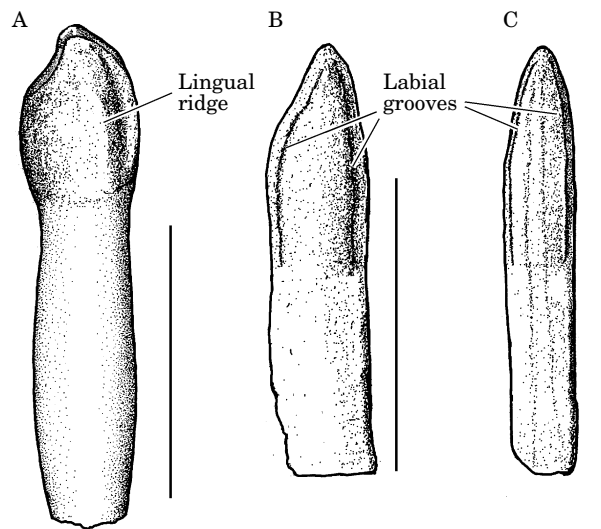C75. 10 or fewer cervicals (0); 12 or more cervicals (1).

Figure 7. Sauropod teeth: A, lingual view of an isolated *Patagosaurus* tooth (specimen number unknown, after Bonaparte, 1986b); B, labial view of *Brachiosaurus* maxillary tooth (HMN t1, after Janensch, 1935–36); C, labial view of an isolated *Dicraeosaurus* tooth (HMN E H, after Janensch, 1935–36). Scale bars = 50 mm.

C76. 12 or fewer cervicals (0); at least 13 cervicals (1).

C77. 13 or fewer cervicals (0); at least 15 cervicals (1).

C78. 15 or fewer cervicals (0); at least 16 cervicals (1).

C79. 16 or fewer cervicals (0); at least 17 cervicals (1). There are difficulties associated with establishing the number of cervical vertebrae in dinosaurs. These difficulties are caused mainly by the absence of any abrupt morphological transition between cervical and dorsal vertebrae. Estimates of the numbers of cervical and dorsal vertebrae are variable because different authors identify the cervicodorsal junction using different criteria. For example, Sereno (1987, 1990) considers the first dorsal vertebra to be the most cranial presacral in which the parapophysis lies above the neurocentral suture. In sauropods, studies have exploited the fact that cervical ribs are fused to their vertebrae (except in smaller and apparently younger individuals), whereas thoracic ribs are usually 'free' (McIntosh, 1990b, and references therein). These two criteria lead to different estimates of cervical number: in sauropods the first one or two vertebrae to possess 'free' ribs usually have parapophyses below the neurocentral suture. In this study, the nature of the rib attachment is used to calculate the number of cervical vertebrae. The use of parapophysis position, although producing a different estimate of cervical number, would still suggest that sauropods have a relatively higher number of cervicals compared to the outgroups.

C80. EI values (see 'Abbreviations') of cervical centra: do not exceed 3.0; exceed 4.0 (1) (Upchurch, 1994a, 1995).

C81. Articulations between cervical centra: are amphicoelous/amphiplatyan (0); are opisthocoelous (1) (Gauthier, 1986; Upchurch, 1995). 'Opisthocoely' refers to a derived state in which the cranial end of the centrum develops a prominent hemispherical 'ball' which articulates with a deep concavity on the caudal end of the adjacent centrum.
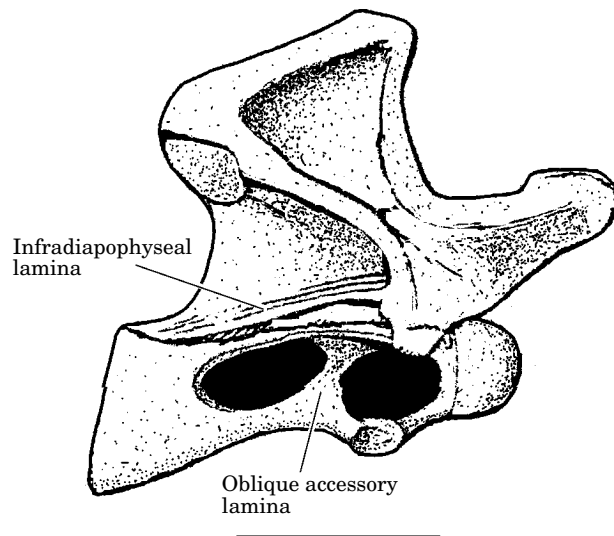
Figure 8. Caudal cervical vertebra of *Haplocanthosaurus* in right lateral view (CMNH 572, after Hatcher, 1903b). Scale bar = 100 mm.

C82. Articulations between middle and caudal dorsal centra: amphicoelous/ amphiplatyan (0); opisthocoelous (1) (Calvo & Salgado, 1995; Upchurch, 1995).

C83. Midline keels on the ventral surfaces of the cervical centra: prominent and plate-like (0); reduced to low ridges or absent (1). Some form of ventral keel (a prominent midline ridge) is present on the cranial halves of the cervical centra of most dinosaurs. In non-sauropods, keels are usually restricted to the most cranial cervicals, but in *Mamenchisaurus*, *Omeisaurus* and possibly several other sauropods, prominent plate-like keels are also found on the most caudal cervicals.

C84. Ventral surface of each cervical centrum: is flat or slightly convex transversely (especially towards the caudal end of each centrum) (0); is transversely concave and bounded by prominent ventrolateral ridges on either side (1).

C85. Height:width ratio of cranial cervical centra: is 1.0 or less (0); is approximately 1.25 (1) (Martin, 1995 [modified]).

C86. Excavation in the dorsal surface of each cervical parapophysis: absent (0); present, and continuous with the pleurocoel (1); present, but separated from the pleurocoel by a longitudinal ridge (2). It is not possible to determine the probable transformation order of states '1' and '2'. This character is therefore unordered.

C87. Lateral surfaces of cervical centra: lack a lateral excavation, or possess only a very shallow depression (0); are deeply excavated (i.e. there is a prominent pleurocoel which ramifies within the body of the centrum), but lack an oblique accessory lamina (1); possess a deep excavation which is divided into cranial and caudal portions by an oblique accessory lamina (2) (McIntosh, 1990b; Russell & Zheng, 1993 [modified]; Upchurch, 1995) (Fig. 8). This character is unordered.

C88. Infraprezygapophyseal laminae on the middle and caudal cervicals: are 'single' (0); bifurcate towards their dorsal ends to form medial and lateral branches (with a triangular hollow in between) (1).

C89. Articular surfaces of middle and caudal cervical prezygapophyses: are flat (0); are convex transversely (1) (Upchurch, 1995).

C90. Infradiapophyseal lamina system: is restricted to the dorsal vertebrae and caudal cervicals (0); is found on all presacral vertebrae (1) (Galton, 1990 [modified]; Upchurch, 1995). The infradiapophyseal laminae form an inverted 'V'-shape structure which supports the dorsal transverse processes from below. In the cervical series of sauropods, these two laminae change their size and orientation: the infraprediapophyseal lamina is small and projects cranioventrally from the transverse process; the infrapostdiapophyseal lamina is very prominent and runs almost horizontally backwards (Fig. 8).

C91. Cervical neural spines: are low (so that the height of the vertebra does not normally exceed the length of the centrum) (0); are high, drawn out into thin processes (so that the height of the vertebra is at least 1.5 times the length of the centrum) (1) (Calvo & Salgado, 1995; Upchurch, 1995).

C92. Bifurcation of presacral neural spines: absent (0); present, without a small process at the base of the bifurcation (1); present, with a small process at the base of the bifurcation (2) (Gauthier, 1986; McIntosh, 1990b; Upchurch, 1995). This character is unordered.

C93. The lateral profile of neural spines on caudal cervical vertebrae: displays steeply sloping cranial and caudal faces (0); displays a steeply sloping cranial face (often nearly vertical) and a noticeably less steep (often subhorizontal) caudal margin (1) (Fig. 8).

C94. Distal shafts of longest cervical ribs: are elongate and form overlapping bundles (0); are short and do not project beyond the caudal end of the centrum to which they are attached (1) (McIntosh, 1990b; Upchurch, 1995).

Dorsal vertebrae and ribs (C95–C119)

C95. Number of dorsal vertebrae: 12 or more (0); 10 or fewer (1) (McIntosh, 1990b).

C96. Pleurocoels in cranial dorsal centra: have rounded caudal margins (0); have tapering, acute caudal margins (1). 'Ancestor', and those sauropods which lack pleurocoels, have been assigned state '?'.

C97. Pleurocoels in dorsal centra: absent (0); present (1).

C98. Pleurocoels in dorsal centra: are moderately deep but simple pits (0); are deep, ramify extensively within the centrum and enter the base of the neural arch (1).

C99. EI values for caudal dorsal centra: are less than 1.0 (0); are greater than 1.0 (1).

C100. Height of dorsal neural arches: low (i.e. less than that of the centrum) (0); high (i.e. subequal to, or greater than, the height of the centrum) (1) (Bonaparte, 1986a).

C101. Cranial face of dorsal neural arch: is flat or shallowly excavated (0); is deeply excavated, forming a large cavity above the neural canal (1) (Bonaparte, 1986a).

C102. Dorsal transverse processes: are directed laterally or slightly upwards (0); are directed strongly dorsolaterally (1).

C103. Transverse processes of caudal dorsal vertebrae: lie caudal, or caudodorsal, to the parapophysis (0); lie vertically above the parapophysis (1).

C104. Laminae linking the prezygapophyses to the transverse processes on dorsal vertebrae: present (0); absent (1) (Bonaparte, 1986a).

C105. Centroparapophyseal lamina: absent (0); present (1). The middle and caudal dorsal vertebrae of many sauropods possess a lamina or ridge which supports the parapophysis from below and behind.

C106. Cavity within some or all of the dorsal neural arches: absent (0); present, totally enclosed within bone (1); present, opens laterally via a foramen beneath the transverse process (2) (Jain *et al.*, 1979: P1. 102; Bonaparte, 1986a: fig. 19.8). Several sauropod genera possess a 'neural cavity' within some or all of their dorsal neural arches (Bonaparte, 1986a). In *Camarasaurus* and *Diplodocus*, this cavity is entirely enclosed by bone, whereas in *Barapasaurus* (Jain *et al.*, 1979) and *Patagosaurus* (Bonaparte, 1986b) the cavity opens laterally via a foramen below the base of the transverse process. This character is somewhat problematic for several reasons. Firstly, the internal structure of dorsal vertebrae is rarely described and is inaccessible unless material is broken or sectioned. Secondly, there appears to be some variation in the size of the neural cavity along the dorsal series: this may lead to the assignment of the incorrect character state in those taxa where complete articulated dorsal series are not available (Upchurch & Martin, in prep.). This character is unordered.

C107. Accessory lamina in the infrapostzygapophyseal cavity of middle and caudal dorsals: absent (0); present (1). This accessory lamina is a short prominent 'ridge' which runs caudodorsally across the neural arch, immediately below the postzygapophysis.

C108. Deep excavation below the transverse process which leaves only a thin septum on the midline (especially in the middle and caudal dorsal vertebrae): absent (0); present (1). This character may be related to the morphologies described in 'C106' (Jain *et al.*, 1979).

C109. Hyposphene-hypantrum system (additional intervertebral articulations in the middle and caudal dorsal vertebrae): present (0); absent (1).

C110. Single midline lamina supporting the hyposphene from below on each of the dorsal neural arches: absent (0); present (1) (Upchurch, 1995).

C111. Horizontal cross-section through the base of a dorsal neural spine: is subrectangular and axially elongate (0); is subtriangular, with a transversely widened caudal margin (1) (Fig. 9).

C112. Prominent suprapostzygapophyseal laminae on dorsal neural spines: absent (0); present (1) (Bonaparte, 1986a). Suprapostzygapophyseal laminae are prominent plates of bone which project from the caudolateral margins of the neural spine (Fig. 9).

C113. Prespinal lamina on the middle and caudal dorsal vertebrae: absent (0); present (1) (Bonaparte, 1986a; Calvo & Salgado, 1995). Prespinal laminae are ridge-like structures located on the cranial midline of dorsal neural spines (Fig. 9).

C114. Postspinal lamina on the middle and caudal dorsal vertebrae: absent (0); present (1) (Bonaparte, 1986a; Upchurch, 1995). The postspinal lamina is a vertical ridge-like structure located on the caudal midline of dorsal neural spines. *Shunosaurus* has been assigned the derived state because a prominent portion of the spine projects caudal to the suprapostzygapophyseal ridges (Fig. 9). This configuration could, however, represent a condition more plesiomorphic than any other seen in sauropods (see 'Discussion'). *Brachiosaurus* may have an incipient postspinal lamina (Janensch, 1950, Abb. 61; Bonaparte, 1986a), but this is usually in the form of a low rounded rugosity rather than a distinct ridge. *Brachiosaurus* is provisionally assigned state '0'.
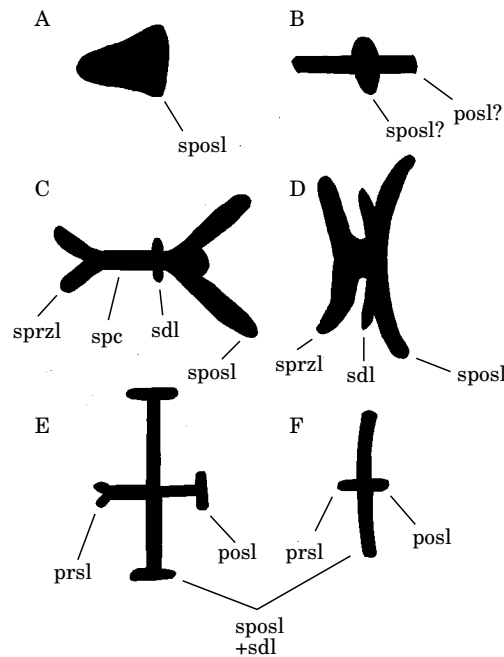
Figure 9. Schematic horizontal cross-sections through the bases of sauropod dorsal neural spines: A, *Lapparentosaurus* (MNHN MAA 91); B, *Shunosaurus* (ZDM T5401); C, *Cetiosaurus* (LCM 468.1968); D, *Camarasaurus* (CMNH 11338); E, *Apatosaurus* (CMNH 3018); F, *Dicraeosaurus* (HMN M); all based on personal observations. Abbreviations: posl=postspinal lamina; prsl=prespinal lamina; sdl=supra-diapophyseal lamina; spc=spine core; sposl=suprapostzygapophyseal lamina; sprzl=suprapre-zygapophyseal lamina. Not to scale.

C115. Neural spines of caudal dorsal vertebrae: are wider craniocaudally than transversely (0); are compressed craniocaudally (1).

C116. 'Triangular processes' on dorsal neural spines: absent (0); present (1) (Upchurch, 1995: fig. 13). In the derived condition, the suprapostzygapophyseal lamina develops a subtriangular lateral projection near the top of the neural spine.

C117. Dorsal neural spines in cranial view: possess subparallel lateral margins (0); possess lateral margins which diverge steadily towards the summit (1) (Fig. 10B).

C118. Supradiapophyseal lamina on middle and caudal dorsal vertebrae: absent (0); present (1). The supradiapophyseal lamina is a relatively small sheet of bone which runs from the dorsal surface of the transverse process to the cranial surface of the suprapostzygapophyseal lamina (Fig. 9).

C119. Proximal portions of cranial thoracic ribs: are shallowly concave on the cranial and caudal faces (0); are deeply concave on the caudal surface and strongly convex on the cranial surface (1) (Upchurch, 1995; McIntosh *et al.*, 1996).

Sacrum and sacral ribs (C120–C127)

C120. Number of sacral vertebrae: is three or fewer (0); is four or more (1) (McIntosh, 1990b; Upchurch, 1995). The number of coalesced vertebrae in the
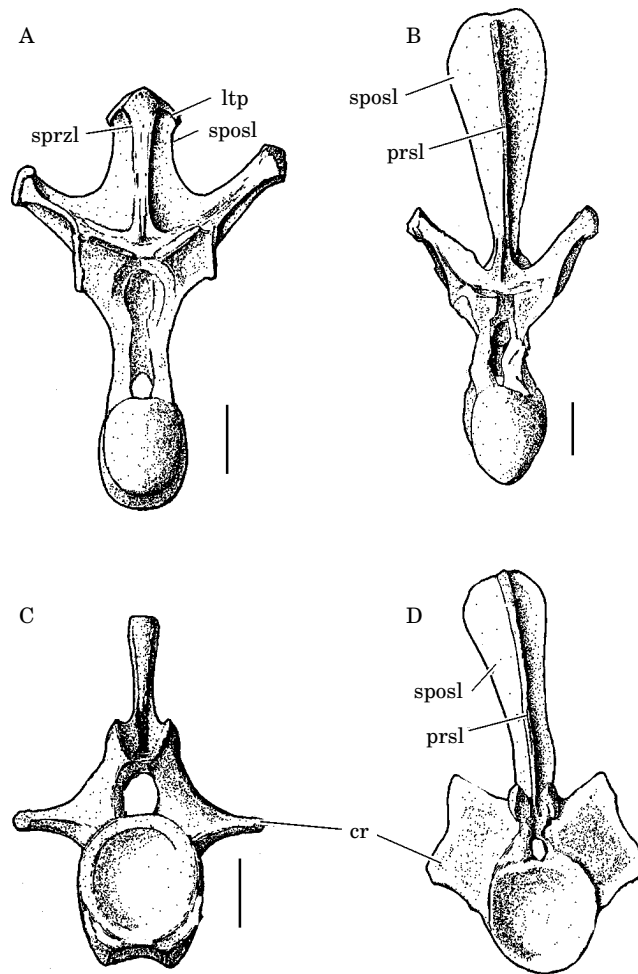
Figure 10. Sauropod vertebrae in cranial view: A, caudal dorsal vertebra of *Haplocanthosaurus*; B, caudal dorsal vertebra of *Dicraeosaurus*; C, cranial caudal vertebra of *Haplocanthosaurus*; D, cranial caudal vertebra of *Dicraeosaurus*. A and C, CMNH 572, after Hatcher (1903b), B and D, HMN M, after Janensch (1929). Abbreviations: cr = caudal rib; ltp = lateral triangular process; prsl = prespinal lamina; sposl = suprapostzygapophyseal lamina; sprzl = supraprezygapophyseal lamina. Scale bars = 100 mm.

sauropod sacrum displays both phylogenetic and ontogenetic variation. For example, Upper Jurassic sauropods typically have five fused sacrals, but a juvenile *Camarasaurus* has no fusion (McIntosh *et al.*, 1996) and 'old' individuals may have six coalesced sacrals (McIntosh, 1990b). Thus, the number of vertebrae fused into the sacrum is not a reliable character for phylogenetic analysis. The number of vertebrae attached to the ilium by a modified sacral rib appears to be more 'stable' and is here used to define sacral number.

C121. Number of sacral vertebrae: is four or fewer (0); is five or more (1) (McIntosh, 1990b; Upchurch, 1995).

C122. Number of sacral vertebrae: is five or fewer (0); is six (1) (McIntosh, 1990b; Upchurch, 1995). The five-vertebra sauropod sacrum is normally considered to

TABLE 1. Comparison of the sacra of *Opisthocoelicaudia* and *Saltasaurus*. The data have been derived from Borsuk-Bialynicka (1977) and Powell (1992)

Structure	Location/orientation in *Opisthocoelicaudia*	Location/orientation in *Saltasaurus*
Transversely narrow centra	S2–S5	S3–S5 (but S2 narrows towards its caudal end)
Position of the parapophysis on S1	Neural arch	Neural arch
Least robust sacral rib	S1	S1
Ribs participating in acetabulum	S3–S6	S3–S6
Sacral ribs in dorsal view	S3–S6 are directed laterally	S3–S6 are directed laterally

possess a dorsosacral, three primary sacrals and a caudosacral. *Saltasaurus* and *Opisthocoelicaudia* possess six sacral vertebrae which are attached to the ilium (Powell, 1992; Borsuk-Bialynicka, 1977). *Saltasaurus* is considered to have acquired the sixth sacral through incorporation of a second dorsosacral (McIntosh, 1990b). *Opisthocoelicaudia*, however, has been described as having a single dorsosacral and two caudosacrals (Borsuk-Bialynicka, 1977). For this reason, the six-vertebra sacra of these two genera appear to be convergently acquired. Table 1 compares a number of different 'landmarks' on the sacra of *Saltasaurus* and *Opisthocoelicaudia*. The close correspondence between the relative positions and orientations of these landmarks suggests that there is no independent evidence supporting the *a priori* assumption of homoplasy.

C123. Sacrum width divided by the average length of a sacral centrum: is 2.5 or less (0); is 4.0 or more (1) (McIntosh, 1990b [modified]).

C124. 'Pleurocoels' or very deep depressions in sacral centra: absent (0); present (1).

C125. Height of neural spines on caudal dorsals, sacrals and cranial caudals: is less than or equal to 1.5 times the height of the centrum (0); is at least 2.0 times the height of the centrum (1) (McIntosh, 1989, 1990b [modified]; Upchurch, 1995). Here, the height of the neural spine is defined as the distance from the top of the spine to the level of the postzygapophyses.

C126. Height of neural spines on caudal dorsals, sacrals and cranial caudals: is less than or equal to 2.0 times the height of the centrum (0); is 3–4 times the height of the centrum (1) (Upchurch, 1995).

C127. Dorsal surfaces of sacral ribs: lie below the dorsal rim of the ilium (0); are level with the dorsal rim of the ilium (1) (Gauthier, 1986).

Caudal vertebrae and ribs (C128–C144)

C128. Number of caudal vertebrae: is 55 or fewer (0); is 70–80 (1) (Berman & McIntosh, 1978; McIntosh, 1989, 1990b). Certain sauropods, such as *Alamosaurus* and *Mamenchisaurus*, lack the distal portion of the tail. Although this means that the exact number of caudals is unknown, it can be argued that these taxa probably possessed the plesiomorphic state. For example, the small size of the last preserved

caudal (Cd30) in *Alamosaurus* (USNM 15560) suggests that it is unlikely that the tail originally possessed more than 40–45 vertebrae.

C129. Articulations between cranial caudal centra: are amphicoelous/amphiplatyan (0); are mildly or strongly procoelous (1) (McIntosh, 1990b: Upchurch, 1995). Here, 'procoely' refers to the presence of concave cranial and convex caudal articular surfaces.

C130. Articulations between cranial caudal centra: are amphicoelous or only mildly procoelous (0); are strongly procoelous (1) (McIntosh, 1990b; Upchurch, 1995). Mildly procoelous caudals possess a weak convexity on the caudal articular surface, whereas strong procoely is characterized by a nearly hemispherical articular 'ball'.

C131. Articulations between middle and distal caudal centra: are amphicoelous/amphiplatyan (0); are strongly procoelous (1) (Jacobs *et al.*, 1993; Upchurch, 1995. In a few sauropods (*Apatosaurus*, *Diplodocus* and *Opisthocoelicaudia*) the most distal caudals have convex articular surfaces at both ends of the centrum, but the middle caudals are amphicoelous.

C132. Centrum length divided by centrum height (in the most cranial caudals): is approximately 1.0 or more (0); is approximately 0.5–0.6 (1) (Gauthier, 1986 [modified]; Upchurch, 1995). 'Centrum length' excludes the length of the articular 'ball' in procoelous and opisthocoelous caudals.

C133. Lengths of caudal centra: remain approximately the same over the first 20 vertebrae (0); increase (by as much as 50%) over the first 20 caudals and then decrease throughout the rest of the series (1).

C134. Distal end of tail: is composed of relatively short caudal centra (EI values of 3.0 or less) (0); is formed into a 'whip-lash' of elongate rod-like caudals (EI values of approximately 5.0) (1) (Berman & McIntosh, 1978 [modified]; Calvo & Salgado, 1995; Upchurch, 1995).

C135. Pleurocoels in cranial caudal centra: absent (0); present (1) (McIntosh, 1990b; Upchurch, 1995).

C136. Ventral surfaces of cranial caudal centra: are transversely rounded or developed into an acute midline ridge (0): are mildly or deeply excavated, with the excavation bounded by a ventrolateral ridge on each side (1) (McIntosh, 1990b; Upchurch, 1995). The extent to which the derived state is present in *Barosaurus* may vary between individuals (B. Curtice, pers. comm. 1995).

C137. Centra of middle caudals: display a subcircular or laterally compressed transverse cross-section (0); display a dorsoventrally compressed transverse cross-section (1).

C138. Neural arches of middle caudals: are situated over the middle of the centrum (0); are situated on the cranial half of the centrum (1) (Calvo & Salgado, 1995; Upchurch, 1995). The middle caudal vertebrae of *Cetiosaurus* display some cranial shift of the neural arches, but this is not as extreme as in those sauropods which have been assigned the derived state.

C139. Caudal 'hyposphenal' ridge: absent (0); present (1). In many sauropods, the cranial caudals possess a 'hyposphenal' ridge which extends from the ventral midline junction of the postzygapophyses to the top of the neural canal.

C140. 'Dorsalization' of the neural spines of the cranial caudals: absent (spines are simple laterally compressed plates which lack laminae) (0); present (spines are very similar to those of dorsal vertebrae) (1) (Fig. 10).

C141. Neural spines of cranial caudals: are transversely compressed (0); are craniocaudally compressed (1).

C142. First caudal rib: is a simple laterally directed process (0); is linked to the lateral surface of neural arch and prezygapophysis by a stout ridge (1).

C143. 'Wing' or 'fan'-like caudal ribs: absent (0); present on first 3–7 caudals (1) (Berman & McIntosh, 1978; McIntosh, 1990b: fig. 16.7; Upchurch, 1995). The derived condition consists of a caudal rib which is subrectangular or trapezoidal in cranial view (Fig. 10). Here, *Rebbachisaurus* is assigned state '0', although Calvo & Salgado (1995) suggest that this genus may possess an intermediate state.

C144. Disappearance of caudal ribs: occurs on Cd20 or more distally (0); occurs on Cds14–16 or more cranially (1).

Haemal arches (C145–C149)

C145. Middle and distal chevrons: have their proximal articular facets joined by a 'bridge' of bone over the haemal canal (0); are 'open' at their proximal ends (i.e. the transverse 'bridge' of bone is absent) (1) (Powell, 1992 [modified]; Upchurch, 1995).

C146. Cranial chevrons: have their proximal facets linked by a transverse 'bridge' of bone (0); are 'open' at their proximal ends (1) (Powell, 1992 [modified]; Calvo & Salgado, 1995; Upchurch, 1995; McIntosh *et al.*, 1996). Nearly all *Camarasaurus* specimens possess the derived state, although McIntosh *et al.* (1996) note that *C. lewisi* (BYU 9047) has the plesiomorphic state.

C147. Ventral blades of middle and distal chevrons: curve backwards and downwards (0); possess a cranially directed process (1). The middle chevrons of many sauropods, including *Apatosaurus*, *Barosaurus*, *Dicraeosaurus*, *Diplodocus*, *Mamenchisaurus*, *Omeisaurus*, and *Shunosaurus*, possess very prominent cranial processes (see 'C148'). In *Camarasaurus*, a small cranial process is present (Gilmore, 1925)—this genus is therefore assigned state '1'.

C148. 'Forked' or 'skid'-like middle and distal chevrons: absent (0); present (1) (Berman & McIntosh, 1978; Upchurch, 1995). 'Forked' chevrons are defined as possessing a prominent cranial process, resulting in the craniocaudal length of the chevron greatly exceeding its height.

C149. Middle and distal chevrons: lack a ventral 'slit' and do not divide into separate left and right rami (0); possess a ventral 'slit' and may divide into separate left and right rami (1) (Upchurch, 1995: fig. 15).

Pectoral girdle and forelimb (C150–C171)

C150. Proximal end of scapula: develops a relatively small dorsal expansion which is rounded in outline (0); develops a prominent dorsally directed plate which is subquadrangular in lateral profile (1) (Yu, 1990) (Fig. 11). In the plesiomorphic state, the width across the proximal end is less than 0.50 of scapula length, whereas in the derived state this ratio is greater than 0.50.
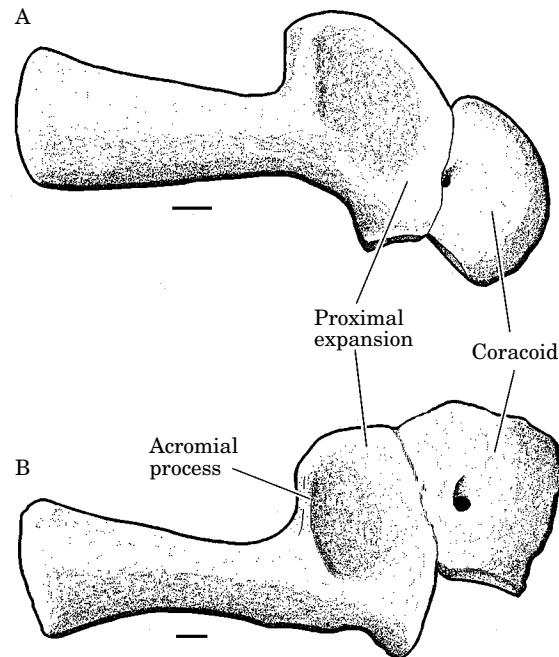
Figure 11. Right scapulae in lateral view: A, *Omeisaurus* (ZDM T5701, after He *et al.*, 1988); B, *Alamosaurus* (USNM 15560, after Gilmore, 1946). Scale bars = 100 mm.

C151. Acromial ridge on lateral surface of the scapular proximal expansion: absent (0); present (1). In state '1', a prominent ridge runs dorsally from the base of the scapular blade to the dorsal margin of the proximal (acromial) expansion. A wide concave area lies cranial to the ridge, as in many other dinosaurs. The presence of the ridge, however, emphasizes the depth of a small concave area which lies caudal to the ridge (Fig. 11).

C152. Dorsal margin of coracoid in lateral view: reaches or projects beyond the dorsal margin of the proximal end of the scapula (0): lies below the dorsal margin of the proximal end of the scapula (1) (Upchurch, 1995 [modified]) (Fig. 11).

C153. Cranial and dorsal margins of the coracoid in lateral view: merge smoothly to form a rounded profile (0); are virtually straight and meet each other at an angle of 90–120°, giving the coracoid a subquadrangular lateral profile (1) (Fig. 11).

C154. Maximum length of sternal plate divided by humerus length: is 0.65 or less (0); is 0.75 or more (1) (McIntosh, 1990b [modified]).

C155. Lateral margin of sternal plate: is straight or convex in dorsal profile (0); is gently or strongly concave (1) (Calvo & Salgado, 1995 [modified]).

C156. Craniolateral expansion of sternal plate: absent (0); present (giving the sternal plate a characteristic 'kidney-shape' in dorsal profile) (1) (McIntosh, 1990b: fig. 16.9).

C157. Prominent, parasagittally elongate ridge on the dorsal surface of the cranial end of the sternal plate: absent (0); present (1).

C158. Forelimb/hindlimb length ratio: is less than 0.60 (0); is 0.66 or more (1) (McIntosh, 1990b; Upchurch, 1994a).
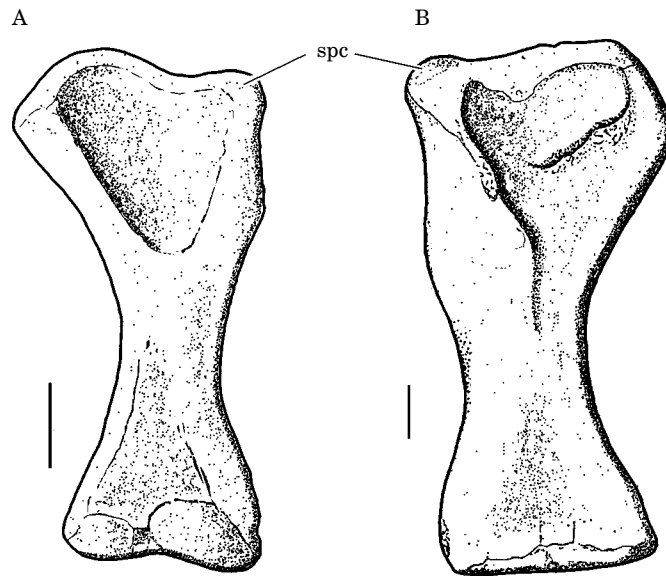
Figure 12. Sauropod humeri in cranial view: A, left humerus of *Saltasaurus* (PVL 4017–67, after Powell, 1992); B, right humerus of *Opisthocoelicaudia* (Z.Pal. MgD-1/48, after Borsuk-Bialynicka, 1977). Abbreviations: spc = insertion for M. supracoracoideus. Scale bars = 100 mm.

C159. Forelimb/hindlimb length ratio: is less than 0.75 (0); is 0.75 or more (1) (Gauthier, 1986; McIntosh, 1990b; Upchurch, 1994a).

C160. Prominent process on the lateral portion of the proximal end of the humerus: absent (proximal end is transversely convex in cranial view) (0); present (proximal end has a sinusoidal cranial profile) (1) (Fig. 12). This process has been interpreted as the point of insertion of the M. supracoracoideus by Borsuk-Bialynicka (1977).

C161. Craniomedial process of the proximal end of the ulna: has a flat proximal surface (0); has a strongly concave proximal surface (1) (Upchurch, 1995: fig. 14).

C162. Radius: slender (maximum width of proximal end is 25% of radius length, or less) (0); robust (maximum width of proximal end is 33% of radius length, or more) (1) (McIntosh, 1990b; Upchurch, 1995).

C163. Number of ossified distal carpals: three or more (0); two or fewer (1). Most dinosaurs, including prosauropods, have three or more distal carpals. McIntosh, (1990b) endorsed Osborn's (1904) suggestion that there are only two elements in the typical sauropod carpus. The evidence currently available, however, indicates that it is difficult to make accurate generalizations about the number of ossified elements in the carpus. For example, there are at least three carpals in *Shunosaurus* (Zhang, Yang & Peng, 1984) and '*Bothriospondylus madagascariensis*' (Lavocat, 1955), and only one carpal has ever been found in *Apatosaurus*. Despite possessing well preserved forelimb material, ossified carpals are currently unknown in *Alamosaurus* and *Opisthocoelicaudia*. The only sauropods described with two carpals are *Brachiosaurus* and *Camarasaurus*, and even here there is some doubt. Marsh (1896) illustrated the forelimb of '*Morosaurus agilis*' (a specimen now referred to *Camarasaurus*) with only a single carpal element. Similarly, Gilmore (1925) described a single 'block-like'

element lying above the proximal ends of metacarpals I and II in *Camarasaurus lentus* (CMNH 11338): there is a very small bone lying near the left wrist, but whether this is another carpal, or a sesamoid displaced from the manus, is not known because most of the important detail is obscured by matrix. A complete forelimb of *Camarasaurus* (FMNH P52120) also possesses a single large carpal element. Finally, it should be remembered that this region of the sauropod skeleton is relatively susceptible to post-mortem disruption and it is possible that the above genera had more carpals than current data suggest.

C164. Number of ossified distal carpals: is two or more (0); is one or none (1). See 'C163'.

C165. Number of ossified distal carpals: is one or more (0); no ossified distal carpals (1). See 'C163'.

C166. Metacarpal I: is shorter than metacarpal II or III (0); is longer than metacarpal III, and is subequal to, or longer than, metacarpal II (1).

C167. Length of the longest metacarpal (usually McIII) divided by the length of the radius: is less than 0.45 (0); is more than 0.45 (1) (McIntosh, 1990b; Wilson & Sereno, 1994; Calvo & Salgado, 1995).

C168. Metacarpal V: is reduced to a splint of bone or absent (0); is large, robust and approximately 90% of the length of the longest metacarpal (1).

C169. Semicircular or 'tubular' arrangement of metacarpals: absent (0); present (1) (McIntosh, 1990b; Upchurch, 1994b). In the derived state, the metacarpals are oriented with their long-axes vertical. In proximal view, the metacarpals are arranged in a semicircular or 'tubular' pattern, with McsII-IV forming the cranial portion of the manus, and McsI and V forming the caudomedial and caudolateral parts respectively (Janensch, 1961: Zu S 194). Figures of the manus of *Shunosaurus* (Zhang *et al.*, 1984: fig. 4A) show the metacarpals lying in a horizontal plane. It is not clear whether this pattern indicates the position in which the metacarpals were found, or merely reflects a convenient lay-out for the purposes of illustration. Examination of the manus of ZDM T5402 suggests that the life-position of the metacarpals would have resembled the derived state seen in other sauropods. *Shunosaurus*, and also *Omeisaurus*, are therefore assigned state '1' in this analysis. Unfortunately, the orientation of the metacarpals in *Vulcanodon* cannot be established now that these elements have been lost (Cooper, 1984).

C170. Manual phalangeal formula: is 2–3–4–5–0 (0): is reduced to 2–2–2–2–1 (1) (Gauthier, 1986; Upchurch, 1995).

C171. Manual phalangeal formula: is 2–2–2–2–1 (or there are more phalanges on digits II–IV) (0); is reduced to 2–2–1–1–1 (1).

Pelvic girdle and hindlimb (C171–C204)

C172. Cranial process of ilium: lies in a vertical plane and is directed cranially or craniolaterally (0); is turned outwards so that it curves laterally into a horizontal plane (1) (McIntosh, 1990b; Powell, 1992; fig. 17; Upchurch, 1995).

C173. Lateral profile of cranial process of the ilium: is triangular and tapers to a point (0); is broad, with a rounded cranial tip (1) (Calvo & Salgado, 1995) (Fig. 13).

C174. Brevis fossa on the caudal process of the iliac blade: present (0); absent (1) (Gauthier, 1986).
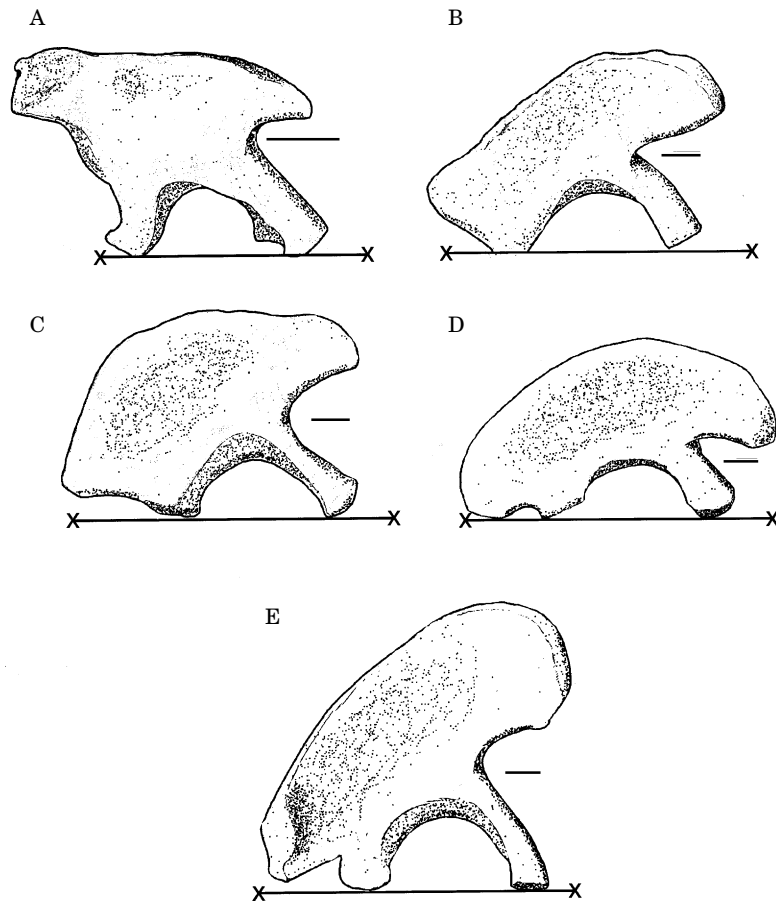
Figure 13. Sauropodomorph ilia in right lateral view: A, *Plateosaurus* (SMNS 13200, after Huene, 1926); B, *Omeisaurus* (ZDM T5701, after He *et al.*, 1988); C, *Patagosaurus* (PVL 4170, after Bonaparte, 1986b); D, *Diplodocus* (based on CMNH 84); E, *Brachiosaurus* (HMN As 13, after Janensch, 1961). X-X defines the chord across the acetabulum (through the pubic and ischiadic articular surfaces). Scale bars = 100 mm.

C175. Lateral profile of the dorsal margin of the ilium: is straight or sinusoidal (0); is strongly convex (1) (Gauthier, 1986) (Fig. 13).

C176. Ischiadic peduncle of the ilium: is large (0); is greatly reduced (1). In the plesiomorphic condition, the ventral margin of the caudal lobe of the ilium lies dorsal to a line drawn through the articular surfaces of the pubic and ischiadic peduncles (i.e. a chord across the acetabulum). The reduction of the ischiadic peduncle in the derived state leads to the ventral margin of the caudal lobe lying level with, or below, the acetabular chord (Fig. 13).

C177. 'Hook'-shaped ambiens process on the pubis: absent (0); present (1) (McIntosh, 1990b).

C178. Ischium:pubis length ratio: is 0.90 or less (0); is 0.90 or more (1) (Yu, 1990 [modified]: Calvo & Salgado, 1995 [modified]).

C179. Middle and distal portion of pubis: forms a transverse sheet of bone which
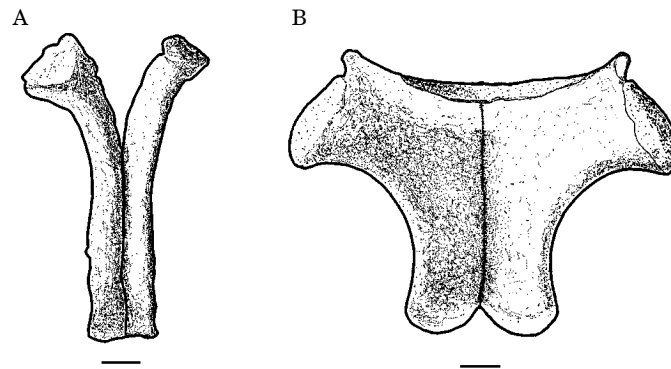
Figure 14. Sauropod ischia in caudodorsal view: A, *Vulcanodon* (SAM QG24, after Cooper, 1984); B, *Alamosaurus* (USNM 15560, after Gilmore, 1946). Scale bars = 100 mm.

is twisted with respect to the proximal end (0); lies in approximately the same plane as the proximal end (1) (Cooper, 1984; Upchurch, 1995 [modified]).

C180. Length of the ischiadic articular surface of the pubis divided by pubis length: is 0.33 or less (0); is 0.45 or more (1) (Calvo & Salgado, 1995 [modified]).

C181. Symphysis between the ischia: terminates at the base of the proximal plates of the ischia (leaving a 'V'-shaped gap cranially in dorsal view) (0); extends to the cranioventral corner of the pubic articular process (which thus obliterates the 'V'-shaped gap between the cranial ends of the ischia) (1) (McIntosh, 1990a [modified]) (Fig. 14). In *Opisthocoelicaudia* the derived condition is carried to an extreme: the pubic and ischiadic symphyses meet each other and obliterate the opening in the ventral 'floor' of the pelvis (Borsuk-Bialynicka, 1977: fig. 13). It is possible that the ventral opening is also closed in at least some other titanosaurids (e.g. *Alamosaurus* and *Saltasaurus*), but at present the relevant material is too poorly preserved to confirm this. In this analysis, therefore, this character is based solely on the structure of the ischium.

C182. Width across the ischiadic shaft (at midlength) divided by the length of the ischium: is less than 0.10–0.15 (0); is 0.20–0.30 (1) (Jacobs *et al.*, 1993 [modified]) (Fig. 15).

C183. Distal end of ischium: is only slightly expanded relative to the rest of the shaft (0); is strongly expanded transversely and especially dorsoventrally (1) (Berman & McIntosh, 1978; McIntosh, 1990b; Upchurch, 1995).

C184. Long-axis of the distal end surface of ischiadic shaft: is directed dorsally or dorsolaterally (0); is directed laterally (1) (Janensch, 1961, Abb. 9–12) (Fig. 16).

C185. Distal shaft of the ischium: is directed caudoventrally at approximately 60° to the horizontal (0); is directed steeply downwards at approximately 80° to the horizontal (1) (Upchurch, 1995).

C186. Femoral shaft: has a sigmoid curve (0); is straight (1) (Gauthier, 1986).

C187. Prominent 'bulge' on the lateral surface of the femur, near the proximal end: absent (0); present (1) (McIntosh, 1990b; Calvo & Salgado, 1995) (Fig. 17). Galton (pers. comm. in McIntosh, 1990b) has suggested that this 'lateral bulge' is the remnant of the lesser trochanter. If correct, this would reverse the polarity of this character. It should be noted, however, that the lateral bulge itself is absent in other dinosaurs, and the lesser trochanter tends to be a ridge-like structure on the
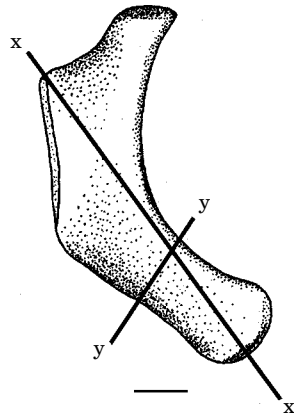
Figure 15. Left ischium of *Andesaurus* in lateral view (MUCPv 132, after Calvo & Bonaparte, 1991); x–x and y–y define the length of the ischium and the breadth of the distal shaft respectively. Scale bar = 100 mm.
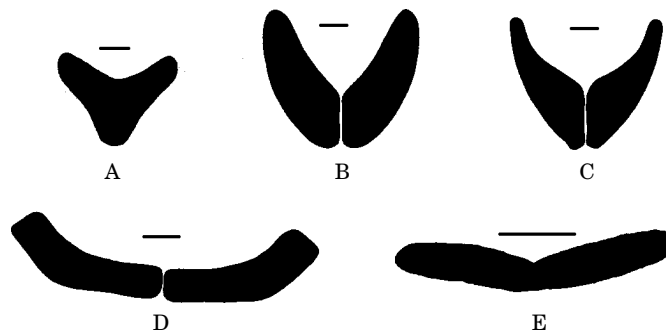
Figure 16. Profiles of the distal ends of sauropod ischia: A, *Vulcanodon* (SAM QG24, after Cooper, 1984); B, *Barosaurus africanus* (HMN K 44, after Janensch, 1961); C, *Dicraeosaurus* (HMN M 7, after Janensch, 1961); D, *Brachiosaurus* (HMN T 2, after Janensch, 1961); E, *Rebbachisaurus* (MUCPv 205, after Calvo & Salgado, 1995). Scale bars = 50 mm.

cranial or craniolateral face of the femoral shaft. Therefore, this analysis follows the polarity used by Calvo & Salgado (1995), and the reduction of the lesser trochanter is treated as a separate character ('C188').

C188. Lesser trochanter on the femur: is well developed (0); is absent or greatly reduced (1) (McIntosh, 1990b).

C189. Fourth trochanter on femur: is situated on the caudal surface, near the midline of the shaft (0); is situated on the caudomedial margin of the shaft (1) (Fig. 17).

C190. Fourth trochanter: is a blade-like structure, often with a 'hook'-shaped or accuminate apex (0); is a low rounded ridge (1).

C191. Horizontal cross-section through the femoral shaft: is subcircular (0); is elliptical or subrectangular (with the transverse diameter wider than the craniocaudal diameter) (1).
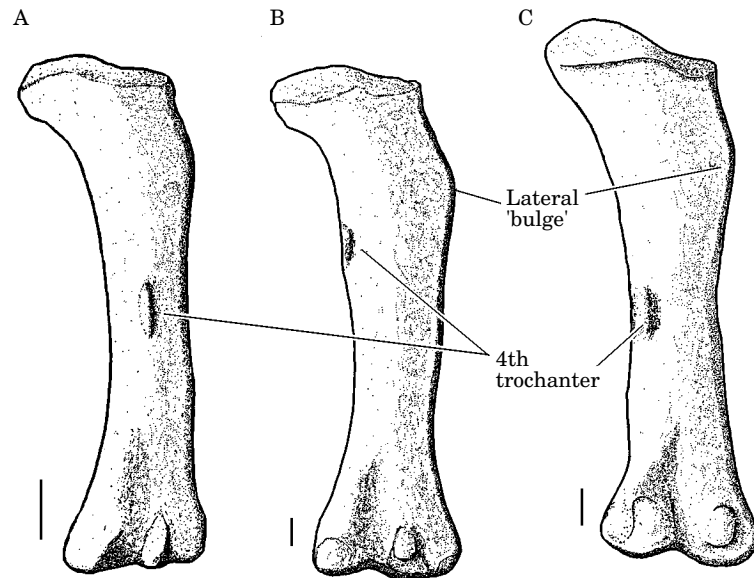
Figure 17. Right sauropod femora in caudal view: A, *Euhelopus* (PMU ex.b, after Wiman, 1929); B, *Brachiosaurus* (HMN St 291, after Janensch, 1961); C, *Opisthocoelicaudia* (Z.Pal. MgD-I/48, after Borsuk-Bialynicka, 1977). Scale bars = 100 mm.

C192. Tibia:femur length ratio: is more than 0.70 (0); is less than 0.65 (1) (McIntosh, 1990b).

C193. Muscle scar on the lateral surface of fibula (at midlength): is oval (0); is an elongate ridge running subparallel to the long-axis of shaft (1) (Powell, 1992).

C194. Ventral surface of the astragalus: is flat or slightly concave transversely (0); is broadly convex transversely (1) (Cooper, 1984; Upchurch, 1995).

C195. Medial end of the astragalus: has a craniocaudal width which is subequal to, or greater than, that of the lateral end (0); has a craniocaudal width which is less than that of the lateral end (i.e. the astragalus tapers medially) (1) (Cooper, 1984; Upchurch, 1995).

C196. Calcaneum: present (0); absent or fails to ossify (1) (McIntosh, 1990b; Upchurch, 1995).

C197. Number of ossified distal tarsals: is two or more (0); is zero (1) (Gauthier, 1986).

C198. Metatarsal I: is either absent or very slender (0); is robust (i.e. maximum length of MtI divided by the transverse proximal width is 1.5 or less) (1) (McIntosh, 1990b: fig. 16.19; Upchurch, 1995).

C199. Laterodistal process on metatarsal I: absent (0); present (1) (Berman & McIntosh, 1978; McIntosh, 1990b; Upchurch, 1995).

C200. Pedal phalangeal formula: is 2–3–4–5–1 (0); is reduced to 2–3–4–3–1 (1) (Upchurch, 1995).

C201. Pedal phalangeal formula: is 2–3–4–3–1 or less reduced (0); is 2–3–4–2–1 (1) (Upchurch, 1995).

C202. Collateral ligament pits on the pedal phalanges: present (0); are greatly reduced or absent (1) (Upchurch, 1995).
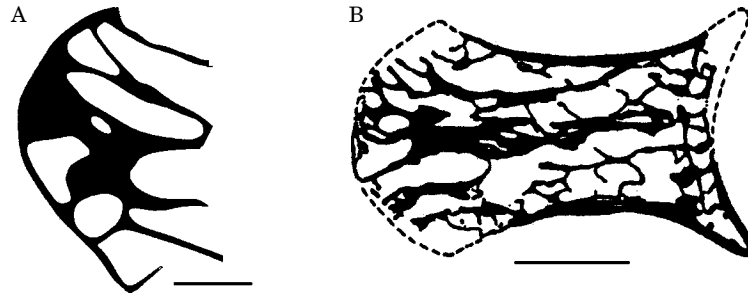
Figure 18. Sections through presacral vertebrae: A, sagittal section through the cranial end of a *Brachiosaurus* cervical centrum (specimen number not known, after Janensch, 1947); B, horizontal section through a *Saltasaurus* dorsal centrum (PVL 4017–43, after Powell, 1992). Scale bars = 50 mm.

C203. Pedal phalanx II-2: is square or rectangular in dorsal view (0); is cranio-caudally compressed (1).

C204. Proximal pedal phalanges: are subrectangular in dorsal view (0); narrow towards their lateral and palmar margins (1).

Miscellaneous (C205)

C205. Osseous tissue structure of presacral vertebrae: is 'spongy' (i.e. a large number of very small spaces within the bone) (0); is composed of a small number of very large 'cancellar' spaces separated by thin bone lamellae (1) (Powell, 1992) (Fig. 18).

ANALYSES AND RESULTS

Cladistic analysis

The data-matrix (Appendix 1) has been analysed using PAUP 3.1.1 (Swofford, 1993). The heuristic search option found two most parsimonious trees ('MPTs') which are identical except for the relationships between *Euhelopus*, *Omeisaurus* and *Mamenchisaurus*. A strict consensus tree based on the two MPTs, with relevant statistics, is shown in Figure 19.

In order to investigate the effect of unordered and ordered multistate characters, a separate data-matrix ('matrix U') has been constructed. Matrix U can be created by converting the following binary coded characters into a series of single columns: C2–3, C15–16, C26–27, C47–48, C62–63, C69–70, C73–74, C75–79, C81–82, C97–98, C120–122, C125–126, C129–131, C145–146, C147–148, C155–156, C158–159, C163–165, C170–171, C200–201. Heuristic analysis of matrix U, with all multistate characters unordered, produced nine MPTs. These trees are similar to that in Figure 19, except: (i) the relationships within the Euhelopodidae are modified; (ii) three MPTs place *Barapasaurus* as the sister-taxon to the cetiosaurid-Neosauropoda clade (i.e. Node F); (iii) the relationships within the Titanosauroidea

Vulcanodon
Barapasaurus
Shunosaurus
Euhelopus
Mamenchisaurus
Omeisaurus
Patagosaurus
Cetiosaurus
Haplocanthosaurus
Nemegtosaurus
Quaesitosaurus
Rebbachisaurus
Amargasaurus
Dicraeosaurus
Apatosaurus
Barosaurus
Diplodocus
Camarasaurus
Brachiosaurus
Lapparentosaurus
Phuwiangosaurus
Andesaurus
Malawisaurus
Alamosaurus
Opisthocoelicaudia
Saltasaurus

D < 50% (2)
E 57%
S 85% (2)
V 97% (6)
R 81% (1)
A
B 72% (1)
C < 50% (1)
F < 50% (1)
G 54% (1)
H < 50% (1)
I < 50% (1)
T 60% (5)
U 88% (5)
W 98% (5)
X 99% (5)
L < 50% (3)
J < 50% (1)
K < 50% (1)
M < 50% (1)
N 80% (3)
O 68% (1)
P < 50% (1)
Q 57% (1)

Named nodes:

A = Sauropoda
C = Eusauropoda
D = Euhelopodidae
I = Neosauropoda
J = 'Brachiosauria'
L = Brachiosauridae
M = Titanosauroidea
P = Titanosauridea
R = Diplodocoidea
S = Nemegtosauridae
V = Dicraeosauridae
W = Diplodocidae

Figure 19. Strict consensus tree based on two MPTs (see text). Tree statistics: length = 346 steps; CI = 0.553; RI = 0.737; RC = 0.448. Bootstrap values are shown as percentages, decay indices are in parentheses. See Appendix 3 for a list of the synapomorphies uniting each of the nodes. 'Brachiosauria' is suggested as an informal name for node J.

are modified. Although the choice of ordered or unordered multistate characters may be responsible for these differences in tree topology, missing data may also be an important factor. As mentioned in the 'Methods' section, binary coding of multistate characters can reduce the amount of missing data in a matrix. The creation of matrix U reversed this process and resulted in an increase in missing data. To test this possibility, a heuristic analysis of matrix U was performed, this time with all the modified multistate characters ordered. This analysis produced seven MPTs of length 363. If the use of ordered versus unordered characters was solely responsible for differences in tree topology, we should expect no difference between the ordered analysis of matrix U and the analysis of the matrix in Appendix 1. Since differences do occur, it seems likely that an increase in missing data has had a significant effect. Given that the author prefers the coding strategy set out in
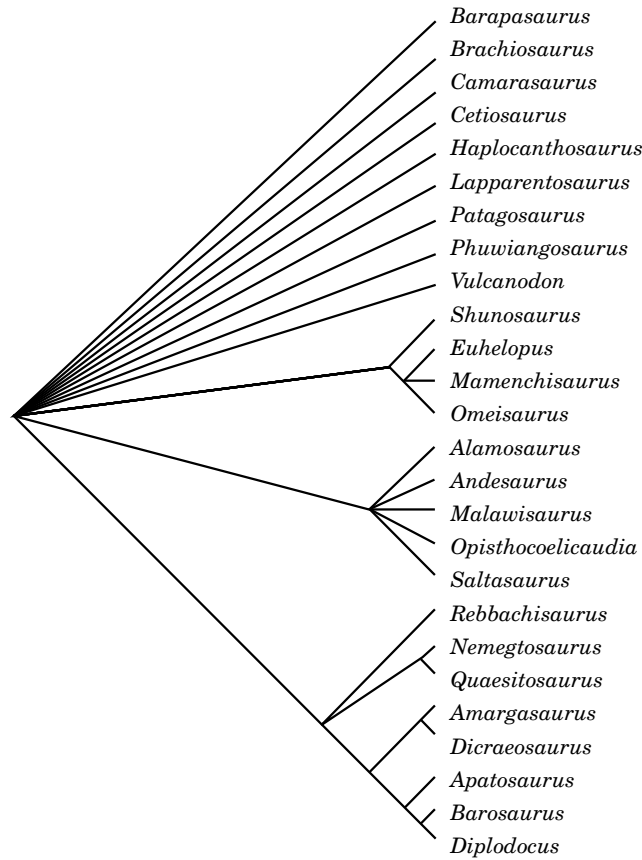
Figure 20. Strict consensus tree based on 35 fundamental trees of length 346 and 347 steps (see text).

the 'Methods' section, the two MPTs summarized in Figure 19 will form the basis for discussion of sauropod phylogeny and classification.

Exploring the data

The strengths and weaknesses of particular relationships, and the data-matrix as a whole, have been explored using a variety of approaches:

(i) Investigation of less parsimonious tree topologies. A heuristic PAUP analysis collected all trees of length 346 (i.e. MPTs) and 347 steps. This analysis produced 35 fundamental trees which have been summarized using strict and Adams consensus methods (Figs 20, 21). The strict consensus tree is poorly resolved: taken at face value, it implies that only the Euhelopodidae, Titanosauroidea (excluding *Phuwiangosaurus*) and Diplodocoidea are common to all fundamental trees. The Adams consensus tree, however, displays considerably higher resolution. This discrepancy may indicate that there is much greater agreement between the fundamental trees than is implied by the strict consensus tree (Wilkinson, 1994). Certain sets of relationships (N-taxon statements), common to all fundamental trees, could be obscured by the variable
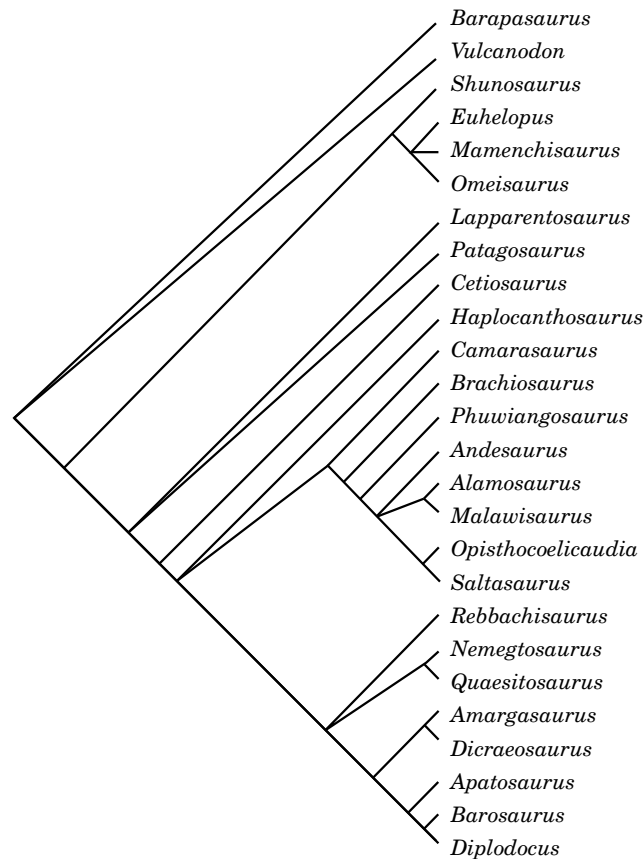
Figure 21. Adams consensus tree based on 35 fundamental trees of length 346 and 347 steps (see text).

position of one or more 'unstable' taxa. This possibility can be explored by 'pruning' (i.e. deleting *a posteriori*) an 'unstable' taxon, and examining whether the recalculated consensus tree has increased in resolution. For example, the deletion of *Lapparentosaurus* produces a marked increase in resolution (compare Figs 20 and 22). Further increases in resolution are achieved by pruning *Barapasaurus* and *Haplocanthosaurus* (Fig. 23). Thus, the fundamental trees share many common relationships, but *Barapasaurus*, *Haplocanthosaurus* and *Lapparentosaurus* are rather 'unstable'. Interestingly, the 'alternative' positions occupied by these three genera correspond with those proposed by some previous studies: *Barapasaurus* and *Lapparentosaurus* could belong to the paraphyletic cetiosaurid assemblage (Bonaparte, 1986a); *Haplocanthosaurus* could be a member of the 'Brachiosauria' (Wilson & Sereno, 1994; Upchurch, 1995).

(ii) Decay analysis. A Decay analysis, using PAUP and Autodecay 3.0.2 (Erikson & Wikström, 1996), discovers the number of additional steps required to break-up a particular set of relationships, and thus can provide an estimate of the relative strengths of nodes. This method therefore represents an alternative approach to the investigation of less parsimonious trees (see (*i*) above). The decay indices for the sauropod MPT are summarized in Figure 19. A majority of the nodes have decay indices of '1', suggesting very weak support for the clades concerned. This poor
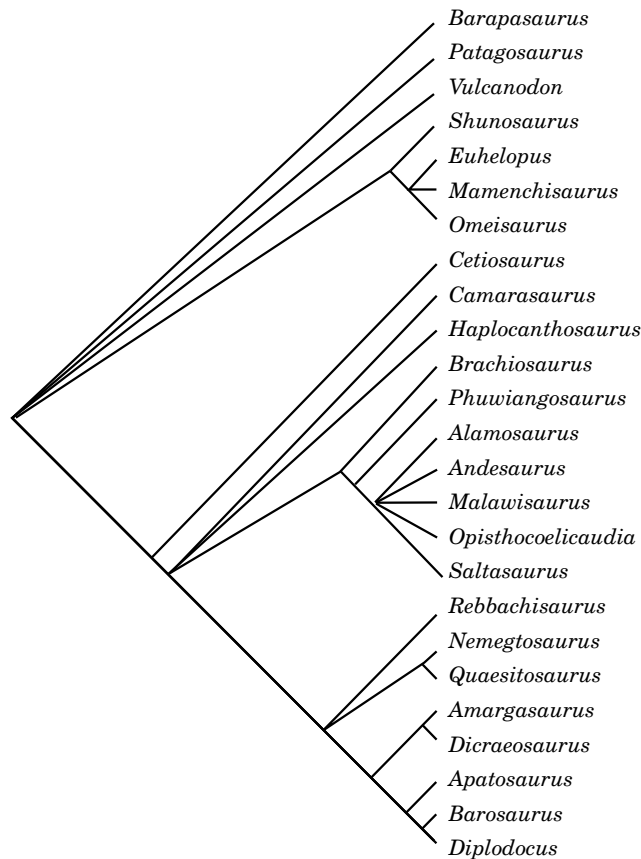
Figure 22. Strict consensus tree based on 35 fundamental trees of length 346 and 347 steps, calculated after *Lapparentosaurus* has been pruned.

performance, however, could be the result of the presence of a few unstable taxa, rather than a 'global' weakness in the data.

(iii) Bootstrapping. A bootstrap analysis (300 replicates) was performed on the data-matrix. The bootstrap support values for each node are summarized in Figure 19. The results suggest relatively low support for most of the relationships in the sauropod MPT: many nodes have bootstrap values of 50% or lower, and only six nodes have values higher than 80%. This poor performance, however, may not be entirely due to character conflict. The data-matrix contains a relatively high proportion of missing data (∼46%). For certain taxa, a small number of 'informative' characters are greatly outnumbered by missing data. Under these circumstances, the random resampling of the original data-matrix (which underlies the bootstrap method), could produce some taxa which are highly unstable.

Whatever the cause of taxon instability, it is certainly possible that an unstable taxon can lower the bootstrap values for clades which are otherwise quite well supported. One way to test this possibility is to prune such unstable taxa, and then recalculate bootstrap supports. Wilkinson (1996) has suggested a method for assessing the impact of such taxa, based on the use of majority-rule reduced consensus trees.
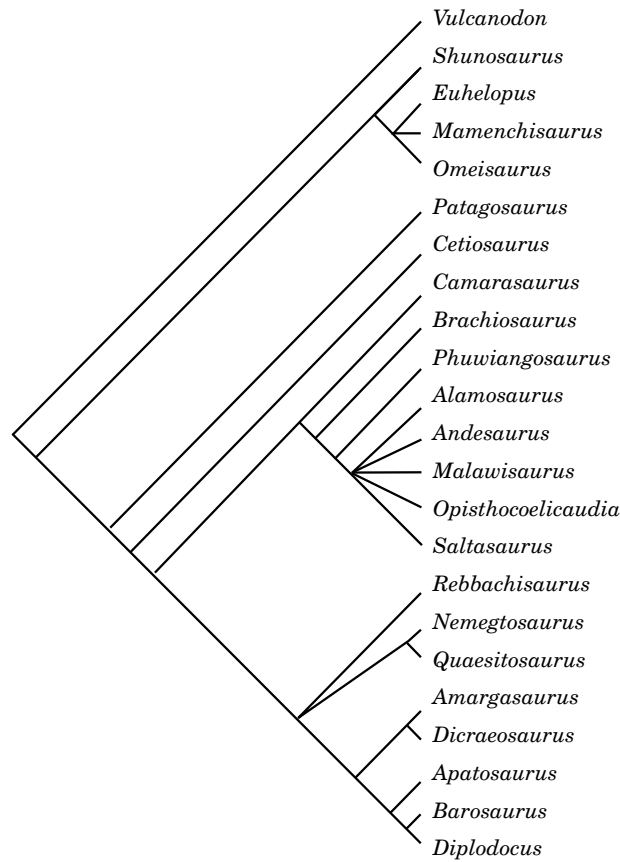
Figure 23. Strict consensus tree based on 35 fundamental trees of length 346 and 347 steps, calculated after *Lapparentosaurus*, *Barapasaurus* and *Haplocanthosaurus* have been pruned.

TABLE 2. Summary of the effect of *a posteriori* taxon deletions on bootstrap support values

Clade	Original bootstrap support	Pruned taxon	New bootstrap support
Node O	68%	*Andesaurus*	89.6%
Node N	80%	*Malawisaurus*	83.1%
Titanosauridae	<50%	*Malawisaurus*	82.0%
Titanosauroidea	<50%	*Phuwiangosaurus*	81.7%
Neosauropoda	<50%	*Haplocanthosaurus*, *Lapparentosaurus*	75%

Applying this approach, some possible deletions and their effects have been identified (Table 2). The most marked increases in bootstrap support occur in the titanosauroid clade when either *Andesaurus* or *Malawisaurus* are deleted. Curiously, the exclusion of one of these genera makes it more likely that the remaining one lies outside the Titanosauridae. Inspection of the data-matrix reveals no obvious character conflicts

TABLE 3. Summary of results of randomization tests. Abbreviations: CC = character conflicts; Full = based on entire data-matrix, including outgroup; Ingroup = based on ingroup only (i.e. 'Ancestor' excluded); N = number of replicates; non-rand. = missing data were not randomized; PTP = permutation tail probability; Rand. = missing data were randomized; S = steps (i.e. tree length)

Test	Matrix	Missing data	Mean Random	Observed	N	PTP
Parsimony	Full	Rand.	472.42 S	283.00 S	99	0.01
Parsimony	Ingroup	Non-rand.	472.49 S	283.00 S	99	0.01
Compatibility	Full	Rand.	3731.54 ± 43.97 CC	2390 CC	999	0.001
Compatibility	Full	Non-rand.	5173.69 ± 160.02 CC	2390 CC	999	0.001

which are removed by the deletion of one of these taxa: the possibility that this result reflects the effects of missing data requires further exploration. Pruning *Lapparentosaurus* and *Haplocanthosaurus* results in an increase in support for the monophyly of the Neosauropoda, but support for the 'brachiosaurian' clade remains low (59%). The latter probably reflects the considerable character conflict caused by convergence between the Titanosauroidea and Diplodocoidea.

(iv) Randomization tests. Randomization tests are based on a comparison of data quality between the original data and replicate data sets. The latter are created by randomly permuting the character states assigned to taxa (independently for each character). This procedure decreases character congruence to the level which would be expected from chance alone (Faith & Cranston, 1991). The null hypothesis, in randomization tests, is that the original data cannot be distinguished from random and phylogenetically uninformative data. The permutation tail probability (PTP) is the proportion of the data sets (original and randomly permuted) with as good a measure of quality as the original data: the PTP therefore provides a test statistic for rejection or acceptance of the null hypothesis. The data-matrix in Appendix 1 has been subjected to four randomization tests (Table 3). Parsimony-based randomization tests use tree length as a measure of data quality (Archie, 1989; Faith & Cranston, 1991), whereas compatibility-based tests employ the number of character conflicts (Wilkinson, 1992b; Alroy, 1994). In all four tests, the lowest possible PTPs were obtained, allowing rejection of the null hypothesis. This suggests that character conflict and missing data, although common in the data-matrix, do not totally obscure the phylogenetic 'signal'.

The different results obtained by the two compatibility tests are of wider interest (Wilkinson, pers. comm., 1997). The mean incompatibility counts are 3731 and 5175 when missing data are randomized or held constant respectively. Although this does not affect the current study, it is possible to conceive a situation in which a data-matrix passes or fails the randomization test depending on how missing data have been treated. Presumably this discrepancy is particularly marked here because of the high proportion of missing data.

The four investigations described above provide some insight into the relative 'reliability' of particular sauropod relationships. In general, the data-matrix contains considerable 'noise' in the form of both homoplasy and missing data. While the former is not abnormally high given the size of the matrix, the latter (at ∼46%) is certainly more numerous than in the majority of cladistic analyses. This 'noise'

results in relatively low support, for the majority of nodes, when bootstrapping and decay analyses are applied. Some of these low support values are deceptive, since they reflect the presence of one unstable taxon within an otherwise well supported clade. In other cases, however, substantial homoplasy means that the evidence in support of the most parsimonious interpretation is only slightly stronger than one or more alternative hypotheses of relationship.

Clearly, some relationships within the Sauropoda are more 'reliable' than others. Diplodocoid monophyly, and the relationships within this group, represent the most robust portion of the cladogram. Many other relationships, including those between the major lineages, receive moderately strong support, but are weakened by uncertainty surrounding the positions of particular constituent taxa. Finally, the relationships of *Barapasaurus*, *Haplocanthosaurus* and *Lapparentosaurus* should be treated with considerable caution: the evidence for the positions of these taxa in Figure 19 is only slightly stronger than that supporting rather different arrangements.

DISCUSSION

Sauropod phylogenetic relationships

The Sauropoda, including *Vulcanodon*, is united by 11 synapomorphies (Node A, Appendix 3). *Vulcanodon* is now widely accepted as the most plesiomorphic sauropod (Gauthier, 1986; Bonaparte, 1986a; McIntosh, 1990b; Yu, 1990; Upchurch, 1995), although this perspective may alter when early Chinese taxa (such as *Kunmingosaurus*) are added to the analysis.

There are currently two main hypotheses concerning the relationships of *Barapasaurus*. The 'majority' view (based largely on the structure of the pubis) considers this Indian genus to be the sister-taxon to the Eusauropoda (Gauthier, 1986; Yu, 1990; Calvo & Salgado, 1995; Upchurch, 1995). Bonaparte (1986a), however, noted some remarkable similarities between the dorsal vertebrae of *Barapasaurus* and *Patagosaurus* (see 'C106' here) and suggested that these genera represent relatively 'advanced' cetiosaurids. Bonaparte's vertebral characters have been incorporated into the present study, but have not caused *Barapasaurus* to cluster with *Patagosaurus* and *Cetiosaurus*. Nevertheless, it must be admitted that the position of *Barapasaurus* is only very weakly supported. For example, of the 36 synapomorphies uniting the Eusauropoda (i.e. excluding *Barapasaurus*), only three can be confirmed as absent in the Indian taxon (and two of these are somewhat equivocal). One additional possibility is that the relationships of *Patagosaurus* have been incorrectly reconstructed: perhaps both *Barapasaurus* and *Patagosaurus* lie outside the Eusauropoda. It will remain difficult to clarify the relationships of these forms until certain key areas of missing data are eliminated.

The Euhelopodidae is a monophyletic group which includes *Shunosaurus* (Upchurch, 1995). Some of the synapomorphies uniting *Shunosaurus* and other euhelopodids, which were originally proposed by Upchurch (1995), have now been discarded. For example, both *Shunosaurus* and *Omeisaurus* were initially considered to possess a tail club (Dong, Peng & Huang, 1989; Dong, 1992). An examination of *Omeisaurus* material (ZDM T5701–T5710), and the description by He *et al.* (1988), indicate that there is no evidence for a tail club in this genus. Thus, the derived condition

in *Shunosaurus* is regarded as an autapomorphy. The current analysis has, however, introduced some new characters which continue to support the inclusion of *Shunosaurus* within the Euhelopodidae (e.g. lateral compression of the cranial cervical centra and the prominent ridge on the dorsal surface of each sternal plate). This phylogenetic hypothesis contrasts with other studies which have generally regarded *Omeisaurus* as being more closely related to cetiosaurids and neosauropods (*sensu* Upchurch, 1995) than *Shunosaurus* (Yu, 1990; Wilson & Sereno, 1994). Some of the problems underlying this disagreement are discussed in the section 'Morphological evolution within the Sauropoda', pp. 84–88.

The inclusion of *Patagosaurus* and *Cetiosaurus* provides new insights into the relationship between the Cetiosauridae and the more 'advanced' neosauropod lineages. Many authors have suggested that the Upper Jurassic and Cretaceous sauropod groups were descendants of the Cetiosauridae (see review in Upchurch, 1995). Cladistic analysis tends to support this view and indicates that *Cetiosaurus* is closer to the neosauropods than is *Patagosaurus*. The relationships of *Cetiosaurus* were poorly resolved in the analysis of Upchurch (1995), with this genus occupying three possible positions on the cladogram. The inclusion of new data from the partial skeleton in the Leicester Museum (LCM 468.1968) (Upchurch & Martin, in prep.), however, has eliminated two of these three possibilities.

Although *Haplocanthosaurus* occupies only one position in the MPTs of the current analysis, a review of recent studies suggests that this taxon is highly problematic. McIntosh (1989, 1990b) regarded this genus as an Upper Jurassic relic of the Middle Jurassic cetiosaurid radiation. While the cladograms of Wilson & Sereno (1994) and Upchurch (1995) differ somewhat in topology, both considered *Haplocanthosaurus* to be closely related to *Camarasaurus* and *Brachiosaurus*. Calvo & Salgado (1995) split *Haplocanthosaurus* into two species (*H. priscus* and *H. delfsi*) and found that this genus is paraphyletic with respect to the Diplodocoidea. Finally, the current analysis has placed *Haplocanthosaurus* as the sister-taxon to the Neosauropoda, which in some respects brings us full circle to McIntosh's (1990b) original interpretation. The inclusion of *Rebbachisaurus* has had some influence on the position of *Haplocanthosaurus*. Although *Rebbachisaurus* is clearly a diplodocoid, it possesses cranial chevrons which are 'open' at their proximal ends ('C146'), and the distal end cross-section of the ischium has a laterally directed long-axis ('C184'). These derived states are also present in *Haplocanthosaurus*, *Camarasaurus*, *Brachiosaurus* and titanosauroids. If *Rebbachisaurus* had been omitted from the analysis, these synapomorphies would have supported the inclusion of *Haplocanthosaurus* within the 'Brachiosauria' (Node J): this has been confirmed by a heuristic PAUP analysis. Such a result illustrates the potential importance of taxa with novel character state combinations.

The Neosauropoda contains the Camarasauridae, Brachiosauridae, Titanosauroidea and Diplodocoidea (Upchurch, 1995). The majority of previous analyses have accepted the view that *Camarasaurus* and *Brachiosaurus* are more closely related to each other than either is to the Diplodocoidea (Gauthier, 1986; Yu, 1990; Wilson & Sereno, 1994; Upchurch, 1995). Calvo & Salgado (1995), however, produced a MPT in which *Camarasaurus* was the sister-taxon to a brachiosaurid–titanosauroid–diplodocoid clade. The latter assemblage is supported by five synapomorphies, but several of these characters are problematic. For example, Calvo & Salgado suggest that *Camarasaurus* possesses a hyposphene-hypantrum system on all of its dorsal vertebrae (the 'primitive' state), whereas this structure is absent on the two most cranial dorsals in brachiosaurids, titanosauroids and diplodocoids. In fact,

McIntosh *et al.* (1996) demonstrate that the hyposphene-hypantrum system is absent on at least the first two dorsals of *Camarasaurus lewisi* (BYU 9047). Given that tree length increases by only five steps when *Camarasaurus* is moved to a position equivalent to that suggested by Calvo & Salgado (1995) (i.e. between nodes H and I), it is certainly conceivable that *Camarasaurus* is not a member of the 'Brachiosauria'. For the present, however, the most parsimonious view of the relationships of *Camarasaurus* will be followed.

The current analysis supports McIntosh's (1990b) view that *Lapparentosaurus* is a brachiosaurid rather than a primitive cetiosaurid. *Lapparentosaurus* is a problematic taxon because it seems to possess an unusual combination of plesiomorphic and derived characters. Upchurch (1995) argued that many of the plesiomorphic states actually reflect the juvenile status of the available material. Certainly, derived features of the scapula, ilium and femur support inclusion of this genus within the Neosauropoda (or closely related cetiosaurids) and the structure of the ischium is very reminiscent of that in *Brachiosaurus*.

One of the most controversial aspects of neosauropod relationships is the position of the Titanosauroidea. Traditionally, diplodocoids and titanosauroids were placed in the same family ('Titanosauridae', Romer, 1956), a view which was supported by preliminary cladistic analyses (Gauthier, 1986; Yu, 1990; Upchurch, 1995). Gilmore (1946), however, noted several similarities between the Brachiosauridae and Titanosauridae (*sensu* McIntosh, 1990b), and a sister-group relationship between these clades has recently been proposed on the basis of cladistic analysis (Wilson & Sereno, 1994; Calvo & Salgado, 1995). The latter possibility is supported by the current work, although inspection of the character-set reveals considerable convergence between the Titanosauroidea and the Diplodocoidea (a sister-group relationship between these two clades increases tree length by only three steps). For example, the teeth, dorsal neural spines, cranial caudal vertebrae and wrist of titanosauroids and diplodocoids share apomorphies which are apparently absent in brachiosaurids. Furthermore, future discoveries may strengthen the evidence supporting a diplodocoid-titanosauroid sister-group relationship. For example, *Saltasaurus* may have small, laterally facing supratemporal fenestrae ('C32', 'C33'). Nevertheless, it remains the case that the brachiosaurid–titanosauroid sister-group relationship is supported by more numerous (and often 'better quality') synapomorphies.

The Titanosauroidea (Upchurch, 1995) is here defined as including all those taxa which are more closely related to 'true' titanosaurids (e.g. *Saltasaurus*) than they are to the Brachiosauridae. One unexpected result of the cladistic analysis is the suggestion that *Phuwiangosaurus* is the sister-taxon to the remaining titanosauroids. Martin *et al.* (1994), who first described this genus, were unable to place it within any of the traditional sauropod families. This difficulty may have resulted from the emphasis on comparisons between *Phuwiangosaurus* and other Asian taxa (mainly the very distantly related euhelopodids). *Phuwiangosaurus* actually possesses a number of apomorphies which place it within the Neosauropoda, and there are four derived states which unite it with the Titanosauroidea. This genus displays an unusual combination of character states which may have played an important role in determining cladogram topology. For example, the dorsal vertebrae of *Phuwiangosaurus* apparently lack the pre- and postspinal laminae found in other titanosauroids and the Diplodocoidea. Thus, the interpretation of *Phuwiangosaurus* as a 'basal'

titanosauroid removes some of the support for a titanosauroid-diplodocoid sister-group relationship.

The relationships within the Titanosauroidea are particularly poorly understood, largely because of the extremely fragmentary nature of most genera. The cladogram in Figure 19 includes some relatively well supported nodes (e.g. Nodes N and O) and may provide a tentative framework for understanding titanosauroid evolution. As proposed by Bonaparte & Coria (1993), it seems that Lower and Middle Cretaceous titanosauroids form a paraphyletic assemblage (the Andesauridae) which gave rise to the Upper Cretaceous Titanosauridae. The relationships of *Opistho-coelicaudia* are particularly significant. This taxon was originally interpreted as a camarasaurid (Borsuk-Bialynicka, 1977; McIntosh, 1990b), but more recently it has been associated with the Titanosauroidea (Upchurch, 1995). This is an important issue since, if correctly identified, *Opisthocoelicaudia* would represent one of the most complete articulated titanosauroid specimens. There now appears to be compelling evidence that, despite the absence of the 'traditional' procoelous cranial caudals, *Opisthocoelicaudia* is a genuine titanosauroid: placement of this genus as the sister-taxon to *Camarasaurus* increases tree length by 23 steps. In this analysis, *Opisthocoelicaudia* is interpreted as the sister-taxon to *Saltasaurus*. These two genera are united by nine synapomorphies, of which four are definitely absent in *Alamosaurus* (Node Q). The appearance of *Alamosaurus* in the Maastrichtian of the south-western U.S.A. has been interpreted as evidence for an influx of South American forms across the Panamanian 'land-bridge' (Bonaparte, 1984; Lucas & Hunt, 1989). While this scenario is supported by several similarities between *Alamosaurus* and South American titanosaurids (e.g. the possession of a biconvex first caudal centrum), the sister-group relationship between *Saltasaurus* (from Argentina) and *Opisthocoelicaudia* (from Mongolia) might indicate a more complex biogeographic history.

The most stable portion of the current cladogram is represented by the Di-plodocoidea. The relationships of the diplodocoid taxa are essentially those found by Upchurch (1995), with the addition of *Rebbachisaurus* in the position proposed by Calvo & Salgado (1995).

Systematic classification of the Sauropoda

The most recent and detailed systematic classifications of the Sauropoda are those of McIntosh (1990b) and Upchurch (1994a). Despite considerable uncertainty concerning sauropod relationships, these two classifications agree in general, although there are some minor differences with respect to the use of subfamilies and the positions of individual taxa. A revised classification of the Sauropoda, based on the present analysis, is proposed in Table 4. This system includes several paraphyletic groups, such as the Vulcanodontidae, Cetiosauridae and Andesauridae. Although generally undesirable, paraphyletic groups can lend stability to a classification: this is an important consideration when dealing with a clade where the evolutionary relationships are problematic. The practice of designating a name for each node in a cladogram has been avoided, although some potentially 'useful' higher taxa are suggested.

TABLE 4. A systematic classification of the Sauropoda. This classification is based on the evolutionary relationships of sauropods proposed in the current study, and the taxonomic work of McIntosh (1990b) and Upchurch (1995). The term 'Vulcanodontidae' is preferred to 'Barapasauridae' (Jain *et al.*, 1979; Hunt *et al.*, 1994) for two reasons. Firstly, although Barapasauridae has 'priority', Vulcanodontidae has been used much more widely in the context of a basal sauropod radiation (Cooper, 1984; Bonaparte, 1986a; McIntosh, 1989, 1990a,b; Upchurch, 1994a, 1995). Secondly, the possibility that *Barapasaurus* may eventually be removed from this family, and placed within the Cetiosauridae, discourages the use of a family name based on this genus. 'Titanosauroidea' is preferred to the earlier equivalent term 'Titanosauria' suggested by Bonaparte & Coria (1993). This decision is based on the view that a set of taxonomic categories of superfamily rank will bring greater consistency and stability to sauropod classification

Sauropodomorpha Huene, 1932
  Sauropoda Marsh, 1878
    Vulcanodontidae Cooper, 1984
      Barapasaurus Jain *et al.*, 1975
      Ohmdenosaurus Wild, 1978
      Vulcanodon Raath, 1972
      Zizhongosaurus Dong, Zhou & Zhang, 1983
  Eusauropoda Upchurch, 1995
    Euhelopodidae (= 'Euhelopodinae', Romer, 1956)
      Datousaurus Dong & Tang, 1984
      Euhelopus Romer, 1956
      Mamenchisaurus Young, 1954
      Omeisaurus Young, 1939
      Shunosaurus Dong *et al.*, 1983
    Cetiosauridae Lydekker, 1888
      Amygdalodon Cabrera, 1947
      Cetiosaurus Owen, 1841
      Haplocanthosaurus Hatcher, 1903a
      Patagosaurus Bonaparte, 1979
  Neosauropoda Upchurch, 1995
    Camarasauridae Cope, 1877a
      Aragosaurus Sanz *et al.*, 1987
      Camarasaurus Cope, 1877b
    Brachiosauridae Riggs, 1904
      Brachiosaurus Riggs, 1903
      Lapparentosaurus Bonaparte, 1986a
      Pleurocoelus Marsh, 1888
  Titanosauroidea Upchurch, 1995
    Andesauridae Calvo & Bonaparte, 1991
      Andesaurus Calvo & Bonaparte, 1991
      Malawisaurus Jacobs *et al.*, 1993
      Phuwiangosaurus Martin *et al.*, 1994
    Titanosauridae Lydekker, 1885
      Alamosaurus Gilmore, 1922
      Opisthocoelicaudia Borsuk-Bialynicka, 1977
      Saltasaurus Bonaparte & Powell, 1980
  Diplodocoidea Upchurch, 1995
    Nemegtosauridae Upchurch, 1995
      Nemegtosaurus Nowinski, 1971
      Quaesitosaurus Kurzanov & Bannikov, 1983
    Dicracosauridae Huene, 1927
      Amargasaurus Salgado & Bonaparte, 1991
      Dicraeosaurus Janensch, 1914
    Diplodocidae Marsh, 1884
      Apatosaurus Marsh, 1877
      Barosaurus Marsh, 1890
      Diplodocus Marsh, 1878
      Seismosaurus Gillette, 1991
  Diplodocoidea incertae sedis
      Cetiosauriscus Huene, 1927
      Rebbachisaurus Lavocat, 1954

Morphological evolution in the Sauropoda

Morphological evolution within the Sauropoda can be examined by mapping character state transformations onto the cladogram. To illustrate the insights which can be gained from such an approach, three important aspects of sauropod morphology will be examined.

Dentition. The evolution of sauropod tooth morphology has been considered elsewhere (Upchurch, 1994a): the results of the current analysis, however, necessitate some revision of these earlier ideas. The most plesiomorphic teeth are found in *Kunmingosaurus* (pers. obs., 1995). These teeth are essentially spatulate in outline, but are rather narrow labiolingually and possess only a very shallow lingual concavity. In *Barapasaurus*, *Patagosaurus* and the Euhelopodidae, the teeth have become larger and more robust but retain their spatulate shape. The labiolingual width of these teeth has increased (especially at the base of the crown) and the lingual concavity is deeper. The teeth of *Shunosaurus* are, in some respects, intermediate between those of *Kunmingosaurus* and other early sauropod groups, particularly with regard to the depth of the lingual concavity. The current position of *Shunosaurus* on the cladogram does not support the view that these dental features represent an evolutionary intermediate stage, and indeed the relatively slender tooth crowns of *Shunosaurus* may be autapomorphic. Large heavy spatulate teeth (which lack serrations) were probably present in cetiosaurids and retained by 'basal' neosauropods.

Within the Neosauropoda there are apparently two independent acquisitions of the more slender, parallel-sided, 'peg'-like tooth shape. The teeth of *Brachiosaurus* can be interpreted as intermediate between the plesiomorphic spatulate condition and the derived 'peg'-like shape. For example, *Brachiosaurus* teeth are relatively large and heavy, and they retain the lingual concavity and labial grooves ('C69'), but the crowns are nearly parallel-sided and have become more elongate. In titanosauroids, the labial grooves are usually retained, but the lingual concavity is absent and the crowns are more slender. In spatulate teeth, the lingual concavity normally contains a 'vertical' ridge which runs from the base of the crown to a point close to the apex. It seems probable that the obliteration of the lingual concavity, in 'peg'-like teeth, was achieved partly by the increased slenderness of the crown, and partly by an increase in the size of the lingual ridge just described. As a result, the lingual surfaces of 'peg'-like tooth crowns resemble the labial surfaces, i.e. a prominent central convex area is separated from the mesial and distal margins of the crown by grooves. Under this interpretation, the relatively sharp mesial and distal edges of 'peg'-like tooth crowns do not represent the acquisition of new features, rather they are remnants of structures present in spatulate teeth.

A similar transition from spatulate to 'peg'-like is assumed to have occurred in 'basal' diplodocoids, although there are currently no examples of any intermediate states. The teeth of diplodocoids become particularly long and slender, with SI values of 5.0 or more. The labial grooves are retained on the teeth of nemegtosaurids, *Rebbachisaurus* and dicraeosaurids, but are greatly reduced or absent in the Diplodocidae.

Neural spine lamination in dorsal vertebrae. Few studies, except Bonaparte (1986a), have considered the detailed structure and evolution of sauropod presacral vertebrae. Description and discussion of vertebral laminae, especially those on the dorsal vertebrae, have been greatly hampered by problems relating to homology and

nomenclature. This section, therefore, examines homology and homoplasy in the structure of the sauropod dorsal neural spine, and addresses problems relating to descriptive terminology.

The dorsal neural spines of non-sauropod dinosaurs are typically laterally compressed plates (known as the 'spine core' here) which lack any supporting laminae. Early sauropods, such as *Barapasaurus*, cetiosaurids and euhelopodids, possess a basic 'tetraradiate' spine (Bonaparte, 1986a), which is formed by the addition of a prominent lamina at each of the craniolateral and caudolateral margins of the spine core. These new structures (the supraprezygapophyseal and suprapostzygapophyseal laminae) create four vertical hollows; one on either side of the spine, one on its cranial face, and one on its caudal face (Fig. 9). In horizontal section, such spines are usually not symmetrical about a transverse plane since the suprapostzygapophyseal laminae are more prominent than the supraprezygapophyseal ones. The supradiapophyseal lamina is also a new acquisition present on the middle and caudal dorsals of these early sauropods. This lamina links the dorsal surface of the transverse process to the lateral surface of the spine core and the cranial face of the suprapostzygapophyseal lamina.

The only 'primitive' sauropods (in this analysis), which do not possess a truly tetraradiate spine, are *Shunosaurus* and *Lapparentosaurus*. In the former, the dorsal neural spines are essentially laterally compressed plates which possess a set of ridges corresponding to the prominent laminae described above. The suprapostzygapophyseal ridges do not run up the caudolateral margins of the spine: instead they lie on the lateral surface, some way cranial to the caudal margin of the spine (Fig. 9). This morphology creates a difficulty in terms of accurate coding of character states for *Shunosaurus*. Either this genus possesses a very primitive condition (implying that the suprapostzygapophyseal laminae have shifted to a more caudal position on the spines of more 'advanced' sauropods) or it has a derived state (implying the presence of a postspinal lamina in *Shunosaurus*). In *Lapparentosaurus*, the dorsal spines are also somewhat laterally compressed, although they widen transversely at the caudal margin. The relatively 'primitive' nature of these spines led Bonaparte (1986a) to propose that *Lapparentosaurus* could represent a grade of sauropod which is less 'advanced' than the cetiosaurids with tetraradiate spines. Upchurch (1995), however, noted the presence of suprapostzygapophyseal, supraprezygapophyseal and supradiapophyseal ridges on the dorsal neural spines of *Lapparentosaurus*, and suggested that many of its plesiomorphic traits may reflect ontogeny rather than phylogenetic relationship.

The basic tetraradiate spine is present in *Haplocanthosaurus* and the 'brachiosaurian' clade. In these taxa, the spine is modified through the addition of laterally projecting subtriangular processes close to the summit ('C116'). Some trend towards a decrease in the prominence of the supraprezygapophyseal laminae occurs, especially at the dorsal end of the spine where these laminae merge into a central rugosity. This trend is carried further in some of the more 'advanced' titanosauroids where a single prespinal lamina is developed on the cranial midline of the spine. In most titanosauroids, the middle and caudal dorsal neural spines also develop a postspinal lamina which is located on the midline of the caudal surface (see 'C114' for comments on this structure in brachiosaurids).

The most profound modifications to the neural spine occur in the Diplodocoidea. As in the titanosauroids, the diplodocoid dorsal neural spine possesses a prespinal lamina, although it is not clear whether this has also developed from a fusion of the

supraprezygapophyseal laminae. The diplodocoid prespinal lamina usually retains a midline groove and bifurcates into craniolaterally directed portions at its base. The more cranial dorsals (where the neural spines are bifurcated) often show both supraprezygapophyseal laminae and a midline rugose ridge on the lower part of the spine.

Diplodocoid dorsal neural spines are generally craniocaudally compressed and transversely expanded. These modifications seem to have been brought about by a shortening of the spine core (perhaps related to prespinal lamina development) and a widening of the prominent suprapostzygapophyseal laminae. The latter are occasionally referred to as the 'supradiapophyseal' laminae because they are positioned vertically above the transverse processes (Calvo & Salgado, 1995). The size, shape and orientation of this lamina suggests that it actually represents a fusion of the supradiapophyseal and suprapostzygapophyseal laminae, and indeed some remnant of each of these can be seen at the base of many diplodocoid neural spines.

Finally, a postspinal lamina also develops in diplodocoids. This has occasionally been interpreted as the result of a fusion between the suprapostzygapophyseal laminae (Calvo & Salgado, 1995): this lamina often possesses a midline groove and bifurcates at its lower end to form ridges which run to the postzygapophyses. Several observations, however, suggest that the postspinal lamina is not homologous to the suprapostzygapophyseal laminae: (i) suprapostzygapophyseal laminae and a postspinal rugosity are simultaneously present on the more cranial dorsal neural spines; (ii) the homologues of the suprapostzygapophyseal laminae are more probably the large laterally directed laminae (see above). The postspinal lamina is therefore regarded as a new structure.

'Forked' chevrons. The possession of 'forked' middle and distal chevrons is derived with respect to non-sauropod dinosaurs. The presence of the derived state in euhelopodids and diplodocoids has, on the basis of parsimony, been previously interpreted as homoplasy (Upchurch, 1995). It should be noted, however, that the brachiosaurid–titanosauroid sister-group relationship now opens up a second possibility. Using the Accelerated Transformation optimization in PAUP, 'forked' chevrons could have been acquired once within the Sauropoda (at or below Node C), and subsequently lost in the 'brachiosaurian' clade. This hypothesis is as parsimonious as that found by the Delayed Transformation optimization (i.e. convergent acquisition of 'forked' chevrons in euhelopodids and diplodocoids). Furthermore, the reversal in the 'Brachiosauria' explains the 'remnant' of the 'forked' chevron condition observed in *Camarasaurus*. At present, it is impossible to determine which of these two optimizations represents the true course of evolution, although information on the chevrons of *Vulcanodon*, *Barapasaurus*, cetiosaurids and/or 'basal' diplodocoids, would settle this issue. If the 'reversal' hypothesis is subsequently confirmed by future discoveries, there could be important implications for the topology of the sauropod cladogram, especially with regard to the monophyly of the Euhelopodidae.

CONCLUSION

Our very incomplete knowledge of the Sauropoda is occasionally cited as a severe obstacle to the application of cladistic analysis to this group. For example, Madsen

et al. (1995: 35) state ". . . because many genera are incompletely known, a meaningful analysis of relationships at this time would be impossible". The data-matrix presented here contains approximately 46% missing data, suggesting that there is certainly a risk that any phylogenetic 'signal' will be swamped by 'noise'. Nevertheless, pessimism with regard to our ability to reconstruct the evolutionary relationships of a group should be based on an *a posteriori* consideration of a cladistic analysis, not an *a priori* assumption. Cladistic analysis of the Sauropoda has produced two MPTs which represent a very high resolution given the amount of missing data in the matrix. Exploration of the data reveals underlying weaknesses, but poor performance on bootstrapping and decay analyses seems to have been caused more by missing data than by character conflict. Furthermore, the randomization tests suggest that the data-matrix contains a genuine phylogenetic 'signal'. Given these results, it seems that cladistic analysis can be usefully applied to the Sauropoda now, and should not be postponed to some unspecified future time when 'complete' data are available.

It is often tempting to examine the 'higher' level phylogeny of a group by concentrating on a few, well-known, representative taxa. The current analysis, however, reveals potential dangers in such an approach. Failure to include taxa with unusual combinations of derived and plesiomorphic character states can have a serious effect on tree topology. In this regard, the inclusion of 26 sauropod taxa represents an 'improvement' over previous analyses. By the same token, there remain yet other sauropods which, if incorporated into this analysis, might result in further modifications in tree topology. The particular relationships proposed here, therefore, represent a 'working' hypothesis and should be treated with caution.

REFERENCES

Alroy J. 1994. Four permutation tests for the presence of phylogenetic structure. *Systematic Biology* **43:** 430–437.

Archie JW. 1989. A randomization test for phylogenetic information in systematic data. *Systematic Zoology* **38:** 239–252.

Berman DS, McIntosh JS. 1978. Skull and relationships of the Upper Jurassic sauropod *Apatosaurus* (Reptilia, Saurischia). *Bulletin of the Carnegie Museum of Natural History* **8:** 1–35.

Bonaparte JF. 1979. Dinosaurs: a Jurassic assemblage from Patagonia. *Science* **205:** 1377–1379.

Bonaparte JF. 1984. Late Cretaceous faunal interchange of terrestrial vertebrates between the Americas. In: Reif W-E, Westphal F, eds *Third Symposium on Mesozoic Terrestrial Ecosystems*. Tübingen: Attempto Verlag, 19–24.

Bonaparte JF. 1986a. The early radiation and phylogenetic relationships of Jurassic sauropod

dinosaurs, based on vertebral anatomy. In: Padian K, ed. *The Beginning of the Age of Dinosaurs*. Cambridge: Cambridge University Press, 247–258.

Bonaparte JF. 1986b. Les Dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosauridés) du Jurassique moyen de Cerro Condor (Chubut, Argentine). *Annales des Paléontologie* **72:** 325–386.

Bonaparte JF, Coria RA. 1993. Un nuevo y gigantesco Sauropodo titanosaurio de la formacion Rio Limay (Albiano-Cenomaniano) de la Provincia del Neuquen, Argentina. *Ameghiniana* **30**(3): 271–282.

Bonaparte JF, Powell JE. 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda-Coelurosauria-Carnosauria-Aves). *Memoires du Societé Geologique de France* **139:** 19–28.

Bonaparte JF, Vince M. 1979. El hallazgo del primer nido de Dinosaurios Triásicos (Saurischia, Prosauropoda), Triásico superior de Patagonia, Argentina. *Ameghiniana* **16:** 173–182.

Borsuk-Bialynicka M. 1977. A new camarasaurid *Opisthocoelicaudia* gen. n. sp. n. from the Upper Cretaceous of Mongolia. *Palaeontologica Polonica* **37:** 5–64.

Cabrera A. 1947. Un saurópdo nuevo del Jurásico de Patagonia. *Notas Museo de La Plata (12 Paleontologia)* **95:** 1–17.

Calvo JO, Bonaparte JF. 1991. *Andesaurus delgadoi* gen. et sp. nov. (Saurischia-Sauropoda), dinosaurio Titanosauridae de la Formacion Rio Limay (Albiano-Cenomaniano), Neuquen, Argentina. *Ameghiniana* **28**(3–4): 303–310.

Calvo JO, Salgado L. 1995. *Rebbachisaurus tesonei* sp. nov. A new Sauropoda from the Albian-Cenomanian of Argentina; new evidence on the origin of the Diplodocidae. *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural* **11:** 13–33.

Chapman RE. 1990. Shape analysis in the study of dinosaur morphology. In: Carpenter K, Currie PJ, eds. *Dinosaur Systematics. Approaches and Perspectives*. Cambridge: Cambridge University Press, 21–42.

Cooper MR. 1981. The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. *Occasional papers of the National Museum of Rhodesia, (B) Natural Sciences* **6:** 689–840.

Cooper MR. 1984. A reassessment of *Vulcanodon karibaensis* Raath (Dinosauria: Saurischia) and the origin of the Sauropoda. *Palaeontologica Africana* **25:** 203–231.

Cope ED. 1877a. On *Amphicoelias*, a genus of saurian from the Dakota epoch of Colorado. *Proceedings of the American Philosophical Society* **17:** 242–246.

Cope ED. 1877b. On a gigantic saurian from the Dakota epoch of Colorado. *Paleontological Bulletin* **25:** 5–10.

Dong Z. 1992. *Dinosaurian Faunas of China*. Berlin: Springer-Verlag.

Dong Z, Tang ZL. 1984. Note on a mid-Jurassic sauropod *Datousaurus bashanensis* (gen. et sp. nov.) from the Sichuan Basin, China. *Vertebrata PalAsiatica* **22:** 69–75.

Dong Z, Peng G, Huang D. 1989. The discovery of the bony tail club in sauropods. *Vertebrata PalAsiatica* **27:** 219–224.

Dong Z, Zhou S, Zhang Y. 1983. The dinosaurian remains from Sichuan Basin, China. *Palaeontologica Sinica, (ser. C)* **23:** 1–145.

Erikson T, Wikström N. 1996. *Autodecay version 3.0.2*. (Computer program distributed by the authors). Botaniska institutionen, Stockholm University.

Faith DP, Cranston PS. 1991. Could a cladogram this short have arisen by chance alone?: On permutation tests for cladistic structure. *Cladistics* **7:** 1–28.

Farris JS, Kluge AG, Eckardt MJ. 1970. A numerical approach to phylogenetic systematics. *Systematic Zoology* **19:** 172–189.

Galton PM. 1990. Basal Sauropodomorpha-Prosauropods. In: Weishampel DB, Dodson P, Osmolska H, eds. *The Dinosauria*. Berkeley and Los Angeles: University of California Press, 320–344.

Gauthier J. 1986. Saurischian monophyly and the origin of birds. In: Padian K, ed. *The Origin of Birds and the Evolution of Flight. Memoirs of the Californian Academy of Sciences* **8:** 1–55.

Gillette DD. 1991. *Seismosaurus halli*, gen. et sp. nov., a new sauropod dinosaur from the Morrison Formation (Upper Jurassic/Lower Cretaceous) of New Mexico, U.S.A.. *Journal of Vertebrate Paleontology* **11**(4): 417–433.

Gilmore CW. 1922. A new sauropod dinosaur from the Ojo Alamo of New Mexico. *Smithsonian Miscellaneous Collection* **72:** 1–9.

Gilmore CW. 1925. A nearly complete articulated skeleton of *Camarasaurus*, a saurischian dinosaur from The Dinosaur National Monument. *Memoirs of the Carnegie Museum of Natural History* **10:** 347–384.

Gilmore CW. 1932. On a newly mounted skeleton of *Diplodocus* in the United States National Museum. *Proceedings of the U.S. National Museum* **81:** 1–21.

Gilmore CW. 1936. Osteology of *Apatosaurus*, with special reference to specimens in the Carnegie Museum. *Memoirs of the Carnegie Museum of Natural History* **11:** 175–300.

Gilmore CW. 1946. Reptilian fauna of the North Horn Formation of central Utah. *U.S. Geological Survey Professional Paper* **210C:** 1–52.

Hatcher JB. 1903a. A new name for the dinosaur *Haplocanthus* Hatcher. *Proceedings of the Biological Society of Washington* **16:** 100.

Hatcher JB. 1903b. Osteology of *Haplocanthosaurus* with description of a new species, and remarks on the probable habits of the Sauropoda and the age and origin of the *Atlantosaurus* beds. *Memoirs of the Carnegie Museum of Natural History* **2:** 1–72.

Hauser DL. 1992. Similarity, falsification and character state order—a reply to Wilkinson. *Cladistics* **8:** 339–344.

He X-L, Li K, Cai KJ, Gao Y-H. 1984. *Omeisaurus tianfuensis*—A new species of *Omeisaurus* from Dashanpu, Zigong. *Journal of the Chengdu College of Geology.* **2** (Suppl.)**:** 13–32.

He X-L, Li C, Cai KJ. 1988. *The Middle Jurassic dinosaur fauna from Dashanpu, Zigong, Sichuan: sauropod dinosaurs (2) Omeisaurus tianfuensis*. Chengdu: Sichuan Publishing House of Science and Technology.

Huene F. 1926. Vollständige Osteologie eines Plateosauriden aus dem Schwäbischen Trias. *Geologische und Palaeontologische Abhandlungen* **15:** 129–179.

Huene F. 1927. Short review of the present knowledge of the Sauropoda. *Memoirs of the Queensland Museum* **8:** 121–126.

Huene F. 1932. Die fossile Reptile-Ordnung Saurischia ihre Entwicklung und Geschichte. *Monographie für Geologie und Palaeontologie, Parts. I and II, ser. I* **4:** 1–361.

Hunt AP, Lockley MG, Lucas SG, Meyer CA. 1994. The global sauropod fossil record. *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural* **10:** 261–279.

Jacobs LL, Winkler DA, Downs WR, Gomani EM. 1993. New material of an early Cretaceous sauropod dinosaur from Africa. *Palaeontology* **36**(3): 523–534.

Jain SL, Kutty TS, Roy-Chowdhury T, Chatterjee S. 1975. The sauropod dinosaur from the Lower Jurassic Kota Formation of India. *Proceedings of the Royal Society of London A* **188:** 221–228.

Jain SL, Kutty TS, Roy-Chowdhury T, Chatterjee S. 1979. Some characteristics of *Barapasaurus tagorei*, a sauropod dinosaur from the Lower Jurassic of Deccan, India. *Fourth International Gondwana Symposium Proceedings (Calcutta 1977)* **1:** 204–216.

Janensch W. 1914. Übersucht über die Wirbeltierfauna der Tendaguru-Schichten, nebst einer kurzen Charakterisierung der neu aufgeführten Arten von Sauropoden. *Archiv für Biontologie* **3:** 81–110.

Janensch W. 1929. Die Wirbelsäule der Gattung *Dicraeosaurus*. *Palaeontographica* **1**(2): 37–133.

Janensch W. 1935–36. Die Schädel der Sauropoden *Brachiosaurus*, *Barosaurus* und *Dicraeosaurus*, aus den Tendaguru-Schichten Deutsch-Ostafrikas. *Palaeontographica* **2:** 147–298.

Janensch W. 1947. Pneumatizität bei Wirbeln von Sauropoden und anderen Saurischiern. *Palaeontographica* **3** (suppl. 7) 1–25.

Janensch W. 1950. Die Wirebelsäule von *Brachiosaurus brancai*. *Palaeontographica* **3:** 27–93.

Janensch W. 1961. Die Gliedmassen und Gliedmaszengürtel der Sauropoden der Tendaguru-Schichten. *Palaeontographica* **7**(Suppl.): 177–235.

Kurzanov SM, Bannikov AF. 1983. A new sauropod from the Upper Cretaceous of Mongolia. *Paleontologicheskyy Zhurnal* **1983:** 91–97.

Lavocat R. 1954. Sur les Dinosauriens du continental intercalaire des Kem-Kem de la Daoura. *Comptes Rendus, 19th International Geological Congress* **1952:** 65–68.

Lavocat R. 1955. Sur un membre antérieur du dinosaurien sauropode '*Bothriospondylus*' recueilli à Madagascar. *Comptes Rendus de l'Academie des Sciences de Paris* **240:** 1795–1796.

Lucas SG, Hunt AP. 1989. *Alamosaurus* and the sauropod hiatus in the Cretaceous of the North American Western Interior. In: Farlow JO, ed. *Paleobiology of the Dinosaurs*. Boulder: The Geological Society of America, Inc., 75–85.

Lull RS. 1919. The sauropod dinosaur *Barosaurus* Marsh. *Memoirs of the Connecticut Academy of Art and Science* **6:** 1–42.

Lydekker R. 1885. Introductory observations. *Palaeontologia Indica (ser. 4)* **1:** V.

Lydekker R. 1888. *Catalogue of the Fossil Reptilia and Amphibia of the British Museum (Natural History), Pt. I*. London.

Maddison WP, Donoghue MJ, Maddison DR. 1984. Outgroup analysis and parsimony. *Systematic Zoology* **33:** 83–103.

Madsen JH. 1976. *Allosaurus fragilis*: a revised osteology. *Utah Geological and Mineralogical Survey Bulletin* **1091:** 1–163.

Madsen JH, McIntosh JS, Berman DS. 1995. Skull and atlas-axis complex of the Upper Jurassic sauropod *Camarasaurus* Cope (Reptilia: Saurischia). *Bulletin of the Carnegie Museum of Natural History,* **31:** 1–115.

Marsh OC. 1877. Notice of some new dinosaurian reptiles from the Jurassic Formation. *American Journal of Science Ser. 3* **14:** 514–516.

Marsh OC. 1878. Principal characters of American Jurassic Dinosaurs Part I. *American Journal of Science Ser. 3* **16:** 411–416.

Marsh OC. 1884. Principal characters of American Jurassic dinosaurs. Pt. VII On the Diplodocidae, a new family of the Sauropoda. *American Journal of Science Ser. 3* **27:** 161–167.

Marsh OC. 1888. Notice of a new genus of Sauropoda and other new dinosaurs from the Potomac Formation. *American Journal of Science Ser. 3* **35:** 89–94.

Marsh OC. 1890. Description of new dinosaurian reptiles. *American Journal of Science Ser. 3* **39:** 81–86.

Marsh OC. 1896. The Dinosaurs of North America. *Sixteenth Annual Report of the U.S. Geological Survey, pt.I.*

Martin V. 1995. Les Dinosaures Sauropodes du Cretace Inferieur de Thailand. Unpublished doctoral thesis, Université Paris VI.

Martin V, Buffetaut E, Suttethorn V. 1994. A new genus of sauropod dinosaur from the Sao Khua Formation (Late Jurassic to Early Cretaceous) of northwestern Thailand. *Comptes Rendus de l'Academie des Sciences de Paris* **319**(II): 1085–1092.

Mateer NJ, McIntosh JS. 1985. A new reconstruction of the skull of *Euhelopus zdanskyi* (Saurischia, Sauropoda). *Bulletin of the Geological Institute of the University of Uppsala* **11:** 125–132.

McIntosh JS. 1989. The Sauropod Dinosaurs: A Brief Survey. In: Culver SJ, ed. *The Age of Dinosaurs. Short Courses in Paleontology, No. 2.* Knoxville: The Paleontological Society, 85–99.

McIntosh JS. 1990a. Species determination in sauropod dinosaurs with tentative suggestions for their classification. In: Carpenter K, Currie PJ, eds *Dinosaur Systematics. Approaches and Perspectives.* Cambridge: Cambridge University Press, 53–70.

McIntosh JS. 1990b. Sauropoda. In: Weishampel DB, Dodson P, Osmolska H, eds *The Dinosauria.* Berkeley and Los Angeles: University of California Press, 345–401.

McIntosh JS, Berman DS. 1975. Description of the palate and lower jaw of the sauropod dinosaur *Diplodocus* (Reptilia, Saurischia) with remarks on the nature of the skull of *Apatosaurus. Journal of Paleontology* **49:** 187–199.

McIntosh JS, Williams ME. 1988. A new species of sauropod dinosaur, *Haplocanthosaurus delfsi* sp. nov., from the Upper Jurassic Morrison Formation of Colorado. *Kirtlandia* **43:** 3–26.

McIntosh JS, Miller WE, Stadtman KL, Gillette DD. 1996. The osteology of *Camarasaurus lewisi* (Jensen, 1988). *Brigham Young University Geology Studies* **41:** 73–115.

Mickevich MF, Weller SJ. 1990. Evolutionary character analysis: tracing character change on a cladogram. *Cladistics* **6:** 137–170.

Novas FE. 1996. Dinosaur monophyly. *Journal of Vertebrate Paleontology* **16**(4): 723–741.

Nowinski A. 1971. *Nemegtosaurus mongoliensis* n. gen., n. sp., (Sauropoda) from the uppermost Cretaceous of Mongolia. *Palaeontologica Polonica* **25:** 57–81.

Ogier A. 1975. Étude de Nouveaux Ossements de Bothriospondylus d'un Gisement du Bathonien de Madagascar. Unpublished doctoral thesis, Université Paris VI.

Osborn HF. 1904. Manus, sacrum and caudals of Sauropoda. *Bulletin of the American Museum of Natural History* **20:** 181–190.

Owen R. 1841. A description of a portion of the skeleton of the *Cetiosaurus*, a gigantic extinct saurian reptile occurring in the oolitic formations of different portions of England. *Proceedings of the Geological Society of London* **3:** 457–462.

Phillips J. 1871. *Geology of Oxford and the Valley of the Thames.* Oxford.

Powell JE. 1992. Osteologia de *Saltasaurus loricatus* (Sauropoda-Titanosauridae) del Cretácico Superior des Noroeste Argentino. In: Sanz JL, Buscalioni AD, eds. *Los Dinosaurios y su entorne biotico: Actas del Segundo Curso de Paleontologia en Cuenca.* Instituto 'Juan de Valdes', 165–230.

Raath MA. 1972. Fossil vertebrate studies in Rhodesia: A new dinosaur (Reptilia, Saurischia) from near the Triassic-Jurassic boundary. *Arnoldia* **5:** 1–37.

Riggs ES. 1903. *Brachiosaurus altithorax*, the largest known dinosaur. *American Journal of Science (ser. 4)* **15:** 299–306.

Riggs ES. 1904. Structure and relationships of opisthocoelian dinosaurs. Part II: The Brachiosauridae. *Field Columbian Museum of Geology* **2:** 229–248.

Romer AS. 1956. *Osteology of the Reptiles.* Chicago: University of Chicago Press.

Russell DA, Zheng Z. 1993. A large mamenchisaurid from the Junggar Basin, Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences* **30**(10–11): 2082–2095.

Salgado L, Bonaparte JF. 1991. Un nuevo sauropodo Dicraeosauridae, *Amargasaurus cazaui* gen. et. sp. nov., de la Formacion la Amarga, Neocomiano de la Provincia del Neuquen, Argentina. *Ameghiniana* **28**(3–4): 333–346.

Salgado L, Calvo JO. 1992. Cranial osteology of *Amargasaurus cazaui* Salgado & Bonaparte (Sauropoda, Dicraeosauridae) from the Neocomian of Patagonia. *Ameghiniana* **29**(4): 337–346.

Sanz JL, Buscalioni AD, Casanovas ML, Santafe JV. 1987. Dinosaurios del Cretacico inferior de Galve (Teruel, Espana). *Estudios Geologias Volumen Extraordinario de Galve-Tremp*: 45–64.

Sereno PC. 1986. The phylogeny of the bird-hipped dinosaurs (Order Ornithischia). *National Geographic Society Research* **2**: 234–256.

Sereno PC. 1987. The ornithischian dinosaur *Psittacosaurus* from the Lower Cretaceous of Asia and the relationships of the Ceratopsia. Unpublished doctoral thesis, Columbia University.

Sereno PC. 1989. Prosauropod monophyly and basal sauropodomorph phylogeny. *Journal of Vertebrate Paleontology* **9**(suppl.): 38A.

Sereno PC. 1990. Psittacosauridae. In: Weishampel DB, Dodson P, Osmolska H, eds. *The Dinosauria.* Berkeley and Los Angeles: University of California Press, 579–592.

Sereno PC, Forster CA, Rogers RR, Monetta AM. 1993. Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. *Nature* **361**: 64–66.

Smith AB. 1994. *Systematics and the fossil record.* Oxford: Blackwell Scientific Publications.

Swofford DL. 1993. *PAUP: phylogenetic analysis using parsimony, version 3.1.1.* Natural History Society, Champaign, Illinois.

Upchurch P. 1994a. Sauropod phylogeny and palaeoecology. *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural* **10**: 249–260.

Upchurch P. 1994b. Manus claw function in sauropod dinosaurs. *Gaia: Revista de Geociencias, Museu Nacional de Historia Natural* **10**: 161–171.

Upchurch P. 1995. The evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London, Series B* **349**: 365–390.

Weishampel DB, Chapman RE. 1990. Morphometric study of *Plateosaurus* from Trossingen (Baden–Württemberg, Federal Republic of Germany). In: Carpenter K, Currie PJ, eds *Dinosaur Systematics. Approaches and Perspectives.* Cambridge: Cambridge University Press, 43–52.

Wild R. 1978. Ein Sauropoden-Rest (Reptilia, Saurischia) aus dem Posidonienschiefer (Lias, Toarcium) von Holzmaden. *Stuttgarter Beiträge zur Naturkunde (Ser. B)* **41**: 1–15.

Wilkinson M. 1992a. Ordered versus unordered characters. *Cladistics* **8**: 375–385.

Wilkinson M. 1992b. *Consensus, compatibility and missing data in phylogenetic inference.* Unpublished doctoral thesis, University of Bristol.

Wilkinson M. 1994. Common cladistic information and its consensus representation: Reduced Adams and cladistic consensus trees and profiles. *Systematic Biology* **43**: 343–368.

Wilkinson M. 1996. Majority-rule reduced consensus methods and their use in bootstrapping. *Molecular Biology and Evolution* **13**: 437–444.

Wilson J, Sereno PC. 1994. Higher-level phylogeny of sauropod dinosaurs. *Journal of Vertebrate Paleontology* **14**(3, suppl.): 52A.

Wiman C. 1929. Die Kreide-Dinosaurier aus Shantung. *Paleontologia Sinica (Series C)* **6**: 1–67.

Young CC. 1939. On a new Sauropoda, with notes on other fragmentary Reptilia from Szechuan. *Bulletin of the Geological Society of China* **19**: 279–315.

Young CC. 1954. On a new sauropod from Yiping, Szechuan, China. *Acta Palaeontologia Sinica* **2**: 355–369.

Young CC, Chao HC. 1972. *Mamenchisaurus hochuanensis* sp. nov.. *Institute of Vertebrate Paleontology and Paleoanthropology Monograph (series A)* **8**: 1–30.

Yu C. 1990. Sauropod phylogeny: a preliminary cladistic analysis. *Journal of Vertebrate Paleontology* **10**(suppl.): 51A.

Zhang Y. 1988. *The Middle Jurassic dinosaur fauna from Dashanpu, Zigong, Sichuan: sauropod dinosaurs (1) Shunosaurus.* Chengdu: Sichuan Publishing House of Science and Technology.

Zhang Y, Yang D, Peng G. 1984. New materials of *Shunosaurus* from the Middle Jurassic of Dashanpu, Zigong, Sichuan. *Journal of the Chengdu College of Geology* **2**(Suppl.): 1–12.

Zheng Z. 1991. Morphology of the braincase of *Shunosaurus*. *Vertebrata PalAsiatica* **4**: 108–118.

APPENDIX 1: DATA-MATRIX

	5	10	15	20	25	30
'Ancestor'	00000	00000	00000	00000	00000	00000
Alamosaurus	?????	?????	?????	?????	?????	?????
Amargasaurus	?????	?????	?????	?????	?????	1?011
Andesaurus	?????	?????	?????	?????	?????	?????
Apatosaurus	11110	110??	21111	10?11	11101	11110
Barapasaurus	?????	?????	?????	?????	?????	?????
Barosaurus	?????	?????	?????	?????	?????	?????
Brachiosaurus	11001	10111	10111	11110	11100	11010
Camarasaurus	11001	10111	10111	11110	11100	11010
Cetiosaurus	?????	?????	?????	?????	?????	?????
Dicraeosaurus	11???	1101?	?1??1	1011?	?????	1?011
Diplodocus	11110	1101?	21111	10111	11101	11110
Euhelopus	11000	00010	00011	00010	1?100	1?110
Haplocanthosaurus	?????	?????	?????	?????	?????	?????
Lapparentosaurus	?????	?????	?????	?????	?????	?????
Malawisaurus	1100?	???10	101??	?????	?????	?????
Mamenchisaurus	1????	???1?	?????	?????	?????	?????
Nemegtosaurus	11110	1101?	211?1	10111	11110	11010
Omeisaurus	11000	00010	00011	01010	10100	10110
Opisthocoelicaudia	?????	?????	?????	?????	?????	?????
Patagosaurus	1100?	0001?	?0111	?101?	?????	?????
Phuwiangosaurus	?????	?????	?????	?????	?????	?????
Quaesitosaurus	11???	1101?	?11??	?0?1?	1?110	1?010
Rebbachisaurus	1111?	?????	?????	????0	?????	1?110
Saltasaurus	?????	?????	?????	?????	?????	???10
Shunosaurus	11000	00010	00011	01010	10100	10110
Vulcanodon	?????	?????	?????	?????	?????	?????

	35	40	45	50	55	60
'Ancestor'	000?0	00000	00000	00000	00000	00000
Alamosaurus	?????	?????	?????	?????	?????	?????
Amargasaurus	1111?	10011	11110	?????	???0	?????
Andesaurus	?????	?????	?????	?????	?????	?????
Apatosaurus	10101	10110	10001	11111	11010	1????
Barapasaurus	?????	?????	?????	?????	?????	?????
Barosaurus	?????	?????	?????	?????	?????	?????
Brachiosaurus	10000	00000	00000	11001	00111	01000
Camarasaurus	10000	00000	00000	11001	00111	01000
Cetiosaurus	?????	?????	?????	?????	?????	?????
Dicraeosaurus	11111	10011	1111?	????1	?10??	?1110
Diplodocus	10101	10110	10001	11111	11010	11110
Euhelopus	1?00?	00???	?????	110?1	000?1	01000
Haplocanthosaurus	?????	?????	?????	?????	?????	?????
Lapparentosaurus	?????	?????	?????	?????	?????	?????
Malawisaurus	?????	?????	?????	?????	?????	?1000
Mamenchisaurus	?????	?????	?????	???01	000?1	?1000
Nemegtosaurus	10110	01000	0000?	1??01	?00?0	11011
Omeisaurus	10000	00000	0000?	1100?	????1	01000
Opisthocoelicaudia	?????	?????	?????	?????	?????	?1000
Patagosaurus	?????	?????	?????	?????	?????	?1000
Phuwiangosaurus	?????	?????	?????	?????	?????	?????
Quaesitosaurus	1010?	01000	00000	????1	??0?1	11011
Rebbachisaurus	11100	00000	1000?	?????	????1	1????
Saltasaurus	11?0?	??010	10?0?	?????	?????	?????
Shunosaurus	10000	00000	0000?	1100?	????1	01000
Vulcanodon	?????	?????	?????	?????	?????	?????

	65	70	75	80	85	90
'Ancestor'	00000	00000	00000	00000	00000	00000
Alamosaurus	?????	1001?	1????	?????	?????	?????
Amargasaurus	?????	?????	????1	?0000	10??0	?0?01
Andesaurus	?????	?????	?????	?????	?1???	?????
Apatosaurus	?????	10011	1?111	11000	10110	22101
Barapasaurus	?????	011??	?????	????0	1000?	01??1
Barosaurus	?????	?????	????1	11101	10110	22111
Brachiosaurus	11111	11110	11101	?0000	11110	22101
Camarasaurus	11111	11100	01101	00000	11100	22001
Cetiosaurus	?????	?????	????1	????0	1?100	11001
Dicraeosaurus	0???1	10111	11111	?0000	10010	00101
Diplodocus	01111	10011	11111	11001	10110	22111
Euhelopus	?1111	11100	01101	11111	11101	?0?01
Haplocanthosaurus	?????	?????	?????	????0	10100	12001
Lapparentosaurus	?????	111?0	?????	????0	10000	00???
Malawisaurus	?????	10110	11?0?	????0	1????	?0?01
Mamenchisaurus	0101?	01100	01?01	11111	11001	?0001
Nemegtosaurus	01111	10111	1011?	?????	?????	?????
Omeisaurus	?1?10	01100	01101	11111	10001	?2001
Opisthocoelicaudia	?????	?????	?????	?????	?1???	?????
Patagosaurus	????1	11100	0??0?	????0	1000?	11001
Phuwiangosaurus	?????	?????	?????	????0	11000	?2001
Quaesitosaurus	?1111	1011?	??11?	?????	?????	?????
Rebbachisaurus	?????	10?1?	?????	????0	10???	?2?01
Saltasaurus	?????	?????	?????	????0	11100	?2001
Shunosaurus	?1010	11100	01101	10000	10001	00?01
Vulcanodon	?????	?????	?????	?????	?????	?????

	95	100	105	110	115	120
'Ancestor'	00000	?0000	00000	00000	00000	00000
Alamosaurus	?0???	?????	?0???	?????	11??0	10?1
Amargasaurus	111?0	?0011	11??1	???0	11111	011?1
Andesaurus	?????	11?11	?0001	?1?0?	11110	??0??
Apatosaurus	02111	01111	10001	?1000	11111	00101
Barapasaurus	00???	01001	10000	20100	11000	001?1
Barosaurus	02111	?1??1	10??1	??01	11111	00??1
Brachiosaurus	00100	?1111	10001	?1000	11000	101?1
Camarasaurus	01100	01101	10000	11000	11000	10111
Cetiosaurus	001?0	010?1	11000	01100	11000	00001
Dicraeosaurus	12110	?0001	11011	?1000	11111	011?1
Diplodocus	02111	01101	10001	11000	11111	00101
Euhelopus	02100	01001	??001	?????	11000	00??1
Haplocanthosaurus	001??	11101	11111	01000	11000	10111
Lapparentosaurus	?????	?00?1	0??0?	??000	10000	001??
Malawisaurus	00?0?	????1	?0???	?????	11?10	10???
Mamenchisaurus	01100	00001	1000?	??00	11000	?0101
Nemegtosaurus	?????	?????	?????	?????	?????	?????
Omeisaurus	00100	01?01	11001	?0?00	11000	001?1
Opisthocoelicaudia	?1??0	11?11	101?1	???10	11110	101?1
Patagosaurus	001??	01001	11000	20100	11000	001?1
Phuwiangosaurus	011??	11?11	?1001	??00	11000	001?1
Quaesitosaurus	?????	?????	?????	?????	?????	?????
Rebbachisaurus	101?0	01??1	11?0?	??0?0	11111	011??
Saltasaurus	001??	11?11	?1101	?111?	11110	101?1
Shunosaurus	001?0	00001	?1001	??0?	10010	001?1
Vulcanodon	?????	?????	?????	?????	?????	????1

	125	130	135	140	145	150
'Ancestor'	00000	00000	00000	00000	00000	00000
Alamosaurus	10??0	0?011	10000	01111	01011	10001
Amargasaurus	10??1	1????	0??0	?????	?????	0???1
Andesaurus	????1	0??00	0??0	001??	????1	1000?
Apatosaurus	10111	01110	01110	00011	11111	01111
Barapasaurus	??000	0??00	0???0	0????	?????	?????
Barosaurus	10?01	0??10	0??11	10011	111?1	01111
Brachiosaurus	10110	01000	01000	00110	01011	10001
Camarasaurus	10110	01000	01000	00110	01011	11001
Cetiosaurus	????0	0??00	01??0	00010	010??	00001
Dicraeosaurus	10101	11?10	010?0	00011	11111	01111
Diplodocus	10111	01110	01111	10011	11111	01111
Euhelopus	001?0	01???	?????	?????	?????	?????
Haplocanthosaurus	10110	01?00	010?0	00010	01011	10001
Lapparentosaurus	??0?	??00	???0	001??	?????	???1
Malawisaurus	????0	0??00	00??0	001?1	010??	?000?
Mamenchisaurus	00?00	01011	010?0	00010	01010	0111?
Nemegtosaurus	?????	?????	?????	?????	?????	?????
Omeisaurus	10000	01000	01000	00010	01010	01111
Opisthocoelicaudia	11100	01000	01000	11111	11011	10001
Patagosaurus	10?00	0??00	01??0	00010	0?0??	0???1
Phuwiangosaurus	1??10	0??00	01??0	0?1?0	010?1	1???1
Quaesitosaurus	?????	?????	?????	?????	?????	?????
Rebbachisaurus	????1	1?000	01010	000?1	1?0??	1???1
Saltasaurus	11100	01?11	10?00	11111	110?1	10001
Shunosaurus	00001	01000	01000	00010	01011	11110
Vulcanodon	??0?	??00	000?0	0?01?	0?01?	0????

	155	160	165	170	175	180
'Ancestor'	00000	00000	00000	00000	00000	00000
Alamosaurus	10111	10??0	11111	1111?	?????	?????
Amargasaurus	1????	??100	00???	?????	?0111	1????
Andesaurus	?????	?????	?????	?????	?????	?0011
Apatosaurus	111?0	00100	00110	00111	10011	10110
Barapasaurus	??0??	?????	?????	?????	?00?1	00?10
Barosaurus	110??	????0	?????	?????	?0011	11110
Brachiosaurus	11101	00110	00100	01111	10111	10111
Camarasaurus	11100	00110	00100	01111	10011	10110
Cetiosaurus	1???0	00??0	00???	?????	?0???	?0?11
Dicraeosaurus	1????	??100	00???	?????	?0011	11110
Diplodocus	11000	00100	00???	?????	?0011	11110
Euhelopus	?????	?????	?????	?????	?0011	00110
Haplocanthosaurus	1?0?1	00???	?????	?????	?0011	10110
Lapparentosaurus	1????	????0	00???	?????	?0111	10?11
Malawisaurus	????1	10???	?????	?????	?????	?????
Mamenchisaurus	?????	?????	?????	?????	?0011	0????
Nemegtosaurus	?????	?????	?????	?????	?????	?????
Omeisaurus	01000	01100	00110	00111	00011	00110
Opisthocoelicaudia	10111	10111	11111	1111?	?1111	10010
Patagosaurus	110??	????0	00???	?????	?0011	00110
Phuwiangosaurus	1?0?1	1?110	01???	?????	?0111	10011
Quaesitosaurus	?????	?????	?????	?????	?????	?????
Rebbachisaurus	111?1	1?100	00???	001??	????1	?0110
Saltasaurus	101?1	10??1	11???	?????	?1111	10?11
Shunosaurus	01000	01100	00000	00111	00011	00110
Vulcanodon	?????	??11?	00???	?01??	?????	?0100

	185	190	195	200	205
'Ancestor'	00000	00000	00000	00000	00000
Alamosaurus	11010	?????	?????	?????	?????
Amargasaurus	?????	10?11	11???	?????	?????
Andesaurus	?10?0	1??1?	?????	?????	????1
Apatosaurus	00100	10111	11011	11111	1111?
Barapasaurus	?00?0	101?0	1????	?????	????0
Barosaurus	00100	10111	11011	??11?	?????
Brachiosaurus	00011	11111	11011	0111?	?1011
Camarasaurus	00010	10111	11011	01101	110??
Cetiosaurus	00??0	10111	1?0??	?????	????0
Dicraeosaurus	00100	10111	11011	??11?	?1???
Diplodocus	00100	10111	11011	11111	1111?
Euhelopus	00000	10101	110?1	??10?	?1?0?
Haplocanthosaurus	00010	10111	11???	?????	????0
Lapparentosaurus	000?1	11111	1?011	??11?	?1???
Malawisaurus	?10?0	?????	?????	?????	?????
Mamenchisaurus	00000	?????	??000	??101	01???
Nemegtosaurus	?????	?????	?????	?????	?????
Omeisaurus	00000	10101	11000	11111	0100?
Opisthocoelicaudia	11010	11111	11111	11101	1101?
Patagosaurus	000?0	10101	110??	?????	????0
Phuwiangosaurus	?0000	11111	11011	?????	?????
Quaesitosaurus	?????	?????	?????	?????	?????
Rebbachisaurus	00010	10111	?1?11	??10?	?????
Saltasaurus	?10?0	11111	111??	??1??	????1
Shunosaurus	00000	10101	11000	01111	0100?
Vulcanodon	00000	10110	11001	0100?	?000?

APPENDIX 2: MATERIALS AND SOURCES OF DATA

This appendix lists sources of information on sauropod anatomy. '*' marks those taxa where personal observations made by the author have contributed to the analysis.

Taxon	Source	Comments
*Alamosaurus**	Gilmore (1946)	
Amargasaurus	Salgado & Bonaparte (1991), Salgado & Calvo (1992)	
Andesaurus	Calvo & Bonaparte (1991)	
*Apatosaurus**	Gilmore (1936), Berman & McIntosh (1978)	
Barapasaurus	Jain *et al.* (1975, 1979)	
*Barosaurus**	Lull (1919)	
*Brachiosaurus**	Riggs (1903), Janensch (1935–36, 1950, 1961)	
*Camarasaurus**	Gilmore (1925), Madsen *et al.* (1995), McIntosh *et al.* (1996)	The holotype of '*Cathetosaurus*' is considered to be congeneric with *Camarasaurus*.
*Cetiosaurus**	Phillips (1871), Upchurch & Martin (in prep.)	Based on material from the U.K. only.
*Dicraeosaurus**	Janensch (1929)	
*Diplodocus**	Gilmore (1932), McIntosh & Berman (1975), Berman & McIntosh (1978)	
Euhelopus	Wiman (1929), Mateer & McIntosh (1985)	
*Haplocanthosaurus**	Hatcher (1903b), McIntosh & Williams (1988)	Includes both *H. priscus* and *H. delfsi*
*Lapparentosaurus**	Ogier (1975), Bonaparte (1986a)	
Malawisaurus	Jacobs *et al.* (1993)	
*Mamenchisaurus**	Young & Chao (1972), Russell & Zheng (1993)	Excludes *Mamenchisaurus constructus*
Nemegtosaurus	Nowinski (1971)	
*Omeisaurus**	He *et al.* (1984, 1988)	Restricted to *Omeisaurus tianfuensis*
Opisthocoelicaudia	Borsuk-Bialynicka (1977)	
Patagosaurus	Bonaparte (1986b)	
Phuwiangosaurus	Martin *et al.* (1994), Martin (1995)	
Quaesitosaurus	Kurzanov & Bannikov (1983)	
Rebbachisaurus	Calvo & Salgado (1995)	Restricted to material from Argentina
Saltasaurus	Bonaparte & Powell (1980), Powell (1992)	
*Shunosaurus**	Zhang *et al.* (1984); Zhang (1988); Zheng (1991)	
Vulcanodon	Raath (1972), Cooper (1984)	

APPENDIX 3: LIST OF SYNAPOMORPHIES

This appendix lists the synapomorphies uniting each of the nodes in Figure 19. The distribution of apomorphies is based on the Delayed Transformation option available in PAUP 3.1.1 (Swofford, 1993). Synapomorphies marked by '*' are those whose presence or absence cannot be established in the node immediately 'below' that under consideration.

Node A – Sauropoda

A1 Fourth vertebra incorporated into sacrum; A2 'hyposphenal ridge' on cranial caudal vertebrae; A3 caudal ribs disappear on Cd16 or more cranially; A4 forelimb:hindlimb length ratio is 0.66 or more; A5 metacarpal V is enlarged and robust; A6 length of ischium is 0.90, or more, of pubis length (reversed in Titanosauroidea); A7 straight femoral shaft; A8 reduced lesser trochanter; A9 craniocaudally compressed femoral shaft; A10 tibia: femur length ratio is less than 0.65; A11 distal tarsals fail to ossify.

Node B – unnamed

*B1 Concave lingual surfaces on tooth crowns (reversed in Diplodocoidea, *Malawisaurus*, and Titanosauridae); *B2 labial surfaces of each tooth crown bear prominent grooves paralleling the mesial and distal margins (reversed in *Alamosaurus* and Diplodocidae); *B3 convexoconcave ('ball-and-socket') articulations between cervical centra; *B4 infradiapophyseal lamina system is present on cranial and middle cervical vertebrae; *B5 prominent excavation of the lateral surfaces of dorsal centra (reversed in *Shunosaurus*, *Mamenchisaurus*, *Lapparentosaurus*, *Malawisaurus* and Dicraeosauridae); *B6 height of dorsal neural arches is equal to, or grater than, the height of the dorsal centra; *B7 cranial faces of dorsal neural arches are deeply excavated (reversed in *Lapparentosaurus*); *B8 deep excavation below the base of the dorsal transverse process (reversed in *Haplocanthosaurus* and Neosauropoda); *B9 subtriangular horizontal cross-section through the base of the dorsal neural spine; *B10 prominent suprapostzygapophyseal laminae on dorsal neural spines (reversed in *Lapparentosaurus* and *Shunosaurus*; *B11 supradiapophyseal lamina on dorsal neural spines (reversed in *Cetiosaurus* and *Shunosaurus*); *B12 strongly convex dorsal margin of the ilium; B13 loss of the 'twist' between the proximal and distal ends of the pubis.

Node C – Eusauropoda

*C1 Cranial end of snout is broadly rounded in dorsal view; *C2 external naris lies rostrodorsal to the antorbital fenestra, or more caudally; *C3 lateral plate on premaxillae, maxillae and dentaries; *C4 maxilla-lacrimal contact lies above the caudal end of the antorbital fenestra; *C5 flange-like structure projects rostromedially from the base of the maxillary ascending process; *C6 'shelf'-like flattened area lies lateral to the external naris (reversed in *Euhelopus* and Diplodocoidea); *C7 loss of bone 'sheet' backing the antorbital fossa; *C8 rostral process of the quadratojugal is 2–3 times the length of the dorsal process; *C9 rostral end of rostral process of the quadratojugal is expanded dorsoventrally; *C10 rostral end of infratemporal fenestra extends forwards below the orbit; *C11 frontals and parietals are short rostrocaudally; *C12 loss of the excavated area around the dorsal margin of the supratemporal fenestra; *C13 maxillary process of the palatine is transversely expanded at its rostral end; *C14 ectopterygoid process of the pterygoid lies below the rostral end of the orbit, or more rostrally; *C15 the rostral process and main 'sheet' of the pterygoid lie in the same plane; *C16 deep excavation in the caudal surface of the quadrate (reversed in *Nemegtosaurus* and the dicraeosaurid–diplodocid clade); *C17 dentary increases in dorsoventral width and robustness towards the symphysis; *C18 external mandibular fenestra is reduced or closed; *C19 jaw articulation lies below the level of the dentary tooth row; C20 loss of denticles on tooth crowns (reversed in *Mamenchisaurus* and *Omeisaurus*): *C21 procumbent teeth (reversed in *Nemegtosaurus*); *C22 tooth row ends below the antorbital fenestra; *C23

at least 12 cervical vertebrae; *C24 caudal cervical neural spines have a steeply inclined cranial face and a more shallowly inclined caudal face; C25 dorsal transverse processes are directed dorsolaterally (highly variable, CI = 0.167); *C26 dorsal surfaces of sacral ribs are level with the dorsal margin of the ilium; *C27 centrum length divided by centrum height is 0.5–0.6 in cranial caudal vertebrae (reversed in *Malawisaurus* and Titanosauridae [except *Opisthocoelicaudia*]); *C28 first caudal rib is attached to the neural arch by a prominent ridge; *C29 dorsal margin of coracoid lies below the dorsal margin of the proximal scapular expansion (reversed in Titanosauridae); *C30 metacarpals are arranged in a semicircular colonnade; *C31 manual phalangeal formula is reduced to 2–2–2–2–1; *C32 loss of brevis shelf on ilium; C33 fourth trochanter is reduced to a low rounded ridge; *C34 metatarsal I is short and very robust; *C35 pedal digit IV has three phalanges or fewer; *C36 loss, or extreme reduction, of collateral ligament pits on pedal phalanges.

Node D – Euhelopodidae

D1 Caudal end of the prefrontal is triangular in dorsal view (convergently acquired in Diplodocidae); D2 13 cervical vertebrae (convergently acquired in *Brachiosaurus* and Diplodocidae); D3 laterally compressed cranial cervical centra; D4 centroparapophyseal lamina on middle and caudal dorsal neural arches (absent in some euhelopodids; convergently acquired in the Neosauropoda); D5 cranial process on middle and distal chevrons (convergently acquired in the dicraeosaurid–diplodocid clade); D6 ventral midline slit on middle and distal chevrons (convergently acquired in the dicraeosaurid–diplodocid clade); D7 prominent parasagittally oriented ridge on the dorsal surface of the sternal plate.

Node E (unresolved polytomy) – unnamed

E1 17 cervical vertebrae; E2 EI values of longest cervical vertebrae are 4.0 or more (convergently acquired in *Barosaurus* and *Diplodocus*).

Node F – unnamed

F1 Loss of caudolateral process on premaxilla; F2 longest tooth crowns (in upper jaw) are found on the premaxilla (convergently acquired in *Euhelopus*); F3 cervical parapophyses are excavated on their dorsal surfaces, but this excavation is not separated from the pleurocoel by a ridge (reversed in Dicraeosauridae); F4 deep pleurocoels in cervical centra (convergently acquired in *Barapasaurus*; reversed in *Lapparentosaurus*, *Malawisaurus*, and Dicraeosauridae); F5 fifth vertebra incorporated into the sacrum (convergently acquired in *Omeisaurus*); F6 proximal end of scapula is developed into a prominent subquadrangular dorsal expansion (convergently acquired in *Omeisaurus*); F7 proximal scapular expansion bears a prominent ridge on its lateral surface.

Node G – unnamed

G1 Loss of midline keels on cervical vertebrae (reversed in Dicraeosauridae); G2 accessory lamina in infrapostzygapophyseal cavity of dorsal vertebrae; G3 fourth trochanter lies on the caudomedial margin of the femoral shaft (convergently acquired in *Vulcanodon*).

Node H – unnamed

H1 Accessory oblique lamina in cervical pleurocoels; H2 pleurocoels in dorsal centra are extensive and enter the base of the neural arch; H3 centroparapophyseal lamina on dorsal neural arches (convergently acquired in *Shunosaurus* and *Euhelopus*); H4 loss of excavation immediately below the bases of the dorsal transverse processes (reversal); *H5 sacrum width divided by average sacral centrum length is 4.0 or more; *H6 pleurocoels in sacral centra; H7 middle and distal chevrons are open at their proximal ends (convergently acquired in *Shunosaurus*); H8 cranial chevrons are open at their proximal ends (convergently acquired in

Shunosaurus; reversed in the dicraeosaurid–diplodocid clade); *H9 reduced ischiadic peduncle on ilium; *H10 the long-axis of the distal end of the ischium is directed laterally (reversed in the dicraeosaurid–diplodocid clade).

Node I – Neosauropoda

*I1 Subnarial foramen faces dorsally; *12 flange at the base of the maxillary ascending process contacts its partner on the midline; *I3 additional antorbital fenestra penetrates the base of the maxillary ascending process; *I4 rostral end of quadratojugal contacts the caudal end of the maxilla; *I5 rostral end of infratemporal fenestra extends forwards to lie below the rostral margin of the orbit; *I6 lateral end of the ectopterygoid contacts the maxilla; *I7 external mandibular fenestra is closed (convergently acquired in *Euhelopus* and *Omeisaurus*); I8 the dorsal surfaces of the cervical parapophyses are excavated and separated from the pleurocoel by a ridge (excavation lost in Dicraeosauridae); I9 neural cavity in dorsal neural arches is entirely enclosed by bone; I10 cranial and dorsal margins of the coracoid meet at approximately 90–120°, giving the coracoid a subquadrangular outline (reversed in *Barosaurus*, *Diplodocus* and *Phuwiangosaurus*); *I11 two or fewer ossified distal carpals (convergently acquired in *Omeisaurus*?); *I12 manual phalangeal formula is reduced to 2–2–1–1–1; *I13 ventral surface of the astragalus is transversely convex; *I14 astragalus narrows towards its medial end (convergently acquired in *Euhelopus* and *Vulcanodon*); *I15 pedal digit IV possesses two phalanges; *I16 proximal pedal phalanges narrow towards their lateral and palmar margins.

Node J – 'Brachiosauria'

J1 Long diameter of the external naris is approximately 40% of skull length; J2 subnarial foramen lies within the external narial fossa; J3 ascending process of the premaxilla is tall, straight, and directed dorsally; J4 'hook' or 'finger'-like process on the pterygoid curls around the basipterygoid process; J5 splenial takes part in the mandibular symphysis; J6 middle and caudal dorsal centra possess a prominent articular 'ball' at the cranial end (reversed in *Lapparentosaurus*; convergently acquired in *Euhelopus* and *Mamenchisaurus*); J7 dorsal transverse processes are directed laterally (reversal, highly variable, CI=0.167); *J8 forelimb:hindlimb length ratio is 0.75 or higher (convergently acquired in *Vulcanodon* and *Omeisaurus*); *J9 longest metacarpal divided by radius length is 0.45 or more.

Node K – unnamed

K1 Tooth crown length divided by mesiodistal width is 4.0 (convergently acquired in Diplodocoidea); K2 tooth crowns have subparallel mesial and distal margins (convergently acquired in Diplodocoidea); K3 EI values for caudal dorsal centra are greater than 1.0 (convergently acquired in *Amargasaurus* and *Apatosaurus*); K4 neural arches of middle caudal vertebrae are located on the cranial half of the centrum; K5 gently/strongly concave lateral margin of the sternal plate (convergently acquired in *Haplocanthosaurus* and *Rebbachisaurus*); K6 cranial process of ilium terminates in a rounded apex (convergently acquired in *Amargasaurus*); K7 length of ischiadic articular surface of the pubis, divided by pubis length, is 0.45 or more (convergently acquired in *Cetiosaurus*); K8 prominent 'bulge' on lateral margin of the proximal end of the femur; *K9 large 'cancellar' spaces in the osseous tissue of the presacral vertebrae.

Node L – Brachiosauridae

L1 Distal shaft of the ischium is directed downwards at approximately 80° to the horizontal; *L2 laterodistal process on metatarsal I (convergently acquired in the dicraeosaurid–diplodocid clade, *Shunosaurus* and *Omeisaurus*).

Node M – Titanosauroidea
*M1 Cranial dorsal pleurocoels have acute caudal margins (convergently acquired in *Haplocanthosaurus*); M2 sternal plates expand craniolaterally to produce a 'kidney'-shaped dorsal outline (convergently acquired in *Rebbachisaurus*); M3 radius proximal width divided by shaft length is 0.33 or more; M4 ischium length divided by pubis length is 0.90 or less (reversal).

Node N – unnamed
N1 Prespinal lamina on dorsal neural spine (convergently acquired in the *Rebbachisaurus*–dicraeosaurid–diplodocid clade); N2 postspinal lamina on dorsal neural spine (convergently acquired in the *Rebbachisaurus*–dicraeosaurid–diplodocid clade); N3 relatively short and broad distal shaft of the ischium.

Node O – unnamed
*O1 loss of concave area on lingual surface of tooth crown (reversal, convergently acquired in Diplodocoidea); O2 subtriangular processes project laterally from the summits of dorsal neural spines (convergently acquired in *Brachiosaurus*, *Camarasaurus* and *Haplocanthosaurus*); O3 cranial caudals possess a prominent articular 'ball' on the caudal articular surface of the centrum (not present in *Opisthocoelicaudia*); O4 centrum length divided by centrum height in cranial caudal vertebrae is greater than 0.60 (reversal; not present in *Opisthocoelicaudia*); *O5 cranial caudal neural spines are 'dorsalized' (convergently acquired in the *Rebbachisaurus*–dicraeosaurid–diplodocid clade).

Node P – Titanosauridae
P1 Middle caudal centra are dorsoventrally compressed; *P2 dorsal margin of the coracoid lies level with, or extends beyond, the dorsal margin of the proximal scapular expansion (reversal); *P3 sternal plate length is at least 75% of the length of the humerus; *P4 concave area on the dorsal surface of the craniomedial proximal process of the ulna; *P5 no ossified distal carpals; *P6 metacarpal I is longer than metacarpals II and III; *P7 symphysis between ischia extends to the ventral end of the pubic articular surface.

Node Q – unnamed
*Q1 Transverse processes of the caudal dorsals lie above the parapophysis (convergently acquired in *Haplocanthosaurus*); *Q2 loss of hyposphene-hypantrum system in middle and caudal dorsal vertebae; Q3 sixth vertebra incorporated into the sacrum; *Q4 loss of pleurocoels in sacral centra (reversal, convergently acquired in the Dicraeosauridae); Q5 cranial caudal centra possess an excavation on their ventral surfaces (convergently acquired in *Barosaurus* and *Diplodocus*); Q6 neural spines of cranial caudal vertebrae are wider transversely than craniocaudally (convergently acquired in the *Rebbachisaurus*–dicraeosaurid–diplodocid clade); Q7 prominent process on the lateral corner of the proximal end of the humerus; *Q8 cranial process of the ilium flares outwards to form a horizontal 'shelf'; *Q9 muscle scar on the lateral surface of the fibula is developed into a ridge which parallels the long-axis of the shaft.

Node R – Diplodocoidea
R1 External nares lie rostrodorsal to the orbit; R2 external nares face dorsally or rostrodorsally; R3 subnarial foramen is elongated along the premaxilla-maxilla suture; R4 internarial bar is absent; R5 premaxilla is narrow at its rostral end and elongate rostrocaudally; R6 loss of shelf-like area lateral to the external naris (reversal); R7 rostrocaudal width of supratemporal fenestra divided by transverse width of the occiput is less than 0.10; R8 long-axis of the quadrate runs caudodorsally; R9 subrectangular dorsal profile of the mandible;

R10 loss of lingual concavity on tooth crowns (reversal; convergently acquired in the *Malawisaurus*–titanosaurid clade); R11 tooth crown length divided by mesiodistal width is 5.0 or more; R12 tooth crowns possess subparallel mesial and distal margins (convergently acquired on the brachiosaurid–titanosauroid clade); R13 tooth row terminates rostral to the antorbital fenestra.

Node S – Nemegtosauridae

S1 Step-like change of direction in the rostral quadratojugal process; S2 squamosal is excluded from the dorsal margin of the supratemporal fenestra by a parietal-postorbital contact; S3 angle between long-axis of mandibular symphysis and long-axis of mandible is 90°.

Node T – unnamed

T1 Basipterygoid processes are directed rostrolaterally (convergently acquired in *Saltasaurus*); *T2 prespinal lamina on dorsal neural spines (convergently acquired in the *Andesaurus*–*Malawisaurus*–titanosaurid clade); *T3 postspinal lamina on dorsal neural spines (convergently acquired in the *Andesaurus*–*Malawisaurus*–titanosaurid clade); *T4 caudal dorsal neural spines are craniocaudally compressed; *T5 neural spines over the sacral region are at least twice the height of the sacral centra (convergently acquired in *Andesaurus* and *Shunosaurus*); *T6 distal caudal centra are elongate rods; *T7 dorsalization of cranial caudal neural spines (convergently acquired in Titanosauridae); *T8 cranial caudal neural spines are widened transversely and craniocaudally compressed (convergently acquired in *Opisthocoelicaudia* and *Saltasaurus*).

Node U – unnamed

U1 Squamosal loses contact with the dorsal process of the quadratojugal; U2 notch in lateral portion of squamosal main body; U3 occipital condyle is directed ventrally (convergently acquired in *Saltasaurus*); *U4 basal articulation on the pterygoid faces caudoventrally; *U5 loss of excavation in the caudal surface of the quadrate (reversal; loss also occurs in *Nemegtosaurus*); *U6 ventral margin of mandible, in the transverse portion leading to the symphysis, forms a thin sharp edge which projects downwards; *U7 cervical vertebrae have concave ventral surfaces (convergently acquired in *Brachiosaurus*); *U8 infraprezygapophyseal laminae, on middle and caudal cervicals, bifurcate toward their dorsal ends (convergently acquired in *Brachiosaurus*); U9 bifurcated neural spines of caudal cervicals and cranial dorsals (convergently acquired in *Euhelopus*, *Mamenchisaurus*, *Camarasaurus*, *Phuwiangosaurus* and *Opisthocoelicaudia*); *U10 shafts of cervical ribs do not extend beyond the caudal end of the centrum to which they are attached; U11 cranial caudal centra have a mildly convex caudal articular surface (a more prominent convexity is present in *Malawisaurus* and Titanosauridae); U12 cranial caudal ribs are 'wing' or 'fan'-shaped; U13 cranial chevrons have closed proximal ends (reversal); *U14 middle and distal chevrons develop prominent cranial processes (convergently acquired in Euhelopodidae); *U15 middle and distal chevrons possess a ventral 'slit' along the midline (convergently acquired in Euhelopodidae); U16 distal end of ischium is dorsoventrally expanded; U17 long-axis of ischium distal end surface is directed dorsolaterally (reversal); *U18 laterodistal process present on metatarsal I (convergently acquired in Brachiosauridae, *Shunosaurus* and *Omeisaurus*).

Node V – Dicraeosauridae

V1 Coalesced frontals; V2 supratemporal fenestrae face laterally (convergently acquired in *Rebbachisaurus* and *Saltasaurus*); V3 postparietal fenestra (convergently acquired in *Nemegtosaurus*); V4 'leaf'-like processes projecting dorsolaterally from the crista prootica; V5 length of basipterygoid process is 1.5 times the distance from the basal tubera to the occipital

condyle; V6 angle between the basipterygoid processes is approximately 20°; V7 a deep pit lies between the bases of the basipterygoid processes; V8 loss of pleurocoels in cervical vertebrae (reversal); V9 loss of excavation in the dorsal surfaces of the cervical parapophyses (reversal); V10 tall cervical neural spines (convergently acquired in *Rebbachisaurus*); V11 loss of pleurocoels in dorsal vertebrae (reversal); V12 middle and caudal dorsal neural spines are narrow at the base and widen transversely towards the summit (convergently acquired in *Rebbachisaurus*); V13 neural spines over the sacrum are 3–4 times the height of the sacral centra (convergently acquired in *Rebbachisaurus*).

Node W – Diplodocidae

*W1 Jugal forms a substantial portion of the caudoventral margin of the antorbital fenestra; *W2 rostral and dorsal processes of the quadratojugal are separated by an angle of approximately 130°; W3 triangular outline of caudal end of prefrontal (convergently acquired in Euhelopodidae); W4 rounded distal ends of paroccipital processes; W5 laterally compressed parasphenoid rostrum, which lacks a groove along its dorsal midline; *W6 ectopterygoid process of the pterygoid lies rostral to the lacrimal; *W7 ectopterygoid process of the pterygoid is reduced and does not project below the ventral margin of the upper jaw; *W8 breadth across main sheet of pterygoid, divided by its rostrocaudal length, is approximately 0.30; W9 loss of grooves on the labial surfaces of tooth crowns (reversal; convergently acquired in *Alamosaurus*); W10 15 cervical vertebrae; W11 10 dorsal vertebrae; W12 transverse processes of the dorsal vertebrae are directed laterally (reversal, highly variable, CI = 0.167); *W13 70–80 caudal vertebrae; W14 lengths of caudal centra gradually increase from Cd1-Cd20; *W15 loss of calcaneum (convergently acquired in *Omeisaurus* and *Opisthocoelicaudia*); *W16 pedal phalanx II-2 is craniocaudally compressed.

Node X – unnamed

X1 EI values of longest cervicals exceed 4.0 (convergently acquired in *Euhelopus*, *Mamenchisaurus* and *Omeisaurus*); X2 articular surfaces of the middle and caudal cervical prezygapophyses are transversely convex; X3 single midline lamina supports the dorsal hyposphene from below, throughout the dorsal series; X4 pleurocoels in cranial caudal centra; X5 ventral excavations in cranial caudal centra (convergently acquired in *Opisthocoelicaudia* and *Saltasaurus*); X6 cranial and dorsal margins of the coracoid merge smoothly to form a rounded lateral profile (reversal); X7 'hook'-shaped ambiens process on pubis (convergently acquired in *Dicraeosaurus*).