

The Evolutionary History of Sauropod Dinosaurs

Paul Upchurch

Phil. Trans. R. Soc. Lond. B 1995 **349**, 365-390
doi: 10.1098/rstb.1995.0125

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: <http://rstb.royalsocietypublishing.org/subscriptions>

The evolutionary history of sauropod dinosaurs

PAUL UPCHURCH

Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K.

CONTENTS

	PAGE
1. Key to abbreviations	366
2. Introduction	366
3. Historical perspective	366
(a) Classification	366
(b) Phylogeny	367
4. Materials and methods	368
5. Sauropod evolutionary relationships	370
(a) The origin of the Sauropoda	370
(b) <i>Vulcanodon</i> and the Vulcanodontidae	370
(c) The Eusauropoda	372
(d) The Euhelopodidae	373
(e) The Neosauropoda	375
(f) <i>Cetiosaurus</i> and the Cetiosauridae	375
(g) The Brachiosauridae and Camarasauridae	376
(h) The Brachiosauridae	376
(i) The Camarasauridae	377
(j) The Titanosauroida and Diplodocoidea	378
(k) The Titanosauroida	378
(l) The Diplodocoidea	380
6. Sauropod phylogeny and biogeography	382
(a) Introduction	382
(b) An overview of sauropod phylogeny and biogeography	383
7. Conclusion	387
References	388

SUMMARY

Most recent studies of dinosaur phylogeny have concentrated on theropods and ornithischians. As a result, the evolutionary relationships of sauropod dinosaurs are poorly understood. In this paper previous studies of sauropod phylogeny are reviewed and contrasted with the results of a recent cladistic analysis. This analysis forms the basis for a reconstruction of sauropod phylogeny.

Sauropods diverged from other dinosaurs at some time in the Upper Triassic, but a large part of their early history is totally unknown. *Vulcanodon* is currently the most primitive sauropod. Many, but perhaps not all, of the Jurassic Chinese sauropods form a monophyletic radiation (the Euhelopodidae) which may reflect the geographic isolation of China during the Lower Jurassic. Members of the Euhelopodidae, such as *Mamenchisaurus*, are not considered to be closely related to the Diplodocidae. 'Forked' chevrons, which have played such an important role in previous studies of sauropod phylogeny, are here considered to have evolved twice within the Sauropoda. This convergence may reflect a correlation between chevron shape and the use of the tail as a weapon within these two sauropod families.

The 'Neosauropoda' (sister group to the Euhelopodidae) contains the Brachiosauridae, Camarasauridae and the new superfamilies Titanosauroida and Diplodocoidea. The Cetiosauridae (here defined in a rather restricted sense) is also provisionally included within the Neosauropoda, but may be removed in future studies. The enigmatic Upper Cretaceous sauropod, *Opisthocoelicaudia*, is thought to be the sister taxon to the Titanosauridae and not a camarasaurid as previously suggested. The Diplodocoidea contains two well established families, the Dicraeosauridae and Diplodocidae, and the new family Nemegtosauridae.

Finally, an overview of sauropod phylogeny is compared with recently published palaeogeographic reconstructions. There are many difficulties associated with the analysis of sauropod biogeographic distribution. Nevertheless, some aspects of sauropod phylogeny may be linked to the break-up of Laurasia and Gondwanaland during the Jurassic and Cretaceous.

1. KEY TO ABBREVIATIONS

BMNH, The Natural History Museum, London.
 CM, Carnegie Museum of Natural History, Pittsburgh.
 HMN, Humboldt Museum für Naturkunde, Berlin.
 LCM, Leicester City Museum and Art Gallery, Leicester.
 OUMZ, Oxford University Museum of Zoology, Oxford.
 PMU, Palaeontological Museum, Uppsala, Sweden.
 PVL, Instituto Miguel Lillo de la Universidad de Tucuman, Tucuman, Argentina.
 SAM, South African Museum, Cape Town, South Africa.
 SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.
 YPM, Peabody Museum, Yale, New Haven.
 Z. PAL., Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

2. INTRODUCTION

Sauropod dinosaurs are familiar to most of us. They can be recognized by their characteristic body form: small head, long neck, quadrupedal stance, long tail and gigantic body size. These 'elephantine' herbivores first appear in the fossil record close to the Triassic–Jurassic boundary and survive to the very end of the Cretaceous period. Sauropods seem to have reached a peak in abundance and diversity during the time interval represented by the Upper Jurassic, and possibly extending into the Lower Cretaceous, when they were the dominant large terrestrial herbivores. Although declining in numbers, it is clear from discoveries in Argentina and elsewhere that they remained an important part of the 'megafauna' in the southern hemisphere right to the end of the Cretaceous.

The familiarity and popularity of sauropods can be misleading. Although studies of their ecology and behaviour have often been undertaken, relatively little work has been done on their evolutionary relationships. For example, in a recent symposium volume (Carpenter & Currie 1990) entitled '*Dinosaur systematics: approaches and perspectives*', six of the papers dealt with theropods, eleven with ornithischians, but only one with sauropods. The studies that have examined sauropod relationships are discussed in section 3.

This work examines sauropod evolutionary history in two main stages. Firstly, the results of a cladistic analysis (Upchurch 1993) of sauropod relationships are presented. The proposed sets of synapomorphies are used to identify the more fragmentary genera which could not be included within the initial cladistic study. Secondly, sauropod phylogeny is compared with recent work on Mesozoic palaeogeography. This allows an assessment of the extent to which sauropod evolution was affected by the break-up of Laurasia and Gondwanaland during the Jurassic and Cretaceous periods.

3. HISTORICAL PERSPECTIVE

(a) Classification

The pioneering studies of R. Owen, H. G. Seeley, R. Lydekker, O. C. Marsh, E. D. Cope and J. B. Hatcher, to name just some of the key 19th century workers, enabled the sauropods to be conveniently divided into several families. For example, Marsh (1896, pp. 231–232) divided the 'order' Sauropoda into six families: Atlantosauridae and Diplodocidae (now generally recognized as one family or subfamily including *Diplodocus* and *Apatosaurus*); Morosauridae (equivalent to Camarasauridae); Pleurocoelidae (now included within the Brachiosauridae, though *Brachiosaurus* itself was not known at the time of Marsh's writing); Titanosauridae; and Cardiodontidae (equivalent to Cetiosauridae). A similar classification was employed by Huene (1927), with minor differences such as the inclusion of the Cardiodontidae and Brachiosauridae within the Cetiosauridae and the acceptance of a separate Dicraeosauridae.

Janensch (1929) 'simplified' this classification by designating these 'families' as subfamilies and placing them in two main families – the Brachiosauridae and Titanosauridae – based on the possession of broad spatulate teeth and narrow 'peg-like' teeth respectively (McIntosh 1990*a*). Romer (1956) expanded this two-fold classification so that the Brachiosauridae included the Brachiosaurinae, Camarasaurinae, Cetiosaurinae and Euhelopodinae (a subfamily containing Chinese

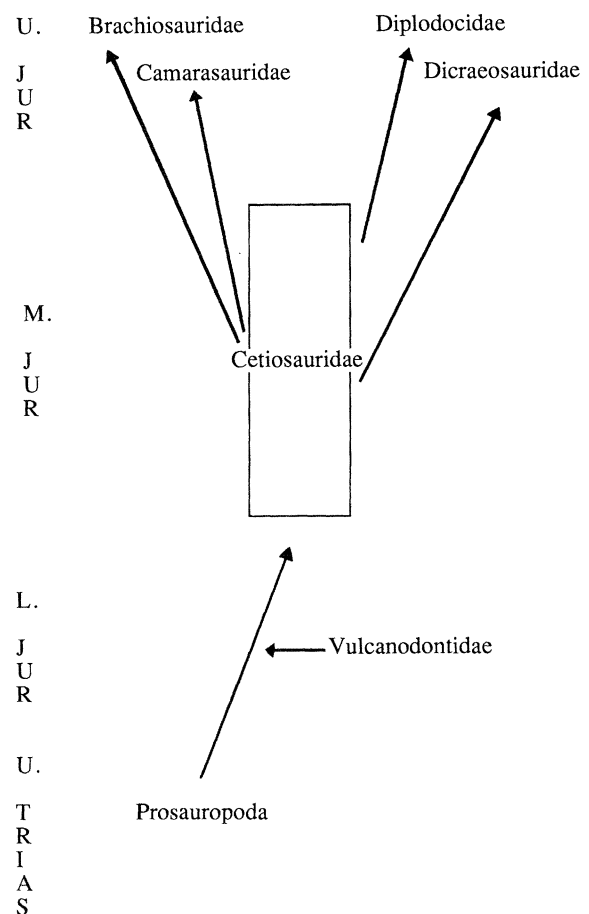


Figure 1. The phylogeny of Jurassic sauropods (redrawn from Bonaparte (1986)).

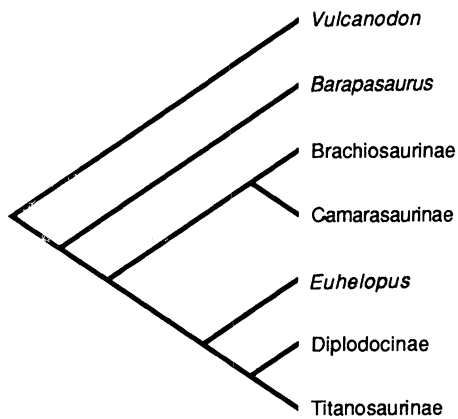


Figure 2. A cladogram of sauropod relationships based on the results of Gauthier (1986).

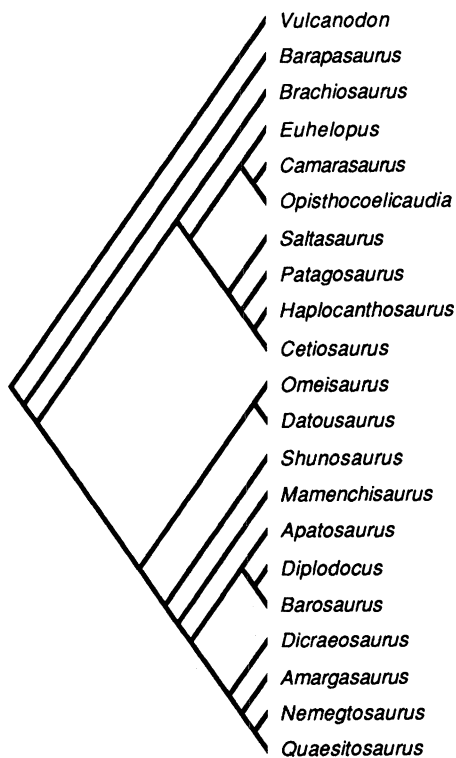


Figure 3. A cladogram of sauropod relationships, based on the phylogeny presented by McIntosh (1989).

forms, principally *Euhelopus*). The Titanosauridae included the Titanosaurinae, Dicraeosaurinae, Apatosaurinae and Diplodocinae.

More recent studies of sauropod systematics have suggested that Janensch's two-fold classification is inadequate. For example, McIntosh (1989, 1990*a, b*) employed six families, and Upchurch (1993) and Hunt *et al.* (1995) have argued for the inclusion of an additional two or three families. These modifications include the raising of the 'Euhelopodinae' to family rank and the introduction of new families such as the Nemegtosauridae (see below).

(b) Phylogeny

Explicit studies of sauropod phylogeny are a relatively recent phenomenon compared with the long history of sauropod systematics. Bonaparte (1986)

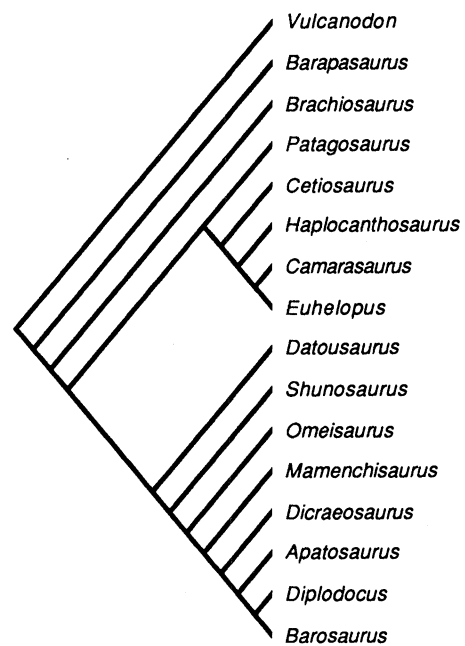


Figure 4. A cladogram of sauropod relationships, slightly simplified from that presented by McIntosh (1990*b*).

produced a phylogeny based on a study of the vertebral columns of Jurassic sauropods. His view of sauropod evolution is represented in figure 1. One unexpected aspect of this work is the suggestion that *Haplocanthosaurus*, previously placed within the Cetiosauridae, is actually a close relative of *Dicraeosaurus*.

Gauthier (1986) gave an outline of sauropod relationships in his paper on theropod and bird evolution. His cladogram (figure 2) showed *Barapasaurus* as one of the most primitive sauropods. *Brachiosaurus* and *Camarasaurus* were viewed as closely related, and were grouped within the 'Camarasauridae'. Similarly, 'titanosaurines' and 'diplodocines' were viewed as sister groups within the 'Titanosauridae'. *Euhelopus* was considered to be the sister taxon of the 'Titanosauridae'.

The most detailed phylogenetic analyses of sauropods are those of McIntosh (1989, 1990*b*). These two phylogenies (figures 3 and 4) tend to include a large number of taxa, but unfortunately consider only a small number of characters. It is highly likely that cladistic analyses based on such a small number of characters would produce a very large number of most parsimonious trees, of which McIntosh's view would be but one. The two phylogenies produced by McIntosh differ in some major ways. For example, figure 3 shows *Camarasaurus* and *Brachiosaurus* as more closely related to each other than either is to *Diplodocus*. But in figure 4, *Diplodocus* and *Camarasaurus* are more closely related than either is to *Brachiosaurus*.

The first published cladistic analysis based on a large number of characters was that of Yu (1990). His data matrix contained 64 osteological characters for 17 sauropod taxa. This study, however, has only been published in the form of an abstract and all the characters were derived from the literature. The resulting cladogram is shown in figure 5.

Russell & Zheng (1993) described important new material which probably belongs to *Mamenchisaurus*.

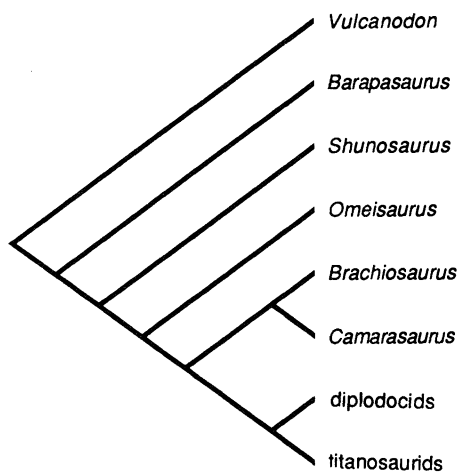


Figure 5. A cladogram of sauropod relationships, based on the description given by Yu (1990).

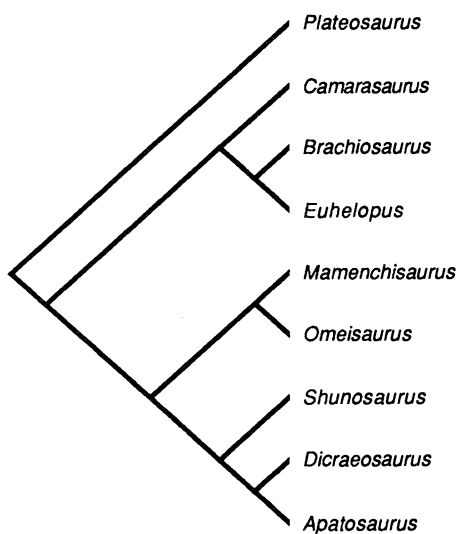


Figure 6. A cladogram of sauropod relationships (after Russell & Zheng 1993).

They provide a data matrix of 21 osteological characters for eight sauropod genera and *Plateosaurus* (the outgroup). When analysed, this data set produced three most parsimonious trees (all very similar in topology) and their 'favoured' cladogram is shown in figure 6. However, as Russell & Zheng acknowledge, 21 characters are insufficient for the adequate analysis of sauropod relationships. The authors themselves express doubts about the position of *Euhelopus*.

Wilson & Sereno (1994) presented a cladistic analysis (in the form of an abstract) of 150 characters for 15 sauropod taxa. The resulting cladogram was partly described by Wilson & Sereno and is shown in figure 7. All sauropods, except *Shunosaurus*, form a monophyletic group which has been named the Neosauropoda. Upchurch (1993) independently coined this term, but applied it to a more restricted group of sauropods (see below). Wilson & Sereno suggest that brachiosaurids and titanosaurids are sister taxa. This rather unexpected result is impossible to assess in the absence of details of the supporting synapomorphies. However, it should be noted that Upchurch (1993) found several derived states present in both families (here interpreted as convergences, see below).

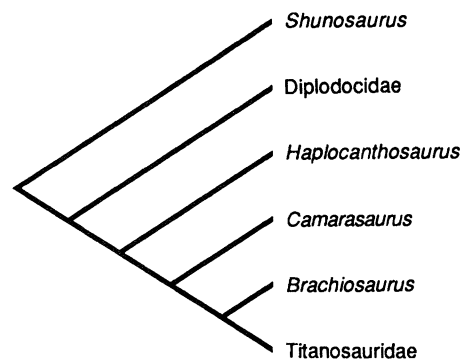


Figure 7. A cladogram of sauropod relationships, reconstructed from the description in Wilson & Sereno (1994).

On reviewing all these cladograms and phylogenies, it is possible to pick out certain points in common. Most of the recent work has concluded that: *Barapasaurus* and *Vulcanodon* are successively more distant outgroups to the rest of the Sauropoda; brachiosaurids and camarasaurids are sister groups; titanosaurids and diplodocids are sister groups; and the Cetiosauridae represent a primitive sauropod stock that gave rise to most of the Upper Jurassic and Cretaceous forms. This 'consensus' masks the fact that there is little agreement concerning the genera placed within the Cetiosauridae (compare Bonaparte (1986), McIntosh (1990*b*) and Upchurch (1993)). The phylogenetic relationships of many of the Asian taxa, such as *Mamenchisaurus*, *Euhelopus* and *Opisthocoelicaudia*, remain poorly understood.

4. MATERIALS AND METHODS

A data matrix of 174 osteological characters and 27 sauropodomorph taxa was developed from an extensive survey of the relevant literature and personal observation of numerous specimens. The genera examined, with institutional catalogue numbers, are listed in appendix 1B in Upchurch (1993). Specimens of particular importance will be mentioned (with catalogue numbers where necessary).

The data matrix was analysed using PAUP version 3.0n (courtesy of Dr David Norman, Department of Earth Sciences, Cambridge). A wide variety of analyses were done, including equally and non-equally weighted, with use of various algorithms ('exhaustive' for smaller numbers of taxa, 'branch and bound' and 'heuristic' for larger numbers). These analyses enabled an assessment of the effects of including or excluding certain taxa and changing the weights of particular characters. Very similar topologies were obtained from each of these studies. Individual analyses tended to produce small numbers of very similar most parsimonious trees. The cladogram in figure 8 is that produced by a unequally weighted Heuristic analysis of 27 taxa. Full details of the osteological characters, polarity determinations and weighting strategy can be found in Upchurch (1993 and in preparation).

Once a tree topology has been chosen, there are several ways in which the state changes can be distributed on that tree. Here I have used DELTRAN

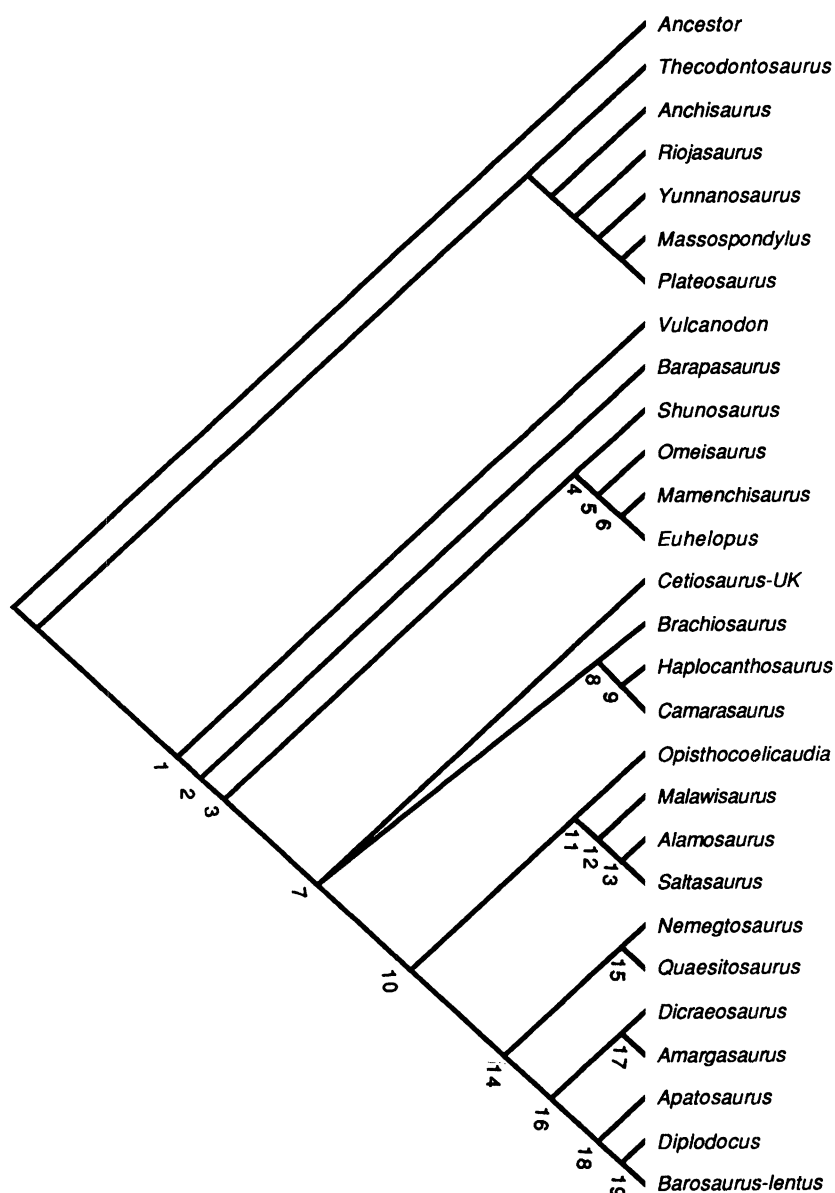


Figure 8. A cladogram of sauropod relationships, based on the results of Upchurch (1993). The cladogram shown here was produced by an unequally weighted heuristic analysis of 174 osteological characters from 27 sauropodomorph taxa. 'Ancestor' is a hypothetical taxon possessing the plesiomorphic condition for every character. The character polarities were determined by using Theropoda and Ornithischia as successively more distant outgroups. The nodes are numbered as follows: 1, 'Sauropoda'; 2, 3, 'Eusauropoda'; 4, 'Euhelopodidae'; 5, 6, 7, 'Neosauropoda'; 8, 9, 'Camarasauridae'; 10, 11, 'Titanosauroidae'; 12, 'Titanosauridae'; 13, 14, 'Diplodocoidea'; 15, 'Nemegtosauridae'; 16, 17, 'Dicraeosauridae'; 18, 'Diplodocidae'; 19.

('delayed transformation') which tends to bias the distribution towards convergences rather than reversals. There are, however, a small number of character state changes that I have preferred to treat as reversals, even though DELTRAN suggests they represent convergence. This can normally be justified on the basis of new data which has been collected since the original analyses were done.

Sauropod material is notorious for its 'missing data'. There are several genera that lack major parts of the skeleton, and indeed there are some where only the skull is known. This leaves ambiguity in the distribution of the derived characters on the cladogram. I have placed the synapomorphies at the highest node possible in each case. Thus, for example, it is known that the sacral neural spines are relatively low in

titanosauroid sauropods (the plesiomorphic state) and relatively high in dicraeosaurids and diplodocids (the derived state). The condition in the nemegtosaurids, *Nemegtosaurus* and *Quaesitosaurus*, is unknown because these genera are only represented by cranial material. The synapomorphy 'relatively high sacral neural spines' could be placed at node 14 (figure 8), thus implying that the nemegtosaurids have the derived state, or at node 16, implying that they have the plesiomorphic state. Both assumptions are currently dubious since nothing is known about the postcrania of these genera. However, we must choose one of these assumptions if we are to use this synapomorphy in the diagnosis of a higher taxon within the Sauropoda. I prefer to assume the presence of the plesiomorphic condition until direct evidence to the contrary becomes

available. Synapomorphies are therefore placed at the 'highest' node possible.

5. SAUROPOD EVOLUTIONARY RELATIONSHIPS

(a) *The origin of the Sauropoda*

Most recent studies have suggested that the Prosauropoda represent the monophyletic sister group to the Sauropoda (Sereno 1989; Galton 1990; Upchurch 1993; Gauffre 1994). The apparent trend within the Prosauropoda, from small bipedal forms to larger quadrupedal forms, is thought to represent convergence on a sauropod-like body form. If this view is correct, we can no longer explain the origin of sauropods in terms of a transition from prosauropod ancestors. What then can we say about the earliest stages of sauropod evolution?

The earliest prosauropod is the poorly known *Azendohsaurus* (Galton 1990; Gauffre 1994). This has been found in rocks of Middle Carnian age (223 Ma, according to Harland *et al.* (1990)). The earliest known sauropod is *Vulcanodon*, found at approximately the Triassic–Jurassic boundary in Zimbabwe (Raath 1972; Cooper 1984), about 208 Ma (Harland *et al.* 1990). Since prosauropods and sauropods are thought to be monophyletic sister groups, the two lineages must have diverged from each other by at least 223 Ma. Thus the first 15 million years of the sauropod lineage is totally unknown to us. It should be borne in mind, however, that absolute geological ages, calculated from radiometric data, may have a substantial margin of error. Nevertheless, this simple comparison suggests that there is much still to be discovered about the first stages in sauropod evolution.

The earliest, and usually most primitive, members of the Ornithischia (e.g. *Lesothosaurus*, *Pisanosaurus*), Theropoda (e.g. *Eoraptor* and *Herrerasaurus*) and the Prosauropoda are all small bipedal forms. It therefore seems likely that sauropods arose from small bipedal ancestors. The exact sequence of anatomical changes, between the earliest sauropods and a form such as *Vulcanodon*, cannot be established. It is probable, however, that an increase in body size, accompanied by a strengthening of the sacrum and lengthening of the forelimbs, occurred during the Upper Triassic. Other changes, such as alterations to the skull and dentition, and even greater lengthening of the neck, may also have occurred during this time, perhaps in relation to a change in feeding preferences. The earliest stages of sauropod evolution will make a fascinating study when appropriate material becomes available.

(b) *Vulcanodon and the Vulcanodontidae*

Vulcanodon karibaensis (Raath 1972) is known from a partial skeleton (and other material) from Zimbabwe. The exact age of the rocks in which it was found is uncertain, but they are generally thought to be of Triassic–Jurassic boundary age or perhaps Hettangian (lowermost Jurassic) (Cooper 1984).

Raath (1972) interpreted *Vulcanodon* as a prosauropod that had convergently acquired some sauropod-like features. He based his view on a number of

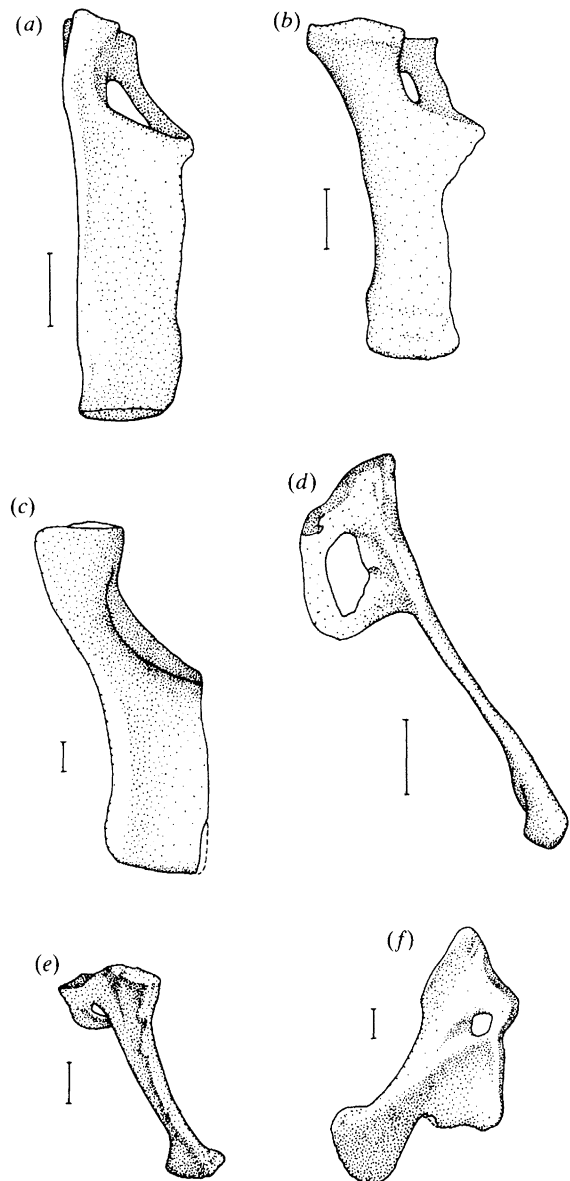


Figure 9. Sauropodomorph pubes in anterior (*a–c*) and lateral (*d–f*) views. (*a, d*) *Plateosaurus engelhardti* (SMNS 13200, after Huene (1926)) (*b, e*) *Vulcanodon karibaensis* (SAM QG24, after Cooper 1984)) (*c, f*) *Brachiosaurus brancai* ((*c*) HMN SII; (*f*) HMN J2, after Janensch (1961)). (*a–e*) Left pubes; (*f*) A right pubis. Scale bars, 100 mm.

features, the most important of which was the structure of the pelvis. In particular, Raath noticed that the pubes of *Vulcanodon* and prosauropods formed a characteristic 'apron'-like structure (figure 9). The proximal portion of the pubis lies in an approximately parasagittal plane. The middle and distal portions, however, are twisted relative to the proximal end, so that they form a flattened plate which lies in a transverse plane. The medial edges of the pubes meet each other on the midline, and together the distal portions form the transverse 'apron'. However, the presence of the pubic 'apron' is not a derived state. Similar structures can also be seen in early theropods (*Herrerasaurus* (Sues 1990), *Coelophysys* (Colbert 1989)) and some of the archosaurs closely related to dinosaurs (*Lagerpeton* (Sereno & Arcucci 1994*a*), *Marasuchus* (Sereno & Arcucci 1994*b*)). There is, in any case,

substantial evidence that *Vulcanodon* shares a number of derived states with other sauropods. These include the following (node 1).

1. The sacrum of *Vulcanodon* appears to have had approximately four coossified sacra. Only three coossified sacral centra can actually be observed, but the two most posterior of these have ribs that join the ilium near the ischiadic peduncle, suggesting that at least four sacra were present in life (Raath 1972; Cooper 1984). Sauropod genera typically have four to six coossified sacral vertebrae (a condition apparently independently acquired by more 'advanced' theropods and ornithischians).

2. The anterior caudals possess a hyposphene-like ridge between the top of the posterior neural canal opening and the bases of the postzygapophyses.

3. Estimates of forelimb/hindlimb ratios suggest that theropods, prosauropods and ornithischians typically have values below 0.60, whereas sauropods have values above 0.65. Indeed, most sauropods have values above 0.75, but this may have been reversed in diplodocids and dicraeosaurids (see below). Unfortunately, the humeri and femora of *Vulcanodon* are damaged, so that exact values for their lengths cannot be obtained. However, reasonable estimates, added to the known lengths of radii, metacarpals, tibiae and metatarsals, give a forelimb/hindlimb ratio of approximately 0.76. So *Vulcanodon* appears to have the long forelimbs characteristic of other sauropods.

4. The femur of *Vulcanodon* has a reduced lesser trochanter (in all other sauropods this has disappeared altogether) and lacks the slight sigmoid curve to the femoral shaft seen in most prosauropods.

5. The ankle bears some similarity to those of later sauropods, including the initial development of the distal 'roller' on the astragalus (Cooper 1984) and the absence of any ossified distal tarsals. The latter might be considered a dubious character since these small disk-shaped elements can easily be lost during post-mortem disruption. There are, however, several specimens, such as the juvenile *Camarasaurus lentus* (CM11338) and *Vulcanodon* itself, where the pes, proximal tarsals and tibia/fibula, have been found in articulation. Indeed, no currently available sauropod material has produced recognizable distal tarsal elements. Distal tarsals are, however, commonly discovered in other dinosaur groups, except stegosaurs, ankylosaurs and ornithomimosaurids (Weishampel *et al.* 1990). These elements are also known in most prosauropods, including the heavily built *Blikanasaurus* (Galton & van Heerden 1985).

The derived states listed above confirm that *Vulcanodon* is a sauropod, but the structure of the pubis, less reduced lesser trochanter and the relatively long metatarsal I (see below) suggest that it is the most plesiomorphic sauropod so far discovered. This view fits well with *Vulcanodon*'s stratigraphic position.

Cooper (1984) placed *Vulcanodon* in the new family Vulcanodontidae, along with the 'Lower' Jurassic Indian form known as *Barapasaurus*. McIntosh (1990*b*) tentatively added *Ohmdenosaurus* and *Zizhongosaurus*, and characterized the family by thirteen diagnostic characters. Most of these characters are symple-

siomorphies, but this is not a criticism since McIntosh does not try to argue for the monophyly of the Vulcanodontidae. However, many of these characters, including absence of pleurocoels, four functional sacra, anterior caudal centra deeply furrowed ventrally, prominent chevron facets, relatively long forelimb, slender femur and presence of the calcaneum, are misleading since they are also found in several other sauropods that would not normally be included within the Vulcanodontidae.

Ohmdenosaurus is represented by a tibia and astragalus from the Middle Toarcian (approximately 180 Ma (Harland *et al.* 1990)) of Germany (Wild 1978). McIntosh (1990*b*) described the astragalus as being of the same general form as that of *Vulcanodon*, but with a concavity on its ventral surface. It would seem, therefore, that the distal 'roller' was not at all well developed in this German form. Despite its younger age, *Ohmdenosaurus* might represent a sauropod that is more plesiomorphic (in the ankle at least) than *Vulcanodon*.

Zizhongosaurus is based on a dorsal neural arch and spine, a portion of humerus and a fragment of pubis (Dong *et al.* 1983, figure 6). This material, and another sauropod called *Sanpasaurus* (about which little is known at present), come from the Lower Jurassic Zilujing Formation of the Sichuan Basin, China (Dong *et al.* 1983; Dong 1992). *Zizhongosaurus* may genuinely belong in the Vulcanodontidae as currently diagnosed, since the dorsal vertebra is sauropod-like and the pubis shares some similarities with those of prosauropods (Dong 1992).

Kunmingosaurus (Chao 1985) is based on a fragmentary sauropod collected in 1954 and some referred lower jaw material from the same site (Dong 1992, figure 28). Very little is known about the anatomy of this form at present. Its importance, however, is potentially very great since it comes from the Lower Lufeng Formation (Hettangian–Pliensbachian, 208–187 Ma, according to Harland *et al.* (1990)) of Wuding, Yunnan Province. This means that *Kunmingosaurus* is the earliest sauropod where some skull material is preserved. Despite its Lower Jurassic age, there is currently no evidence to suggest that *Kunmingosaurus* should be assigned to the Vulcanodontidae.

Barapasaurus is represented by disarticulated remains from several skeletons, providing examples of all parts except the skull and feet (Jain *et al.* 1975, 1979). It was found in the 'Lower' Jurassic Kota Formation of Andhra Pradesh, India. There are several derived states uniting *Barapasaurus* and the remaining sauropods, including the following (node 2).

1. Presence of spatulate teeth.
2. Complex lamination on the anterior and middle cervical neural arches and spines.
3. Cervical centra are strongly opisthocoealous.
4. Prominent lamination developed on dorsal neural spines.
5. Increased height of the dorsal neural arches.
6. Pubis is more robust and the apron-like area is reduced.

Unfortunately, all but the last of these characters cannot be examined in *Vulcanodon*. However, Jain *et al.*

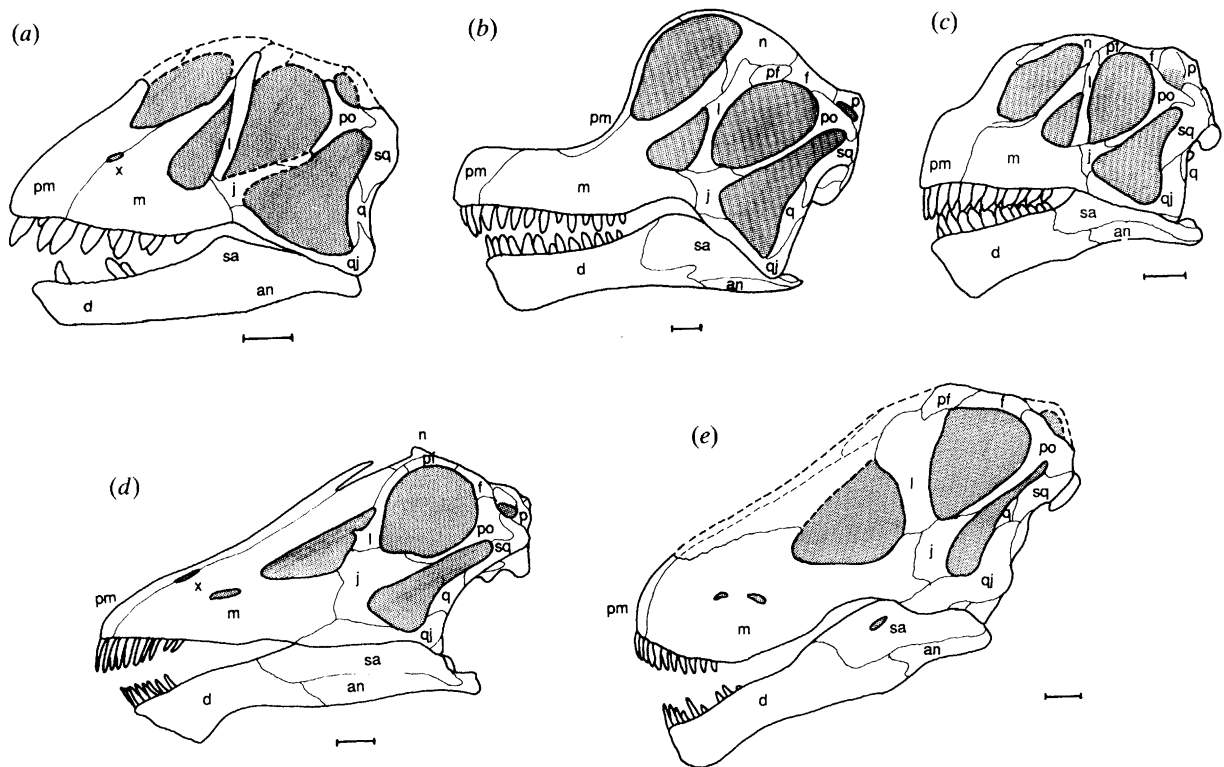


Figure 10. Sauropod skulls in left lateral view. (a) *Euhelopus zdanskyi* (PMU R233a- δ , after Mateer & McIntosh (1985)), (b) *Brachiosaurus brancai* (HMN SII, after Janensch (1935–36)), (c) *Camarasaurus lentus* (CM11338, after Gilmore (1925)), (d) *Diplodocus longus* (based on CM11161), (e) *Nemegtosaurus mongoliensis* (Z. Pal. no. MgD-1/9, after Nowinski (1971)). Scale bars, 50 mm. Abbreviations: an, angular; d, dentary; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pf, prefrontal; pm, premaxilla; po, postorbital; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal; x, premaxilla-maxilla foramen.

(1979) suggest that the pubes of *Barapasaurus* and other sauropods are derived relative to those of *Vulcanodon* and prosauropods. These modifications include an increased robustness of the pubis and an increase in the depth of the 'U'-shaped 'pelvic basin' which can be seen between the proximal ends of the pubes in anterior view (Jain *et al.* 1979, plate 97A–C; Cooper 1984, figure 17A–C). Most recent studies agree upon the relative phylogenetic positions of *Vulcanodon*, *Barapasaurus* and other sauropods (Gauthier 1986; McIntosh 1990b; Yu 1990; Upchurch 1993). Bonaparte (1986) suggested that the dorsal vertebrae of *Barapasaurus* are as derived as those of *Cetiosaurus* and *Patagosaurus*, and are more derived than those of certain other sauropods, such as *Lapparentosaurus* and *Volkheimeria*. He noted, for example, that *Patagosaurus* and *Barapasaurus* possess unusual cavities within the dorsal neural arches. Each of these cavities opens to the exterior via a foramen below the transverse process. This condition has not been observed in any other sauropod. It is possible that the 'Lower' Jurassic age of *Barapasaurus* has influenced the interpretation of its phylogenetic position. Bandyopadhyay (verbal report 1991) has suggested that the Kota Formation is actually of Middle Jurassic age. It would therefore not be too surprising if subsequent redescription of *Barapasaurus* indicated that it should be removed from the Vulcanodontidae.

(e) *The Eusauropoda*

Upchurch (1993) found that all sauropods, except the vulcanodontids, formed a monophyletic assemblage. A new taxonomic group, the 'Eusauropoda', is erected to contain these forms. The Eusauropoda is diagnosed by numerous specializations, including the following (node 3, see figures 10 and 11).

1. Partial (or more extreme) retraction of the external nares.
2. Shortened skull roof.
3. Anterior corner of the lower temporal opening extends (at least partly) underneath the orbit.
4. Ascending process of the maxilla meets the lacrimal at the posterodorsal corner of the antorbital fenestra.
5. 'Lateral plate' on premaxillae, maxillae and dentaries (figure 12; Barrett & Upchurch 1995).
6. External mandibular fenestra is greatly reduced.
7. Tooth crowns are procumbent (i.e. lean forwards).
8. Tooth rows end below or in front of the antorbital fenestra.
9. Addition of at least two cervicals to the vertebral column (from ten to twelve cervicals).
10. Manual phalangeal formula reduced to at most 2–2–2–2–1.
- 11*. Pubis even shorter and more robust.
- 12*. The torsion between the distal and proximal ends of the pubis is much less pronounced.
13. Pedal digit IV reduced to three phalanges.

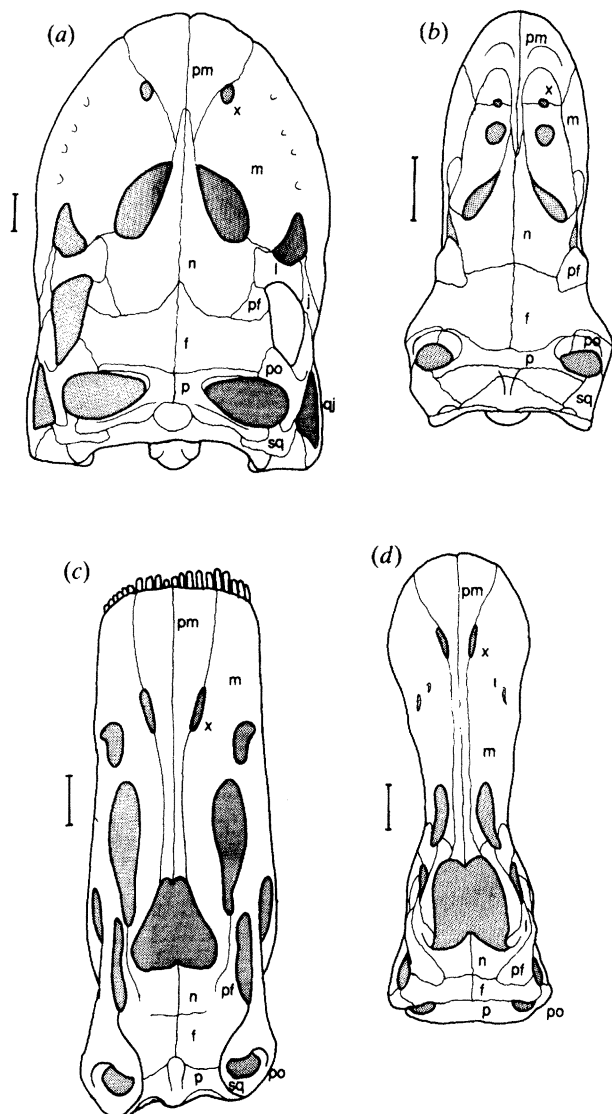


Figure 11. Sauropod skulls in dorsal view. (a) *Brachiosaurus brancai* (after Janensch (1935–36)); (b) *Camarasaurus lentus* (after Gilmore (1925), with some modifications based on personal observation); (c) *Diplodocus longus* (based on CM11161), (d) *Nemegtosaurus mongoliensis* (Z. Pal. no. MgD-1/9, after Nowinski (1971)). Scale bars, 50 mm. For abbreviations see legend for figure 10.

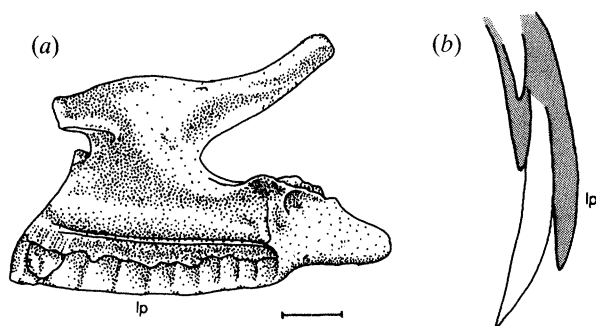


Figure 12. The sauropod 'lateral plate'. (a) Medial view of the right maxilla of *Camarasaurus* (unnumbered specimen from the Dinosaur National Monument, Utah; after White 1958); (b) generalized transverse section through the maxillary lateral plate (the stippled and plain areas denote the bone of the maxilla and the teeth respectively). Scale bar, 50 mm; lp, lateral plate.

14*. Metatarsal I is very short and robust. Only those synapomorphies marked by * can be confirmed as absent in at least some vulcanodontids. Some additional derived states based on the structure of the femur are being investigated currently and may eventually strengthen the support for this node. The Eusauropoda can be divided into two distinct monophyletic groups, the Euhelopodidae and the Neosauropoda.

(d) The Euhelopodidae

The Euhelopodidae contains *Shunosaurus*, *Omeisaurus*, *Mamenchisaurus* and *Euhelopus*. This is a rather different assemblage from those suggested by other authors (figures 3–6) although it should be noted that many Chinese workers have tended to place all or some of these genera within this family (Dong *et al.* 1983; Dong 1992). The Euhelopodidae is diagnosed by the following derived states (node 4).

1. Dorsal process of quadratojugal loses contact with ventral process of squamosal (independently acquired by diplodocids).

2. Cervical number increased from twelve to thirteen (also may have occurred in the lineage leading to the diplodocids).

3. Presence of a bony club at the end of the tail (state not known in *Mamenchisaurus* and *Euhelopus*).

4. Possession of forked chevrons on the middle caudal vertebrae (independently acquired in diplodocids and dicraeosaurids).

5. First caudal rib is fan-shaped in anterior view (independent acquisition in diplodocids and dicraeosaurids).

It will immediately strike the reader that most of these derived states are not unique to the Euhelopodidae: they also occur in the Diplodocidae and sometimes the Dicraeosauridae. Why then do the euhelopodids and diplodocids–dicraeosaurids not cluster more closely on the cladogram in figure 8? The answer is that there is substantial support for the monophyly of the Neosauropoda (node 7). The derived conditions found in euhelopodids and diplodocids–dicraeosaurids are, therefore, more parsimoniously interpreted as convergences.

Omeisaurus, *Euhelopus* and *Mamenchisaurus* are further united by the possession of at least seventeen cervicals (a condition not found in any of the diplodocids, which have fifteen or sixteen) and possession of particularly elongate cervical centra (which are found in *Diplodocus* and *Barosaurus*, but not *Apatosaurus* or dicraeosaurids) (node 5). *Mamenchisaurus* and *Euhelopus* are further united by the presence of bifurcate posterior cervical and anterior dorsal neural spines (node 6). Presacral spine bifurcation is also found in *Camarasaurus*, *Opisthocoelicaudia*, dicraeosaurids and diplodocids. The situation in the two Chinese genera is more like that in diplodocids and dicraeosaurids because the bifurcation forms a 'V'-shaped notch rather than the 'U'-shaped notch found in *Camarasaurus* and *Opisthocoelicaudia*. However, the notch in the diplodocids and dicraeosaurids is much deeper than in the Chinese forms.

The presence of a distal tail club in some sauropods

is of great interest. Tail clubs, formed from three to five coossified caudal vertebrae, have been recovered from the Lower Shaximiao Formation (Middle Jurassic) of Dashanpu, Sichuan Province, China, which is already well known as the site where many *Shunosaurus* and *Omeisaurus* skeletons have been discovered (Dong *et al.* 1989). The fifteen tail clubs described by Dong *et al.* are of two types and have been referred to *Shunosaurus* and *Omeisaurus*. Unfortunately, no tail material of *Euhelopos* has been found, and the distal end of the tail in *Mamenchisaurus* is also unknown (Young & Chao 1972). It is interesting and rather intriguing to note that Young & Chao, long before the discovery of ossified sauropod tail clubs, stated that *Mamenchisaurus hochuanensis* (holotype) probably had a 'cartilaginous' tail club. This must remain doubtful, however, since these authors did not discuss the evidence that led them to this view. The view that *Mamenchisaurus* is a diplodocid (Young & Chao 1972; McIntosh 1989, 1990*b*) may have encouraged the reconstruction of this form with a whiplash tail (see, for example, the restorations in Hallett (1987)). The last caudal preserved in the holotype of *Mamenchisaurus hochuanensis* is the 35th. The centrum of this caudal is 108 mm long and 56 mm high at the anterior end. The 35th caudal centrum in *Apatosaurus louisae* is 155 mm long and approximately 60 mm high. The greater elongation of the centrum in *Apatosaurus* is typical of forms possessing whiplash tails. The presence of the shorter caudals, combined with the proposed phylogenetic position of *Mamenchisaurus*, suggest that this genus would be more plausibly reconstructed with a distal tail club.

Charig (1980) suggested that forked chevrons were correlated with the use of the tail as a weapon. The anterior and posterior extensions on each chevron would help protect vulnerable subvertebral blood vessels and nerves. This hypothesis is supported by the discovery of forked chevrons in euhelopodids and diplodocids, which clearly possess two distinct types of tail weapon (club and whiplash).

Several other Chinese sauropods may also be referable to the Euhelopodidae. *Datousaurus* (Dong & Tang 1984) is based on two partial skeletons from the Dashanpu site in the Sichuan Basin. A robust skull, with spatulate teeth, was found in association with one of the skeletons. This skull resembles those of other euhelopodids, with laterally facing premaxilla-maxilla foramina – a plesiomorphic state not found in neosauropods. *Datousaurus* has thirteen cervicals and forked chevrons, suggesting that it may have been a euhelopodid similar to *Shunosaurus*.

Klamelisaurus (Zhao 1993) comes from the Middle Jurassic of the Junggar Basin, Xinjiang Province, China. It has large spatulate teeth, an estimated sixteen cervicals and forked chevrons. This genus may have been related to forms such as *Omeisaurus*, *Mamenchisaurus* and *Euhelopos*.

'*Nurosaurus*' is a new sauropod from the Qagannur Formation of Inner Mongolia (Dong 1992). A full description of this form is not yet available, although one is planned by Dong & Li. The single photograph of this sauropod in Dong (1992, figure 76) suggests that it may belong to the Euhelopodidae. The neck is long,

with around sixteen or seventeen cervicals. The middle and posterior cervicals and anterior dorsals appear to have bifurcate neural spines. Forked chevrons may be present. As in most non-diplodocoid sauropods, the cervical ribs are long and slender so that the shaft of one rib extends posteriorly well beyond the posterior end of the centrum to which it is attached. The forelimbs are longer than would be expected in a diplodocid sauropod. The age of the Qagannur Formation is not known, but it appears to be older than Upper Cretaceous.

Some of the Chinese genera cannot be so easily referred to the Euhelopodidae. *Bellusaurus* (Dong 1990) is a small sauropod (up to about 4.8 m in length) known from seventeen partial skeletons (Dong 1992). These individuals were all found in the same quarry in the Middle Jurassic Wucaiwan Formation, Junggar Basin, and it seems probable that they represent a herd of juveniles. The strongly developed procoely of the anterior caudals led Jacobs *et al.* (1993) to suggest that *Bellusaurus* might represent a very early titanosaurid. It should be noted, however, that prominent procoely is also found in all caudals of *Mamenchisaurus*. No other titanosaurid synapomorphies are present in *Bellusaurus*. The teeth are spatulate, the neck is short, the chevrons do not fork and there is no sign of a tail club. The affinities of *Bellusaurus* cannot be determined at present.

Tienschanosaurus (Young 1937) is known from a partial skeleton from the Upper Shaximiao Formation (Upper Jurassic) of the Junggar Basin. This genus was provisionally placed in the Camarasauridae by McIntosh (1990*b*). However, the derived characters shared by camarasaurids and *Tienschanosaurus*, such as elongate cervical ribs, are here considered to be symplesiomorphies. The fact that the posterior dorsal centra of *Tienschanosaurus* are amphicoelous and the chevrons of the anterior caudals have a bridge of bone above the haemal canal does not support the referral of this genus to the Camarasauridae (see diagnosis of Neosauropoda, section 5*e*). Dong (1992) placed *Tienschanosaurus* within the Euhelopodidae, but there seems little justification for this at present.

Rhoetosaurus is based on a fragmentary sauropod from the Lower(?) Jurassic of Queensland, Australia. This form may actually be of Bajocian age according to Molnar (personal communication in Weishampel 1990). The material includes a cervical centrum, several dorsal vertebrae, a portion of sacrum showing at least four coossified vertebrae, a large part of the tail, and poorly preserved parts of the pelvis and hindlimb (Longman 1926, 1927). The affinities of this form are uncertain, but it is mentioned here because McIntosh (1990*b*) placed it within the 'Shunosaurinae' (a subfamily of the Cetiosauridae). McIntosh (1989) mentioned that the chevrons are 'apparently forked', which may have influenced his decision to place *Rhoetosaurus* in the same subfamily as *Shunosaurus*, *Omeisaurus* and *Datousaurus*. However, it is not clear from the original description (Longman 1926) whether the chevrons are genuinely forked in a manner similar to euhelopodids and diplodocids. The rest of the material generally suggests that *Rhoetosaurus* is a neosauropod. The posterior dorsal vertebrae have well

developed pleurocoels and opisthocoelous centra. The proximal ends of the anterior chevrons are not closed by a bridge of bone. The pubis does seem to be relatively longer and more slender than those of most sauropods, but there is no sign that it formed the plesiomorphic 'apron'-like structure (Longman 1927, plate IV). *Rhoetosaurus* may have an important role to play in our future understanding of sauropod phylogeny and biogeography. Unfortunately, the currently available information makes it difficult to determine the relationships of this form and it is here regarded as 'Neosauropoda *incertae sedis*'.

(e) *The Neosauropoda*

The Neosauropoda contains most of the familiar sauropod genera from the Upper Jurassic and Cretaceous. This new assemblage of sauropods is diagnosed by the following derived states (node 7).

1. Premaxilla-maxilla foramen faces dorsally, not laterally.
2. The infratemporal fenestra extends far forwards beneath the orbit so that its anterior edge lies level with, or in front of, the anterior margin of the orbit.
3. The base of the ascending maxillary process produces a flange of bone which projects anteromedially and meets its partner from the opposite side at a midline junction.
4. External mandibular fenestra is completely closed.
5. Teeth in the upper jaw become larger anteriorly.
6. Well developed pleurocoels in the cervical centra (absent in dicraeosaurids and some titanosaurs).
7. Cervical pleurocoels are divided into anterior and posterior portions by a prominent accessory lamina (not developed in titanosaurs and *Cetiosaurus*).
8. Number of coossified sacral vertebrae increases from four to five.
9. Left and right proximal ends of the anterior chevrons are not connected to each other by a 'bridge' of bone above the haemal canal (reversed in dicraeosaurids and diplodocids; plesiomorphic state probably present in *Cetiosaurus*).
10. Metacarpals held in a vertical 'colonnade'.
11. Manual phalangeal formula reduced to 2-1-1-1-1.
12. Femoral distal condyles extend prominently anteriorly as well as posteriorly.
13. Extreme reduction or loss of collateral ligament pits from the distal ends of the metatarsals and pedal phalanges.
14. Pedal digit IV is reduced to two phalanges.

The Neosauropoda currently contains the Cetiosauridae (*sensu* Upchurch 1993), a brachiosaurid-camarasaurid clade and a titanosaurid-diplodocid clade. As explained below, future work may suggest the exclusion of the Cetiosauridae from the Neosauropoda.

(f) *Cetiosaurus and the Cetiosauridae*

Cetiosaurus (Owen 1841) was one of the first sauropod genera to be named. Unfortunately, Owen's original type material is too fragmentary for an adequate

generic diagnosis. In addition, *Cetiosaurus* has served as a convenient 'label' for a large amount of fragmentary sauropod material from the Jurassic and Lower Cretaceous of England. The genus is therefore in need of extensive revision, a project that is already in progress (P. Upchurch & J. Martin, in preparation). In the cladogram (figure 8), '*Cetiosaurus-UK*' is based on data derived from the best preserved English material, available at the museums in Oxford (OUMZ) and Leicester (LCM). The partial skeletons at these institutions provide information about nearly all parts except the skull. A nearly complete skeleton of *Cetiosaurus* (*C. mogrebiensis*), from Morocco, is being described by P. Taquet (personal communication 1992) but it is not yet known whether this form and the English material genuinely belong to the same genus. The Moroccan material is particularly important since it includes the skull.

The main reason why the analyses of Upchurch (1993) found more than one most parsimonious tree was the instability of the position of *Cetiosaurus-UK*. This instability seems to have been caused by the presence of many plesiomorphic states in *Cetiosaurus* (relative to other neosauropods) and the lack of data for several important characters. The three possibilities suggested by these analyses are that *Cetiosaurus* is the sister taxon to the brachiosaurid-camarasaurid clade, the sister taxon to the titanosaurid-diplodocid clade, or the sister taxon to a monophyletic group containing all remaining neosauropods. The uncertainty in the position of *Cetiosaurus* is expressed in figure 8 by the trichotomy at node 7. Recent work (P. Upchurch & J. Martin in preparation) tentatively suggests that *Cetiosaurus* is the sister taxon to the remaining neosauropods. If this proves to be the case, I propose that 'Neosauropoda' should apply at the node uniting brachiosaurids, camarasaurids, titanosaurids and diplodocids, thus excluding *Cetiosaurus*. This revision would, of course, necessitate some redistribution of the derived states diagnosing the Neosauropoda at present.

Cetiosaurus has been used as the basis for the family Cetiosauridae (Lydekker 1888). As discussed earlier, the cetiosaurids are frequently regarded as a paraphyletic assemblage of primitive sauropods that gave rise to separate lineages leading to each of the more familiar Upper Jurassic and Cretaceous forms. This 'consensus' may obscure the fact that this family requires detailed revision. McIntosh (1990*b*) divided the Cetiosauridae into two subfamilies, the Shunosaurinae and the Cetiosaurinae. Upchurch (1993) argued that the 'shunosaurines' should be removed from the Cetiosauridae and placed within the Euhelopodidae (see above). The remaining 'cetiosaurines' (here regarded as the family Cetiosauridae) include *Cetiosaurus* and two Middle Jurassic Argentinian genera, *Patagosaurus* and *Amygdalodon*. Work on the relationships of these cetiosaurids is in progress (P. Upchurch, in preparation) and suggests that they lie close to the base of the neosauropod clade.

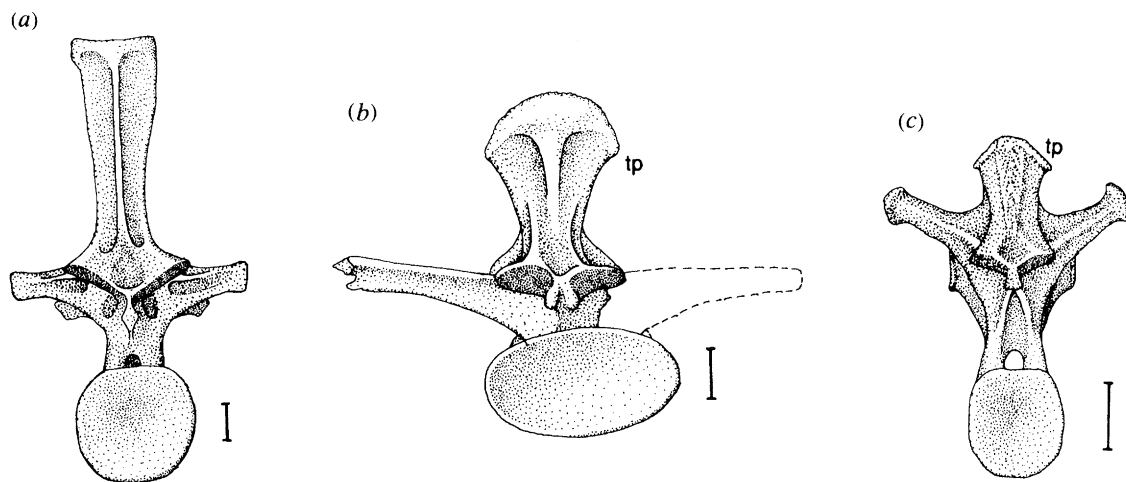


Figure 13. Sauropod dorsal vertebrae in posterior view. (a) *Apatosaurus louisae* (dorsal 8, CM3018, after Gilmore (1936)); (b) *Brachiosaurus brancai* (dorsal 10(?), HMN SII, after Janensch (1950)); (c) *Haplocanthosaurus priscus* (dorsal 12(?), CM572, after Hatcher (1903)). Scale bars, 100 mm; tp, triangular process (see text).

(g) *The Brachiosauridae and Camarasauridae*

The Brachiosauridae and Camarasauridae share a number of derived features, including the following (node 8).

1. Enlarged external nares (longest diameter is approximately equivalent to 40% of skull length).
2. Strongly anterodorsally arched internarial bar.
3. Premaxilla–maxilla foramen lies within the external narial fossa.
4. Flattened, dorsally facing area at the anterior end of the maxilla ('maxillary shelf' (see McIntosh 1990b)).
5. Muzzle-like region present in front of the internarial bar (short in camarasaurids, long in brachiosaurids).
6. The tops of the middle and posterior dorsal neural spines flare laterally to form characteristic triangular processes (figure 13).
7. Metacarpals are relatively long and slender (possibly a reversal to the plesiomorphic state found in other dinosaurs).

Characters 1–5 may be correlated, forming a single character complex. Nevertheless, even taken as a single character, these modifications to the skull are very unusual and strongly suggest a close phylogenetic relationship between brachiosaurids and camarasaurids.

(h) *The Brachiosauridae*

In the cladistic analyses of Upchurch (1993) the brachiosaurids were only represented by *Brachiosaurus*. This genus is known from partial skeletons from the Upper Jurassic Morrison Formation (Colorado) and Tendaguru Formation (Tanzania). This large form (length up to 23 m) is well known for its long vertical neck and relatively long forelimbs. The humerus is virtually the same length as the femur. Although humerus/femur ratios are rather variable among dinosaur genera (P. Upchurch, in preparation), the particularly high ratio in *Brachiosaurus* is not found

elsewhere, apart from other brachiosaurids. *Brachiosaurus* possesses several other derived states, at least some of which may diagnose the entire family. These include the following.

1. Internarial bar is extremely slender relative to skull size (figure 10).
2. The 'muzzle' region, anterior to the internarial bar, is relatively long (figure 10).
3. Tooth crowns arranged in an 'imbricate' pattern (i.e. the distal margin of a given crown overlaps labially the mesial edge of the tooth that follows immediately posterior to it).
4. The thoracic ribs possess foramina that lead into internal cavities.
5. Humerus/femur ratio is approximately 0.9–1.0.
6. The claw on manual digit I is extremely reduced.
7. The shaft of the ischium is directed steeply downwards.

On the basis of these characters, several other forms can be included within the Brachiosauridae.

The material now known as *Lapparentosaurus* was previously referred to *Bothriospondylus* by Ogier (1975). The type material of *Lapparentosaurus* consists of three or four partial skeletons (lacking skull material, apart from teeth) of apparently juvenile sauropods from the Bathonian of Madagascar. Bonaparte (1986), who recognized the distinct nature of this material, believed it to belong to a form more plesiomorphic than *Barapasaurus*, *Cetiosaurus* and *Patagosaurus*. He noted the poor development of the lamination on the dorsal neural spines and the lack of pleurocoels in the cervical and dorsal centra. The dorsal neural arches are also relatively lower than those of typical sauropods. These plesiomorphic features would tend to place *Lapparentosaurus* somewhere within the Vulcanodontidae. However, re-examination of this material (P. Upchurch, personal observation) indicates that these characters should be treated with some caution. The dorsal neural spines, for example, are not simple transversely compressed plates as in other dinosaurs. Instead they are triangular in horizontal section (widest along the posterior margin) as in other sauropods. Supraprezygapophysial, suprapostzygapo-

physical and supradiapophysial laminae are moderately developed. The absence of pleurocoels is not a good guide to the relationships of this genus. Within the Neosauropoda alone, pleurocoels seem to have been lost at least twice independently, once within the Titanosauridae (*Malawisaurus*) and once within the Dicraeosauridae. Until we know more about sauropod growth and development, we cannot be sure whether the 'plesiomorphic' features in *Lapparentosaurus* reflect phylogeny or ontogeny. McIntosh (1990*b*) placed *Lapparentosaurus* within the Brachiosauridae, although he did not provide any evidence for this. The material assigned to this genus includes femora with distal condyles that project strongly anteriorly as well as posteriorly (suggesting a close relationship with the Neosauropoda). The ischia display very steeply inclined shafts and the humeri are relatively elongate. *Lapparentosaurus* is therefore provisionally referred to the Brachiosauridae.

Another relatively early 'brachiosaurid', *Volkheimeria*, has been recovered from the Middle Jurassic of Argentina (Bonaparte 1979). It was included within the Brachiosauridae by McIntosh (1990*b*) and is apparently similar to *Lapparentosaurus* (Bonaparte 1986).

Bothriospondylus was originally based on very fragmentary remains from Wiltshire, England (Owen 1875). Since Owen's description, several other sets of remains have been referred to this genus, including substantial material from Madagascar (Lydekker 1895; Thévenin 1907; Ogier 1975). In many cases this Madagascan material can only be identified as an indeterminate sauropod. Well preserved material from the Upper Jurassic of Damparis, France, has also been referred to *Bothriospondylus* by Dorlodot (1934) and Lapparent (1943). The shaft of the ischium is directed very steeply downwards, but the humerus/femur ratio is lower than expected, around 0.80. Further evidence for the presence of brachiosaurids in the Upper Jurassic of Europe comes from the discovery of fragmentary remains from Portugal (*Brachiosaurus atalaiensis*) and brachiosaurid humeri known as '*Ischyrosaurus*' and '*Cetiosaurus humerocristatus*' from the Kimmeridgian of Dorset, England (Upchurch 1993).

Brachiosaurus may not have been the only brachiosaurid present in the Upper Jurassic of North America. *Ultrasaurus* and *Dystylosaurus* were named by Jensen (1985), based on rather fragmentary material. Until more details are available, it cannot be fully demonstrated that these genera are distinct from *Brachiosaurus* (McIntosh 1990*b*), although *Ultrasaurus* does appear to represent a form somewhat larger than currently known *Brachiosaurus* specimens.

There is good evidence that brachiosaurids remained abundant (in at least some areas) during the Lower and early Middle Cretaceous. Examples include the indeterminate brachiosaurid known as '*Pelorosaurus conybeari*', based on an elongate humerus from the Wealden Formation (Valanginian) of Sussex, England. A large amount of fragmentary material has also been recovered from the Wessex Formation (Barremian) of the Isle of Wight, England. These specimens are usually referred to '*Ornithopsis*' (or one of its numerous

synonyms). Some of the material does not belong to a brachiosaurid (see Upchurch (1993) for a discussion), but the dorsal vertebrae are almost identical to those of *Brachiosaurus*. A partial skeleton of a brachiosaurid has recently been discovered on the Isle of Wight (S. Hutt, verbal report, 1992). Taxonomic revision of '*Ornithopsis*' should be greatly facilitated by this new specimen.

'*Dinodocus mackesoni*' is based on a very poorly preserved partial skeleton from the Lower Greensand (Aptian) of Kent, England. Most of the preserved elements cannot be identified, but portions of humerus suggest that this bone was very long and slender, resembling those of other brachiosaurids (Upchurch 1993). Another fragmentary sauropod, assigned to a fourth 'species' of *Brachiosaurus* (*B. nougaredi* (Lapparent 1960)), comes from the Albian of Algeria. McIntosh (1990*a*), however, has pointed out that this material is too poorly preserved to be identified at the generic level.

Pleurocoelus is known from the Hauterivian–Barremian of Maryland and the Aptian–Albian of Texas. Much of the material, especially that from the Arundel Formation of Maryland, appears to come from juveniles, whereas the Texas material indicates a sauropod of approximately 9–10 m in length (Langston 1974). No dorsal neural spines have been reported, but the relative lengths of the humeri and metacarpals, the structure of the dorsal centra (with extremely extensive pleurocoels) and some aspects of the caudal vertebrae strongly suggest that this genus is a brachiosaurid. Small spatulate teeth, from the Wealden Formation (Valanginian) of Sussex, England, have been referred to this genus (Lydekker 1890), but there are no derived features shared by the English and American specimens to justify this. Brachiosaurids may also have been present in the Lower Cretaceous of western U.S.A. (see section 5*k*).

Chubutisaurus (Corro 1975) is based on fragmentary cervicals and dorsals, several caudal vertebrae and most limb elements. It is an interesting form mainly because it comes from the Albian of South America. McIntosh (1990*b*) has tentatively placed this genus within the Brachiosauridae, largely on the basis of limb ratios (for example, humerus/femur ratio of 0.87). The fragmentary nature of this material means that its status as a brachiosaurid is far from definitely established.

In summary, brachiosaurids seem to have occupied North America, Europe, South America and Africa up to the Albian, but there is no evidence that this family survived beyond this point.

(i) *The Camarasauridae*

Camarasaurus material is abundant in the Upper Jurassic Morrison Formation of the U.S.A. It is a medium-sized sauropod with a short high skull and relatively short neck. Although the forelimbs are long compared with diplodocids and dicraeosaurids, they tend to be shorter than in euhelopodids and brachiosaurids. Figure 8 shows *Haplocanthosaurus* (also from the Upper Jurassic of North America) to be the sister taxon

to *Camarasaurus*. These two genera share the following derived states (node 9).

1. Cervical vertebrae have broad flat ventral surfaces (independently acquired in at least some titanosaurids, such as *Saltasaurus*).

2. The posterior surfaces of the proximal portions of the anterior thoracic ribs are deeply excavated.

3. The distal shafts of the ischia are strongly twisted relative to the plane of the proximal plate.

Two other 'unusual' characters, of uncertain status, are also found in these two genera. Firstly, the supraprezygapophysial laminae are not strongly developed on the posterior cervicals and anterior dorsals of *Camarasaurus* and *Haplocanthosaurus*, in contrast to the situation in other sauropods. Secondly, the pedicels of the dorsal centra in *Haplocanthosaurus* and *Camarasaurus grandis* (YPM 1901, 1905) are relatively tall and meet over the top of the neural canal. As a result, the neurocentral suture lies above the neural canal. This does not occur in every dorsal vertebra of these specimens, and this unusual feature is not found in *Camarasaurus lentus* and *C. supremus* (McIntosh 1990*a*). Another Upper Jurassic camarasaurid is *Cathetosaurus* from Colorado (Jensen 1988). This form is very similar to *Camarasaurus*, and J. S. McIntosh (personal communication 1991) has suggested that they may be congeneric.

The Camarasauridae is perhaps the most problematic of all of the commonly employed sauropod families. McIntosh (1990*b*) lists the following taxa as members of this family: *Camarasaurus*, *Aragosaurus*, *Tienseosaurus*, *Euhelopus* (within the 'Camarasaurinae'); *Opisthocoelicaudia* and *Chondrosteosaurus* (within the 'Opisthocoelicaudinae'). I have already argued for the removal of *Euhelopus* and *Tienseosaurus* from this family. In section 5*k* it is suggested that *Opisthocoelicaudia* is most parsimoniously interpreted as the sister taxon to the Titanosauridae. These results further restrict the geographic and stratigraphic distribution of the Camarasauridae.

Camarasaurids were certainly present in the Upper Jurassic of North America. They may also have occurred in Europe from the Oxfordian to Barremian. '*Camarasaurus alenquerensis*' is known from a partial skeleton (lacking skull and cervical vertebrae) and other material from the Oxfordian–Kimmeridgian of Portugal (Lapparent & Zbyszewski 1957). At present the available data are insufficient to confirm the inclusion of this material within *Camarasaurus* itself. McIntosh (1990*a*), however, has noted similarities in the limb proportions between the Portugese and North American materials.

'*Chondrosteosaurus*' (Owen 1876) is based on a few isolated cervical centra from the Wessex Formation of the Isle of Wight, England. These cervical centra are strongly opisthocoelous and have prominent pleurocoels. The ventral surfaces are broad and flat and the pleurocoels are divided into anterior and posterior portions by a prominent accessory lamina. Although '*Chondrosteosaurus*' is probably a camarasaurid, it is too fragmentary to allow diagnosis at the generic level.

Aragosaurus is based on a partial skeleton (lacking skull, presacrals and sacrum) from the Barremian of

Spain (Sanz *et al.* 1987). As with the Portugese '*C. alenquerensis*', this potentially important form requires further study.

(j) *The Titanosauroidae and Diplodocoidea*

These two new superfamilies contain familiar sauropod families, such as the Titanosauridae, Diplodocidae and Dicraosauridae, as well as some less expected forms (see below). The titanosaurids and diplodocids have frequently been considered to be closely related (Janensch 1929; Romer 1956; Gauthier 1986; Yu 1990), although it should be noted that some supposed similarities in the morphology of their skulls are now thought to be dubious (Jacobs *et al.* 1993). The two superfamilies are united by the possession of the following derived states (node 10).

1. The lingual surfaces of the tooth crowns are convex mesiodistally (reversal to plesiomorphic state).

2. Teeth relatively long and slender.

3. Tooth crowns start to taper at midlength or nearer to the crown tip, rather than close to the base.

4. Dorsal neural spines have a postspinal lamina (see below).

5. Anterior caudal centra are at least mildly procoelous (not found in *Opisthocoelicaudia*).

6. Loss of calcaneum.

In most sauropods, a vertically elongate hollow is formed on the posterior surface of the neural spine of each middle or posterior dorsal vertebra. This is brought about by the presence of prominent, posterolaterally directed, suprapostzygapophysial laminae. In the titanosauroids and diplodocids, the postspinal hollow contains a stout vertical 'postspinal' lamina running up the midline. This lamina is explicitly described by Borsuk-Bialynicka (1977, figure 2) and Jacobs *et al.* (1993) in *Opisthocoelicaudia* and *Malawisaurus* respectively. This structure has also been observed by the author in all dicraosaurids and diplodocids. The presence of this lamina cannot be demonstrated in *Alamosaurus* and *Saltasaurus* owing to poor preservation and a lack of detailed descriptions. However, *Andesaurus* (a recently described titanosaurid from South America) does possess the derived condition (Calvo & Bonaparte 1991).

(k) *The Titanosauroidae*

The Titanosauroidae includes the familiar but poorly understood Titanosauridae and the single genus *Opisthocoelicaudia* (figure 8). The latter is based on a partial skeleton (lacking the skull and neck) from the Nemegt Formation (Campanian–Maastrichtian) of the People's Republic of Mongolia. This 'unusual' genus has previously been referred to the Camarasauridae (Borsuk-Bialynicka 1977; McIntosh 1990*b*). There are, however, very few derived states shared by *Camarasaurus* and *Opisthocoelicaudia*. One of these, the presence of bifurcate presacral neural spines, seems to have occurred several times independently within the Sauropoda (Upchurch 1993). The remaining characters cited by Borsuk-Bialynicka are symplesiomorphies

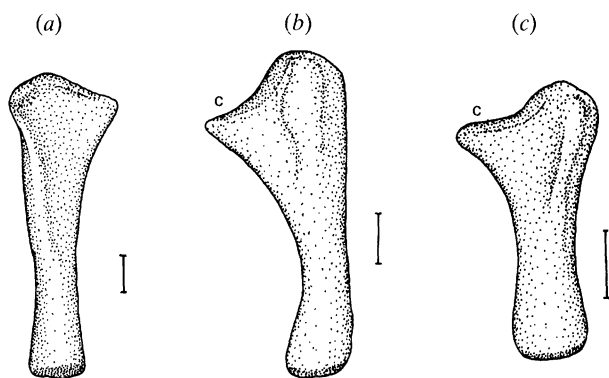


Figure 14. Left sauropod ulnae in anterior view. (a) *Apatosaurus louisae* (CM3018, after Gilmore (1936)); (b) *Janenschia robusta* (HMN P12, after Janensch (1961)); (c) *Saltasaurus loricatus* (PVL4017-72, after Bonaparte & Powell (1980)). Scale bars, 100 mm. The position of the concave profile of the anteromedial proximal process is marked c.

(e.g. simple caudal ribs, unforked chevrons). *Opisthocoelicaudia* shares the following derived states with the Titanosauridae (node 11).

1. The neural arches of the middle caudals are situated on the anterior half of the centrum (also found in *Cetiosaurus*, *Brachiosaurus* and other brachiosaurids).

2. Ulna and radius are extremely robust.

3. Anteromedial proximal process of the ulna bears a prominent concave area dorsally (figure 14). The proximal end of a typical sauropod ulna is divided into two processes by a concavity on the anterior surface. The dorsal (proximal) surfaces of these anterolateral and anteromedial processes are flat in most sauropods. In titanosaurids, however, the dorsal surface of the anteromedial process has a strongly developed concave profile in side view.

4. The anterior blade of the ilium is turned outward to form an almost horizontal plate.

5. The pubis has become much less robust (reversal to the plesiomorphic state).

Borsuk-Bialynicka (1977) also noted that *Opisthocoelicaudia* possessed opisthocoelous anterior caudals, unlike titanosaurids where they are prominently procoelous. This difference was considered to be evidence against a close relationship between these taxa. The condition found in *Opisthocoelicaudia*, however, is an autapomorphy of that genus (at least at present) and thus tells us little about its relationships. Borsuk-Bialynicka (1977) noted several of the character states listed at node 11 (and others besides), but did not regard them as significant indicators of phylogenetic relationship. The rejection of these characters seems to be based on the view that certain aspects of sauropod anatomical evolution were 'progressive'. She argued that certain derived states can be 'expected in the Late Cretaceous sauropods representing the final stage of the evolutionary tendencies in this infraorder, irrespective of what family they belong to' (Borsuk-Bialynicka 1977; p. 57). This argument is rejected here because it assumes, *a priori*, that the derived states shared by titanosaurids and *Opisthocoelicaudia* arose via convergence. In addition, there is currently no evidence that any aspects of sauropod evolution were confined to any 'progressive' trends. At present,

therefore, the most plausible interpretation of the relationships of *Opisthocoelicaudia* is that shown in figure 8.

Nevertheless, some similarities between titanosaurids and *Opisthocoelicaudia* are probably the result of convergent evolution. For example, their sacra have six coossified vertebrae (compared with four or five in other sauropods). In titanosaurids, this appears to have been brought about by the addition of an extra dorsosacral, whereas in *Opisthocoelicaudia* an anterior caudal has been incorporated.

The Titanosauridae are united by the following derived states (node 12).

1. The anterior caudals are prominently procoelous (independently acquired in *Mamenchisaurus* and *Bellusaurus*).

2. The distal shaft of the ischium is particularly short (longitudinally) and wide (transversely).

3. Presence of ossified dermal scutes.

In figure 8 the titanosaurids are represented by three taxa. *Malawisaurus* is known from disarticulated remains of several individuals from the Lower Cretaceous of Malawi. Until recently, there was very little known about the skulls of titanosaurids. However, the discovery of *Malawisaurus* demonstrates that early titanosaurids had an external nostril placed close to the anterior end of the skull and the premaxillae were more like those of non-diplodocoid sauropods (Jacobs *et al.* 1993). *Saltasaurus* is based on several partial skeletons from the Upper Cretaceous of Argentina and *Alamosaurus* is known from a partial skeleton and other fragmentary remains from the Upper Cretaceous of southwestern U.S.A. Most titanosaurid genera are too poorly diagnosed to be included within a cladistic analysis. Nevertheless, there are characters that may play an important role in understanding the relationships within this family. For example, *Saltasaurus* and *Alamosaurus* are united by the possession of the following derived states (node 13).

1. Six coossified sacral vertebrae as a result of the addition of another dorsosacral (state not known in *Malawisaurus*).

2. First caudal centrum is biconvex. Although there is some doubt surrounding the presence of this derived state in *Saltasaurus* (J. F. Bonaparte, personal communication, 1994; J. S. McIntosh, personal communication, 1995), there are several other South American titanosaurids that possess biconvex first caudal centra (Jacobs *et al.* 1993).

3. Procoely extends into the middle and distal caudal centra (independent acquisition in *Mamenchisaurus*).

4. The dorsal margin of the coracoid projects above the dorsal margin of the proximal plate of the scapula.

Titanosaurid sauropods have been reviewed recently by McIntosh (1990*b*) and Jacobs *et al.* (1993) and here I shall restrict myself to a few comments on their evolution and distribution.

The earliest titanosaurid may be *Janenschia* (= '*Tornieria*', see Wild 1991), from the Upper Jurassic of Tendaguru, Tanzania. Jacobs *et al.* (1993) accepted the titanosaurid nature of the caudal vertebrae assigned to *Janenschia*, but were less confident about the

presacral vertebrae and limb elements. There is some uncertainty regarding the field relationships of this material. It is also possible that 'Tornieria' was based on material left over after Janensch had identified and assigned remains belonging to *Brachiosaurus*, *Dicraeosaurus* and *Barosaurus africanus* (McIntosh 1989). It is interesting to note, however, that the ulna and radius referred to *Janenschia* seem to possess the extreme robustness expected in a titanosauroid, and the ulna has the characteristic concave area on the anteromedial proximal process (figure 14). This provides additional support for the view that the titanosauroids had appeared by the Upper Jurassic.

Titanosaurids are poorly represented in the Lower Cretaceous. Ostrom (1970) described fragmentary sauropod material from the Lower Cretaceous Cloverly Formation of Montana and Wyoming. Some of these remains may belong to a single individual, and include dorsal vertebrae and limb elements. Ostrom tentatively assigned this form to the Titanosauridae. However, none of the caudal vertebrae are procoelous, the ulna is slender and the ischium is not short and wide. The humerus is apparently rather *Brachiosaurus*-like (Ostrom 1970), and the amphicoelous caudal vertebrae have the neural arch on the anterior portion of the centrum. These features suggest that the material belonged to a brachiosaurid.

The only reliable Lower Cretaceous titanosaurid material, apart from *Malawisaurus*, comes from Europe, especially England. The earliest of these forms may be represented by the forelimb of '*Pelorosaurus becklesii*' (Mantell 1852) from the Valanginian of Sussex. This specimen was considered to be *Sauropoda incertae sedis* by McIntosh (1990*b*). However, a skin impression shows polygonal plates of a similar shape and size to those found in *Saltasaurus* (Bonaparte & Powell 1980). The ulna and radius are robust and the ulna bears the typical concavity on its anteromedial proximal process. Upchurch (1993) therefore argued that this form should be provisionally included within the Titanosauridae. Caudal vertebrae, very similar to those of *Titanosaurus* from the Upper Cretaceous of India, are known from the Wessex Formation (Hauterivian–Barremian) and younger Greensand deposits of the Isle of Wight.

The titanosaurids are also poorly known in the Middle Cretaceous. One of the best preserved forms is *Andesaurus* from the Albian–Cenomanian of Argentina (Calvo & Bonaparte 1991). This genus is known from most parts, except the skull and neck. It appears to be a true titanosaurid, but still possesses amphicoelous middle caudal vertebrae. Other mid-Cretaceous titanosaurs include *Aegyptosaurus* (from the Cenomanian of Egypt) and an unnamed form from the Turonian–Santonian of Kazakhskya. Unfortunately, the type specimens of the former were destroyed during World War II (McIntosh 1990*b*), while few details are currently available concerning the Kazakhskya material. The caudal vertebrae of *Macrurosaurus*, displaying strong procoely in the anterior ones and amphicoely more distally, have been recovered from the Greensand of Cambridgeshire, England. These rocks are of Cenomanian age, but the vertebrate fossil

content has been reworked from Albian deposits (Rawson *et al.* 1978).

Upper Cretaceous titanosaurids include: *Titanosaurus*-like forms, *Magyarosaurus* and *Hypselosaurus* in Europe; *Argyrosaurus*, *Laplatasaurus* and *Saltasaurus* from South America; a species of '*Titanosaurus*' from Madagascar; *Titanosaurus* from India; and material from Laos. *Alamosaurus* appeared in the southwestern part of the U.S.A. in the Late Maastrichtian and may have reinvaded this area via the Panamanian land-bridge from South America (Bonaparte 1984; Lucas & Hunt 1989).

(1) *The Diplodocoidea*

The Diplodocoidea is a new superfamily which contains the Diplodocidae, Dicraeosauridae and the new family, Nemegtosauridae. The relationships between these families can be seen in figure 8.

The Nemegtosauridae currently contains only two genera, both based on skulls alone. As a result only cranial characters can diagnose the Diplodocoidea at present (see figures 10 and 11). These include the following (node 14).

1. Fully retracted external nares (anterior rim of nostril lies far behind the anterior margin of the antorbital fenestra). This is probably correlated with characters 4 and 5 below.
2. External nares face dorsally (rather than laterally).
3. Loss of internarial bar.
4. The premaxilla–maxilla foramen is extremely elongate.
5. The premaxilla is axially long and transversely narrow; the maxilla forms the anterolateral corner of the snout.
6. The quadrate slopes strongly anteroventrally.
7. The mandible is rectangular in dorsal view (rather than 'U'-shaped). This is caused by the anterior portion of each dentary running at right angles to the sagittal plane.
8. The teeth are restricted to the extreme anterior ends of the upper and lower jaws.

The Nemegtosauridae includes *Nemegtosaurus* (Nowinski 1971) and *Quaesitosaurus* (Kurzanov & Bannikov 1983), both from the Upper Cretaceous of the Mongolian People's Republic. *Quaesitosaurus* may be slightly older (Santonian or possibly Campanian) compared with *Nemegtosaurus* (Late Campanian or Maastrichtian). McIntosh (1989) proposed a sister group relationship for these two genera. Synapomorphies supporting this view were suggested by Upchurch (1993) (node 15).

1. The squamosal is excluded from the dorsal rim of the supratemporal fenestra by a postorbital–parietal contact.
2. The anterior process of the quadratojugal bends downwards towards its anterior end.
3. The long axis of the mandibular symphysis is at approximately 90° to the long axis of the mandible, rather than 130° or more as in other sauropods.

The Diplodocidae and Dicraeosauridae share the following derived states (node 16).

1. A small notch in the posterior process of the squamosal exposes the proximal end of the quadrate in occipital view.

2. The occipital condyle is directed ventrally (rather than posteroventrally).

3. Basipterygoid processes are directed anteriorly.

4. Deeply bifurcate presacral neural spines.

5. Small rugosity at the base of each notch in the bifurcate presacral neural spines (independent acquisition in *Euhelopus*).

6. Shortened cervical ribs so that their shafts no longer form overlapping bundles.

7. The neural spines of posterior dorsal vertebrae are widened transversely and flattened anteroposteriorly.

8. Sacral neural spines are at least twice the height of their centra (independent acquisition in stegosaurs and 'higher' ornithomorphs).

9. Complex lamination is found on the anterior caudal neural spines.

10. Chevrons of the middle caudals are 'forked' and possess a midline ventral slit (figure 15). Those of more posterior caudals separate into left and right rami.

11. Forelimb/hindlimb ratio reduced to 0.67–0.70 (approaching a reversal to the plesiomorphic condition).

12. Distal end of the ischiadic shaft becomes dorsoventrally expanded.

13. The lateroventral margin of the distal end of metatarsal 1 develops a small projection (independent acquisition in at least some brachiosaurids).

The Dicraeosauridae includes *Dicraeosaurus* from the Upper Jurassic of Tanzania and *Amargasaurus* from the Lower Cretaceous (Hauterivian) of Argentina (Janensch 1929; Salgado & Bonaparte 1991). These genera share a number of derived features (Salgado & Calvo 1992; Upchurch 1993) (node 17).

1. Very slender and elongate basipterygoid processes which are separated by an angle of approximately 20° or less, compared with 45° in other sauropods including diplodocids.

2. Supratemporal fenestrae are very small and face laterally (rather than dorsolaterally or dorsally).

3. The frontals are thoroughly fused on the midline (rather than merely tightly sutured).

4. Extreme vertical elongation of the cervical neural spines.

5. Neural spines over the sacral region are three to four times as high as their centra.

The best known dicraeosaurid is *Dicraeosaurus* itself. This is a relatively small form (around 10 m long). The short neck is composed of 12 cervicals. The presacrals lack pleurocoels, a very unusual condition among neosauropods. Although several skeletons are available, none of them are complete enough for the presence of a whiplash tail to be confirmed, but diplodocid-like forked chevrons suggest that one should be expected. The forelimbs of both *Dicraeosaurus* and *Amargasaurus* appear to be relatively short, as in diplodocids.

Rebbachisaurus is represented by material from the Albian of Morocco and Niger. The specimens are rather fragmentary and there is no guarantee that they

all belong to the same genus. McIntosh (1990*b*), however, has noted that a posterior dorsal belonging to the Moroccan specimen possesses a neural spine that has the characteristic shape and great height indicative of a dicraeosaurid. It seems likely, therefore, that dicraeosaurids were present in the Middle Cretaceous of North Africa.

The Diplodocidae contains familiar forms from the Upper Jurassic of North America and elsewhere. This family is diagnosed by a large number of derived states, some of which are listed below (node 18) (see also Berman & McIntosh 1978).

1. The jugal forms a large portion of the margin of the antorbital fenestra.

2. The angle between the anterior and dorsal rami of the quadratojugal has been increased to approximately 135°.

3. The distal end of the paroccipital process forms a rounded 'tongue-shaped' structure.

4. The parasphenoid rostrum is a very thin spike.

5. The ectopterygoid processes of the pterygoids are greatly reduced and no longer project below the ventral margin of the skull.

6. Each infraprezygapophysial lamina, on the middle and posterior cervicals, bifurcates towards its dorsal end so that the prezygapophysis is supported from below by two laminae. A triangular hollow is created between these two branches.

7. Addition of three cervicals (an increase from twelve to fifteen), at least two of which were probably converted dorsals (dorsal number decreases from twelve to ten).

8. The tail ends in a distal whiplash (possibly also present in dicraeosaurids).

Material from England may have much to add to our knowledge of the evolution of the Diplodocidae and related forms. *Cetiosauriscus* comes from the Callovian of Cambridgeshire and therefore predates the North American genera. This genus is based on a large part of the tail, a portion of sacrum, a forelimb lacking the manus, parts of the pelvis and an almost complete hindlimb (including most of the pes). Bonaparte (1986) cast doubt on the diplodocid nature of *Cetiosauriscus* because none of the characteristic dorsal vertebrae had been preserved. However, it should be clear from the list of synapomorphies for node 18 that the Diplodocidae can be diagnosed even when dorsal vertebrae are not available. Berman & McIntosh (1978), McIntosh (1989, 1990*b*) and Upchurch (1993) concluded that *Cetiosauriscus* was a member of the Diplodocidae based on the presence of the following derived states: elongate sacral neural spines, forked chevrons with a ventral slit and eventual complete separation of rami, calcaneum absent, relatively short forelimbs and the characteristic laterodistal projection on metatarsal I. However, although these synapomorphies place *Cetiosauriscus* within the Diplodocoidea, they do not identify the family-level status of this early English form. *Cetiosauriscus* does possess a whiplash tail, as in other diplodocids. As mentioned above, however, fragmentary preservation makes it impossible to confirm that this derived state is absent in the Dicraeosauridae. *Cetiosauriscus* could be a basal

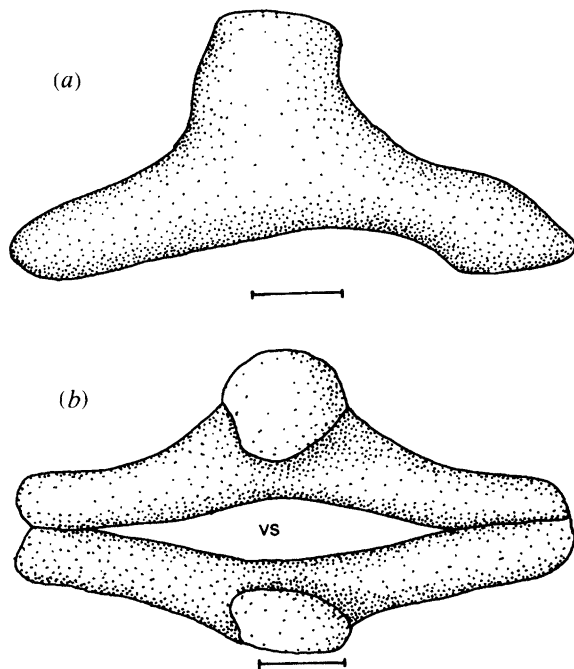


Figure 15. 'Forked' chevron of *Diplodocus carnegii* (CM84) in (a) left lateral view and (b) dorsal view. This is approximately the 17th chevron (from the anterior end of the tail). Scale bar, 50 mm; vs, ventral slit (see text).

member of either the dicraeosaurid or diplodocid radiations, or even a basal diplodocoid. For the present, therefore, this English genus is regarded as *Diplodocoidea incertae sedis*. The absence of pleurocoels and ventral excavations in the anterior caudal centra does suggest that *Cetiosauriscus* lies outside the *Barosaurus*–*Diplodocus* clade.

The Diplodocidae includes forms such as *Diplodocus*, *Apatosaurus*, *Barosaurus*, *Supersaurus* and *Seismosaurus*. These are all known from the Upper Jurassic of North America. McIntosh (1990*b*) has confirmed Janensch's identification of some Tendaguru material as belonging to *Barosaurus*. Although there may be some problems with this identification with regard to particular specimens, it is true that certain Tendaguru material represents a *Barosaurus*-like or *Diplodocus*-like sauropod. For example, metatarsal II, in *Barosaurus africanus* (HMN Nr. 28, XIII 10) and *Diplodocus* (CM84), possesses a characteristic rugosity on the dorsolateral margin close to the distal end. This structure has not been observed in any other sauropod.

According to the cladogram in figure 8, *Diplodocus* and *Barosaurus* are more closely related to each other than either is to *Apatosaurus*. The former genera share the following derived states (node 19).

1. Relatively more elongate cervical centra (independent acquisition in some euhelopodids).
2. The prezygapophysial articular facets on the middle and posterior cervicals are transversely convex (rather than flat).
3. All dorsal vertebrae possess a vertical midline lamina on the posterior face of the neural arch, supporting the hypospine from below.
4. Anterior caudal centra possess lateral pits ('pleurocoels').
5. Anterior caudal centra are deeply excavated on

their ventral surfaces (independently acquired in *Opisthocoelicaudia* and *Saltasaurus*).

6. The pubis possesses a hook-like ambiens process (also found in *Dicraeosaurus*).

It seems that *Seismosaurus* (from New Mexico) and *Supersaurus* (from Colorado) are also more closely related to *Diplodocus* and *Barosaurus* than either is to *Apatosaurus*. *Supersaurus* is poorly known at present, with much material awaiting preparation (Jensen 1985). However, two middle caudals referred to this genus apparently possess centra with excavated ventral surfaces. *Seismosaurus* is known from a single partial skeleton and is remarkable for its incredible size. Gillette (1991) estimates its total length to have been somewhere between 37 and 53 m. The anterior caudals of this form possess 'pleurocoels' and ventral excavations.

Material from the Isle of Wight suggests that diplodocids–dicraeosaurids persisted into the Lower Cretaceous of Europe. Charig (1980) described a large forked chevron (possessing a ventral slit) from the Wessex Formation (Hauterivian–Barremian). Several other specimens from these deposits, including a large metatarsal I (BMNH 11187) and a very small neural spine and arch from an anterior caudal (on display in the Sandown Museum of Geology), also possess characteristic diplodocid–dicraeosaurid features.

Weishampel (1990) lists a possible diplodocid ('? *Barosaurus lentus*') from the Late Aptian–Cenomanian of the 'Dakota Formation' of Utah. Little information is currently available concerning this specimen.

'*Antarctosaurus*' (Huene 1929) is normally included within the Titanosauridae, and probably does contain some genuine titanosaurid material (Jacobs *et al.* 1993). However, the type specimen, from the Campanian–Maastrichtian of Argentina, includes a fragmentary cranium with some striking diplodocoid synapomorphies. The teeth are slender and restricted to the anterior end of the mandible, and the lower jaw has the characteristic rectangular outline in dorsal view (characters 7 and 8 at node 14, 'Diplodocoidea'). The braincase has a slender parasphenoid rostrum, suggesting that it belonged to a member of the Diplodocidae, but the skull roof appears to differ from those of all other sauropods (McIntosh 1990*b*). Although it seems highly probable that this South American material belongs to the Diplodocoidea, currently available information does not allow it to be easily assigned to any of the three diplodocoid families employed here. Nevertheless, this enigmatic form does indicate that the Mongolian nemegtosaurids were not the only diplodocoids present in the Upper Cretaceous.

6. SAUROPOD PHYLOGENY AND BIOGEOGRAPHY

(a) Introduction

The following is an attempt to integrate data on sauropod evolution, stratigraphic and geographic distribution, with information on Mesozoic palaeogeography. First, however, it is important to appreciate the uncertainty surrounding each of the sources of data.

1. The proposed set of sauropod relationships could be inaccurate.

2. Taxonomic problems may obscure the true distribution of sauropods.

3. Absence from the fossil record does not mean that the organism was not alive at the particular time and place concerned. Thus, dates of origin and extinction are little more than speculation constrained by the periods of time in which the organism is currently known to have been present. For the same reason, the geographic point of origin of a group is usually impossible to establish with any rigour.

4. There are often difficulties associated with the absolute and relative geological ages of sauropod genera and species. Frequently, the most precise estimate of the age and temporal extent of a particular genus may be as vague as 'Middle Jurassic' or 'Lower Cretaceous'. There are even instances where the age of the deposits concerned is based mainly on the kinds of dinosaurs found in them (see Dong 1992 for some examples). This practice can introduce a circular argument into estimates of the times of origin and extinction of particular sauropod groups.

5. Our knowledge of palaeogeography is constrained by the fact that, although palaeomagnetism can be used to find palaeolatitude, it cannot determine palaeolongitude. Data on 'sea-floor spreading' may allow some estimate of palaeolongitude, but this is only available as far back as the Middle Jurassic (Smith *et al.* 1994).

6. Smith *et al.* (1994) provide palaeocoastline reconstructions, for the Mesozoic and Cenozoic, at an average resolution of one map per 8 million years. These maps represent the most detailed and highly resolved reconstructions currently available. However, substantial variation in sea level (and thus coastline) can occur within 8 million years (see Maastrichtian example in Smith *et al.* (1994, p. 11)). Much evolutionary change and dispersal could occur within such a geologically narrow period of time.

7. Other factors, such as floral distribution, climatic zones, adaptations of particular sauropod groups and chance events, may all have had a significant effect on sauropod distribution. The extent to which these factors are more or less important than continental movement and sea level changes is difficult to gauge at present.

Given all these difficulties, is it worth even attempting an understanding of the interaction between sauropod evolution and palaeogeography? I believe it may be; after all, despite the uncertainties, the observed data do not support all 'scenarios' equally. In any case, the pattern suggested below predicts when and where particular kinds of sauropod should and should not be found. As such, it forms a hypothesis that can easily be falsified by future discoveries. In addition, some aspects of sauropod distribution are not entirely compatible with the palaeogeographic reconstructions of Smith *et al.* (1994). Although these inconsistencies may reflect problems with our understanding of sauropod taxonomy and phylogeny, they may also be taken as indications of previously unsuspected aspects of Mesozoic palaeogeography. If, for example, a land

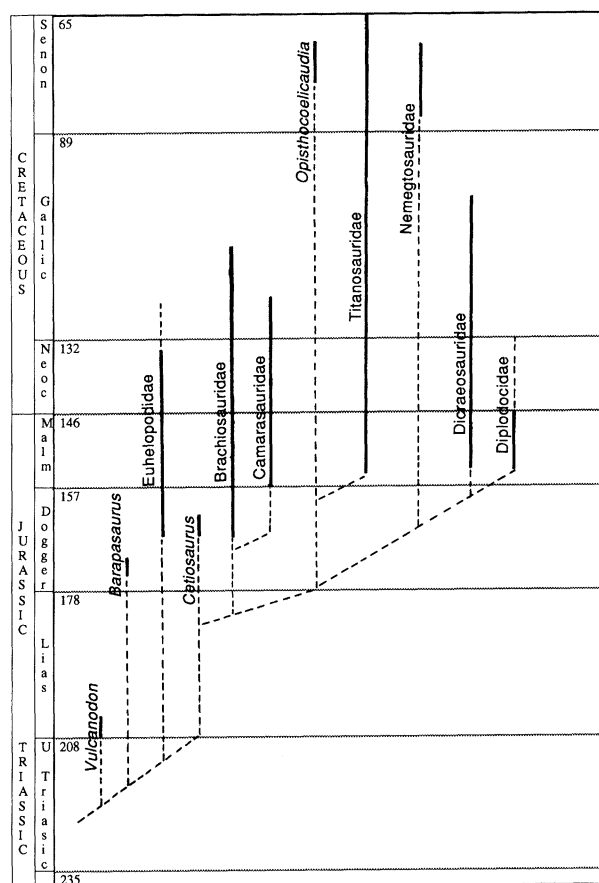


Figure 16. Sauropod phylogeny reconstructed by using the cladogram of figure 8 and the stratigraphic distributions discussed in the text. The time values on the Y-axis are in millions of years before present (based on data in Harland *et al.* (1990)). Abbreviations: Neoc, Neocomian; Senon, Senonian.

bridge appeared and disappeared during the period between two consecutive maps in Smith *et al.*, a sauropod group might seem to cross an 'impassable' barrier, resulting in an apparent contradiction. I believe, therefore, that this overview is worth presenting now, not only because it may form a useful framework for future studies of the Sauropoda, but also because it contains information of potential value to those interested in the reconstruction of Mesozoic palaeogeography.

(b) *An overview of sauropod phylogeny and biogeography*

Sauropod phylogeny is shown in figure 16. Although doubts remain concerning the status of the various vulcanodontid genera, the presence of *Vulcanodon* (Africa), *Ohmdenosaurus* (Germany), *Rhoetosaurus* (Australia), *Kunmingosaurus*, *Zizhongosaurus* and *Sanpasaurus* (China) in the Lower Jurassic suggests that sauropods were already geographically widespread and perhaps taxonomically diverse even at this early stage in their evolution. This observation is consistent with the view that the sauropod lineage underwent a substantial amount of evolutionary change during the Upper Triassic.

Sauropod distribution in the Lower Jurassic gives no

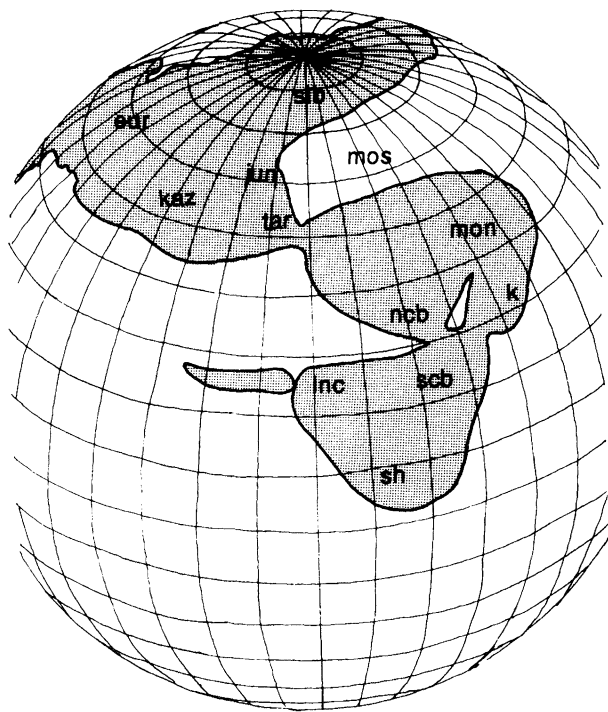


Figure 17. Palaeogeographic map of eastern Eurasia during the Lower Jurassic (redrawn from Enkin *et al.* (1992)). Abbreviations: eur, Europe; inc, Indochina; jun, Junggar block; k, Korea; kaz, Kazakhstan; mon, Mongolian block; mos, Mongol-Okhotsk Sea; ncb, North China block; scb, South China block; sh, Shan Thai; sib, Siberia; tar, Tarin block.

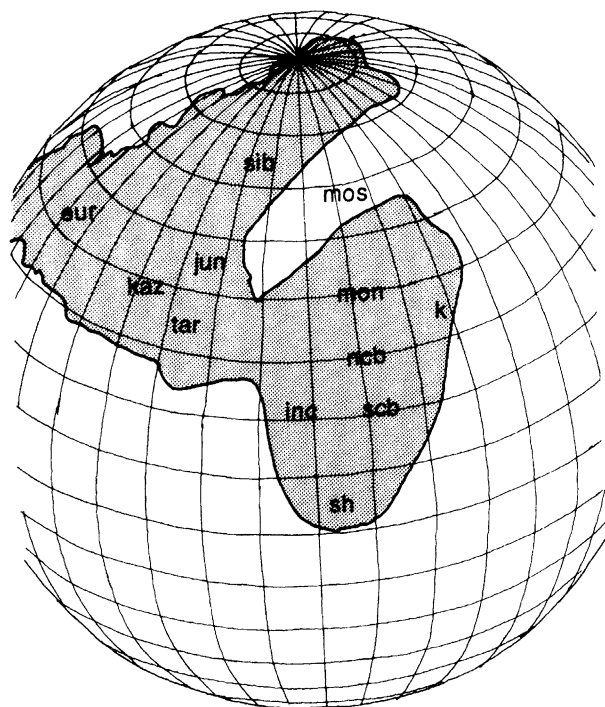


Figure 18. Palaeogeographic map of eastern Eurasia during the Upper Jurassic (redrawn from Enkin *et al.* (1992)). For abbreviations see legend for figure 17.

clue to the place of origin of this group. The Upper Triassic map (map 29) in Smith *et al.* (1994) shows Gondwanaland and North America in contact. This 'supercontinent', however, was separate from Eurasia. Thus, it would have been difficult for sauropods to

have crossed from Eurasia to North America–Gondwanaland (and vice versa) during the Upper Triassic. Maps 28–25 (Hettangian to Toarcian respectively) suggest that a connection between these two continental areas (via western Europe) was present in the Lower Jurassic. We might expect Upper Triassic sauropods, if and when they are discovered, to occur either in North America–Gondwanaland or in Eurasia, but not in both. However, the presence of prosauropods and other dinosaurs in the Upper Triassic of North America, Gondwanaland and parts of Eurasia indicates that dispersal between the two main continental areas was possible even at this time.

The Euhelopodidae first appear in the Middle Jurassic and persist into the Lower Cretaceous. The observation that this monophyletic group contains only Chinese forms suggests that this branch of the Eusauropoda may have been geographically isolated at some point during the Lower or Middle Jurassic. Geographical isolation of Chinese sauropods has also been proposed by Dong (1992), Russell & Zheng (1993) and Russell (1993). Dong (1992) suggested that southwest China was a landlocked area of Gondwanaland, which does not seem likely given the work of Smith *et al.* (1994) and Enkin *et al.* (1992). Russell & Zheng (1993) noted the distinct nature of at least some of the Middle Jurassic Chinese sauropods, but did not provide any suitable isolating mechanism. Russell (1993) suggests at least two isolating mechanisms: (1) a Lower Jurassic land bridge between South Asia and Central Asia could have been disrupted; (2) Central Asia may have become cut off from Europe (and the rest of Pangaea) during the Bathonian as the result of spreading epicontinental seas. Evidence based on the affinities of Chinese and Mongolian mammals, dinosaurs and lizards suggests that South Asia remained isolated until at least the early Cretaceous. Russell notes that the biogeographic evidence for the isolation of South Asia is more clear than the palaeogeographic evidence. However, recent work on Mesozoic palaeogeography lends support to Russell's view. The maps in Smith *et al.* indicate that China was linked to the rest of Eurasia, during most of the Triassic and Jurassic, by a long narrow land bridge. Enkin *et al.* (1992) have investigated the geodynamic history of China from the Permian to the present. Modern China is composed of several continental blocks ('cratons') which were accreted to each other, and to the rest of Eurasia, during the Mesozoic. The sequence of events is summarized below (see also figures 24–27 in Enkin *et al.* (1992) and figures 17 and 18 here).

The eastern margin of Eurasia was formed by Siberia and Kazakhstan during the Triassic and much of the Jurassic. The most important cratons forming modern China are: the South China block (scb), which includes Sichuan Province; the North China block (ncb), which includes northern provinces such as Shanxi and Shandong; the Mongolian block, including the administrative area of Inner Mongolia; and the Tarin and Junggar blocks, which now form Xinjiang Province in western China. During the Middle and Upper Triassic, the scb, ncb and Mongolian block were probably in contact with each other. The

Mongolian block was separated from Siberia by the Mongol–Okhotsk sea, but its western end was probably linked to Kazakhstan by a land bridge partly composed of the Tarin and Junggar blocks. This land bridge closed the southwestern end of the Mongol–Okhotsk sea. In the Lower Jurassic, the scb, ncb and Mongolian block were even more closely assembled, but remained widely separated from the rest of Eurasia. The Junggar and Tarin blocks were more firmly joined to Eurasia, but the junction between the Tarin block and the western end of the Mongolian block is reconstructed as being far less substantial than that present in the Upper Triassic (figure 17). During the Middle and Upper Jurassic, the western end of the Mongolian block collided with the Tarin and Junggar blocks, establishing a more substantial land bridge between Eurasia and the rest of China (figure 18). The Mongol–Okhotsk sea closed during the Lower Cretaceous when Mongolia and the rest of China collided with Siberia.

It is possible that the Junggar–Tarin–Mongolian land bridge was breached at times during the Triassic and Jurassic. This area may have been particularly prone to submergence during the Lower Jurassic when the land bridge was at its most tenuous. When this land bridge was disrupted, sauropods in the Yunnan and Sichuan areas, for example, would have been effectively cut off from the rest of Eurasia. Another possibility is that the land bridge remained intact but became unsuitable for the dispersal of sauropods. The land bridge occupied palaeolatitudes 35–50 °N in the Upper Triassic, but only a few degrees either side of 50 °N during the Lower Jurassic and 30–40 °N in the Upper Jurassic. The restriction of this area to a narrow and higher band of palaeolatitude during the Lower Jurassic may have affected its climate and/or flora in such a way as to ‘discourage’ the passage of sauropods. This scenario must remain speculative until more data on the Lower–Middle Jurassic environments of the Tarin–Junggar area become available.

The second isolating mechanism suggested by Russell (1993), involving the formation of epicontinental seas between Europe and Central Asia during the Bathonian, cannot be easily examined by using the sauropod fossil record. There are virtually no sauropod fossils from the Lower and Middle Jurassic of Central Asia (Weishampel 1990). When such material does become available, its euhelopodid or neosauropod affinities may help identify the region responsible for isolation. Of course, it should be remembered that the Europe–Central Asia separation and the Tarin–Junggar land bridge may both have played a role in the isolation of China–Mongolia (perhaps at different times). It is also tempting to speculate that the closure of the Mongol–Okhotsk sea during the early Cretaceous was in some way related to the decrease in endemism in China and Mongolia during the Middle and Upper Cretaceous.

If Chinese sauropods were isolated from the rest of Eurasia during the Lower Jurassic, forms such as *Kunmingosaurus* (from Yunnan), *Zizhongosaurus* and *Sanpasaurus* (from Sichuan) probably represent early members of the euhelopodid clade. The relative positions of Australia and China at this time, however,

make it highly unlikely that *Rhoetosaurus* also belongs to this group.

While euhelopodids followed their separate course of evolution in eastern Asia, the Neosauropoda were diversifying elsewhere. The Cetiosauridae, as defined here, is restricted to *Cetiosaurus* from the Bathonian of England (and Morocco?), *Amygdalodon* (Bajocian) and *Patagosaurus* (Callovian) of Argentina. It is difficult to interpret the geographic distribution of cetiosaurids, partly because there are so few representatives now that the ‘shunosaurines’ have been removed from the family, and partly because their relationships to each other and to the rest of the Neosauropoda are not well understood. Nevertheless, the Cetiosauridae demonstrate that sauropods closely related to the Neosauropoda were geographically widespread as early as the Bajocian or Bathonian (see below).

The Lower Jurassic to Upper Cretaceous sequence of palaeocoastline reconstructions in Smith *et al.* (1994) suggests that faunal exchange between Laurasia and Gondwanaland was possible up to and including the Bajocian. From the Callovian onwards, however, North America–Europe was separate from South America–Africa. Theoretically, this separation can be used to estimate the times of divergence of various neosauropod lineages. Brachiosaurids, titanosaurids and diplodocoids all have Upper Jurassic and/or Lower Cretaceous representatives in Laurasia and Gondwanaland. This implies that the divergences between the brachiosaurids, camarasaurids, diplodocoids and titanosaurids occurred before the Callovian. A Pre-Callovian divergence of neosauropod lineages is also consistent with the view that *Lapparentosaurus* (from the Bathonian) represents an early brachiosaurid. The distribution of neosauropod groups that arose after the Callovian should also have been affected by the separation of Laurasia and Gondwanaland. For example, apart from *Barosaurus*, all members of the Diplodocidae are found in Europe and North America. Dicraeosaurids, in contrast, are only known from South America and Africa. It is tempting to regard these two families as separate (albeit closely related) northern and southern hemisphere radiations.

There are difficulties, however, with this simple picture of neosauropod biogeography. In particular, the presence of *Brachiosaurus* and *Barosaurus* in both Africa and North America (during the Kimmeridgian) is somewhat puzzling. If Gondwanaland and Laurasia were completely separate from the Callovian onwards, the only explanation of this distribution is that these two genera originated before the Callovian and survived (with virtually no osteological modification) into the Kimmeridgian. It is not inconceivable that a genus might survive for 10–15 million years. Nevertheless, no well diagnosed sauropod genus is known to persist across three or four stratigraphic stages. An alternative possibility is that a connection did exist between Laurasia and Gondwanaland during the Upper Jurassic (Galton 1977; Russell 1993; Sereno *et al.* 1994). The most probable location for this ‘land bridge’ would have been between North Africa and the eastern margin of North America, via western Europe. Although no such land bridge is shown in the

Upper Jurassic maps of Smith *et al.* (1994), the distance between Spain and North Africa was relatively small at this time. A small drop in sea level would have exposed a land connection between the two areas (Serenio *et al.* 1994) and there may have been occasions when sauropods could have waded or swam across this short, and probably shallow, stretch of sea.

No titanosaurs have been discovered in the Upper Jurassic of Europe and North America. This cannot be explained easily in terms of geological factors since these regions have produced large numbers of other sauropods. The earliest (and most plesiomorphic) titanosaurid is *Janenschia* from the Upper Jurassic of Tanzania. Lower Cretaceous titanosaurids are known from Europe ('*Pelorosaurus becklesii*' and other fragmentary material) and again from Africa (*Malawisaurus*). It is possible that titanosaurs originated in Africa (or elsewhere in Gondwanaland) and invaded Europe via the Upper Jurassic land bridge proposed above.

In summary, the Neosauropoda probably diverged into several lineages (Brachiosauridae–Camarasauridae, Titanosauroidae, Diplodocoidea) before the Callovian. Post-Callovian neosauropod radiations would then have been influenced by the separation of Laurasia and Gondwanaland. During the Upper Jurassic diplodocids and camarasaurids were largely restricted to Laurasia, while dicraeosaurids and titanosaurs were found only on Gondwanaland. Towards the end of the Upper Jurassic (Kimmeridgian–Tithonian) *Brachiosaurus* and *Barosaurus* may have been able to cross from North America to Africa (or perhaps vice versa in the case of *Brachiosaurus*). At the same time, or possibly a little later, titanosaurs may have spread from Africa into Europe. Although this scenario provides a plausible explanation for many aspects of neosauropod biogeography, it leaves several questions unanswered. For example, why was a Laurasia–Gondwanaland exchange possible for *Barosaurus*, *Brachiosaurus* and titanosaurs but not other sauropods? Differences between sauropods, in terms of their habitat preferences, may have had a significant effect on their dispersal and consequent biogeographic distribution. In addition, the above scenario is largely based on a comparison of the Morrison and Tendaguru faunas. Hunt *et al.* (1995) have noted that the Morrison Formation represents an 'interior plains' environment, whereas the Tendaguru beds seem to have been deposited in a coastal environment. These authors suggest, therefore, that differences in the sauropod faunas of these two formations may reflect palaeo-ecological rather than biogeographic factors.

The diverse Upper Jurassic sauropod fauna may have remained relatively unaltered in the Lower and earliest Middle Cretaceous of Europe. At this time, brachiosaurids, diplodocoids, titanosaurs and camarasaurids are all represented. Various sauropod families did persist elsewhere, including: brachiosaurids and diplodocids in North America; brachiosaurids, camarasaurids (Serenio *et al.* 1994), titanosaurs and dicraeosaurids in Africa; brachiosaurids and dicraeosaurids in South America; and euhelopodids in eastern Asia. In general, however, the 'Upper Jurassic type' sauropod

fauna did not survive intact into the Middle Cretaceous in most areas.

Middle and Upper Cretaceous sauropod faunas are dominated by titanosaurs. The sauropod fossil record is particularly poor from the Aptian to the Turonian. For example, our knowledge of Middle Cretaceous titanosaurs is largely restricted to fragmentary material from the Albian of South America (Lucas & Hunt 1989, and references therein), *Andesaurus* from the Cenomanian of South America and *Aegyptosaurus* from the Cenomanian of northern Africa. However, data on titanosaurid distribution during the Upper Cretaceous, combined with knowledge of the break-up of Gondwanaland, can increase our understanding of the Middle Cretaceous faunas. India was effectively isolated from the rest of Gondwanaland as early as the Aptian (Smith *et al.* 1994). Thus, even though titanosaurs do not appear in India until the very end of the Cretaceous, we can predict that they were present on the subcontinent as early as the Aptian. Africa may have been the centre for the dispersal of titanosaurs into South America and India during the Middle Cretaceous.

As in the Jurassic, the Upper Cretaceous sauropod fauna of East Asia contains rather unusual forms. Cladistic analysis indicates that *Opisthocoelicaudia* and the Nemegtosauridae were not descendants of the endemic Euhelopodidae. Neosauropods were abundant in the rest of Laurasia as early as the Upper Jurassic, and it is probable that members of this group invaded East Asia at some point in the Lower or Middle Cretaceous. For example, titanosaurs are first represented in Asia by the Middle Cretaceous material from Laos and Kazakhstan. This view is consistent with the palaeogeographic evidence. Russell (1993) has suggested that the isolation of Central and eastern Asia ended during the Aptian–Albian, when land connections to Europe and North America were established.

According to figure 16, *Opisthocoelicaudia* and the Nemegtosauridae diverged from their respective sister taxa during the Upper Jurassic (or even earlier). Yet the lineages leading to these East Asian forms are not represented by fossil material until the Upper Cretaceous. The lengths of these missing lineages ('ghost taxa') would be reduced by reassigning *Opisthocoelicaudia* and the Nemegtosauridae to the Camarasauridae and Dicraeosauridae respectively, but this would conflict with the cladistic data. The interpretation preferred here is that the lengths of the 'ghost' lineages reflect the poverty of the fossil record. Lower–Middle Cretaceous European sauropods are very fragmentary, and their taxonomy is consequently rather poorly known. In addition, little sauropod material has been recovered from the Cretaceous of Central and eastern Asia. The poorly known *Mongolosaurus*, from the Barremian–Albian of Mongolia (Gilmore 1933), possesses slender 'peg-like' teeth. This form may eventually shed light on the origins of the Asian titanosaurs or nemegtosaurids.

The appearance of *Alamosaurus* in southwestern North America, in the latest Maastrichtian, is perhaps best explained by Bonaparte's (1984) hypothesis that

titanosaurids invaded from South America across the Panamanian land bridge (see Lucas & Hunt (1989) for a more detailed discussion). However, no land bridge is shown in the Maastrichtian map in Smith *et al.* (1994). This probably only reflects the exact point in the Maastrichtian chosen for reconstruction by Smith *et al.* Nevertheless, this clearly illustrates how even a resolution of one palaeogeographic map per 8 million years may be inadequate for the purposes of studying sauropod biogeography.

Elsewhere during the Campanian–Maastrichtian, flourishing sauropod faunas were present in South America, India, Europe and Madagascar. These faunas were rather different from those of the Upper Jurassic. One obvious difference is the greatly reduced diversity of sauropod families during the Upper Cretaceous. The factor(s) responsible for the shift from the diverse ‘Upper Jurassic type’ sauropod fauna to the titanosaurid dominated Upper Cretaceous faunas is not well understood. It is interesting to note, however, that only sauropods with slender ‘peg-like’ teeth appear to have survived to the Upper Cretaceous. In addition, titanosaurids possessed body armour, tended to be smaller (10–15 m in body length) and more robust than Upper Jurassic sauropods. Unfortunately, palaeoecological comparisons between titanosaurids and other sauropod families are severely hampered by our very poor knowledge of titanosaurid anatomy and interrelationships.

7. CONCLUSION

It has become something of a cliché (not without reason) to regard sauropod taxonomy and phylogeny as highly problematic. Nevertheless, recent studies have produced a partial consensus, with most authors agreeing on the relationships between the Brachiosauridae, Camarasauridae, Titanosauridae and Diplodocidae. The most controversial aspects of sauropod phylogenetic studies are normally associated with the relationships of various Asian taxa. There are severe limitations on the use of palaeogeographic data in conjunction with phylogenetic studies, but for the Euhelopodidae our current knowledge of the tectonic history of China is consistent with the monophyletic and endemic nature of this group.

Although geological and taxonomic factors obscure the pattern of sauropod phylogeny and biogeography, some broad trends can be detected. Most sauropod families may have been distinct by the Middle Jurassic. During the Upper Jurassic, brachiosaurids and diplodocoids dominated the sauropod faunas of North America, western Europe and Gondwanaland, while the Euhelopodidae radiated in eastern Asia. The ‘Jurassic’ sauropod fauna survived almost unaltered into the Lower Cretaceous of Europe and possibly elsewhere, but was largely absent after that time. Middle and especially Upper Cretaceous faunas were dominated by titanosaurids, a family that seems to have been relatively rare during the Upper Jurassic. *Antarctosaurus* and the Nemegtosauridae indicate that at least some diplodocoids survived into the Upper Cretaceous. The derived features displayed by these

Upper Cretaceous diplodocoids suggest that they cannot be regarded merely as ‘relicts’ of their Upper Jurassic counterparts. Despite the apparent Upper Cretaceous revival in sauropod fortunes, they became extinct, along with all other dinosaurs, at the end of the Maastrichtian.

Gaps in the sauropod fossil record, and inconsistencies between their phylogeny and biogeography, emphasize how much we still have to learn about these gigantic animals. *Rhoetosaurus*, *Austrosaurus* (from the Albian of Australia), the diplodocoid remains of *Antarctosaurus*, and many other poorly known forms cannot be easily integrated into our current picture of sauropod evolutionary history. In addition, our understanding of titanosaurid taxonomy and phylogeny is particularly unsatisfactory. The discovery of new material would be of obvious benefit. However, it should also be remembered that there are several long-established forms, such as *Cetiosaurus* and *Barapasaurus*, which have not yet been described in detail. New data, from whatever source, will no doubt necessitate a major re-evaluation of the results presented here. Nevertheless, it is hoped that the proposed sauropod phylogeny, and supporting osteological characters, will form a useful framework for future studies.

This paper summarizes results from my Ph.D. research and work produced subsequently. The following institutions provided financial support during the course of my Ph.D.: the Science and Engineering Research Council (studentship no. 89302816), St John’s College, Cambridge, the Department of Zoology, University of Cambridge, and the Cambridge Philosophical Society. I also thank Sidney Sussex College, Cambridge, whose award of a Junior Research Fellowship has allowed me to further my research and write this paper.

I am very grateful to the following for allowing access to the material in their care: Angela Milner and Sandra Chapman (Natural History Museum, London), Phillip Powell (Oxford University Museum of Zoology), John Martin and Arthur Cruickshank (Leicester City Museum), the staff of the Yorkshire Museum, York, David Norman and the late David Price (Sedgwick Museum of Geology, Cambridge), Phillipe Taquet (Museum National d’Histoire Naturelle, Paris), Wolf-Dieter Heinrich and the late Hermann Jaeger (Humboldt Museum für Naturkunde, Berlin), Mary Dawson and David Berman (Carnegie Museum of Natural History, Pittsburgh), John Ostrom and Mary Anne Turner (Peabody Museum, Yale), Mark Norrell (American Museum of Natural History, New York), Michael Brett-Surman (United States National Museum of Natural History, Washington D.C.), Cathy Forster and Paul Sereno (Department of Organismal Biology and Anatomy, University of Chicago) and Bill Simpson and John Bolt (Field Museum of Natural History, Chicago). I am also grateful to John S. McIntosh for useful discussions concerning sauropod taxonomy during my research in the U.S.A. David Norman and John McIntosh provided helpful reviews of this paper.

I thank the following members of the departments of Zoology and Earth Sciences, University of Cambridge, for their helpful advice and encouragement: Jenny Clack and David Norman (my Ph.D. supervisor and ‘adviser’ respectively), and also Adrian Friday, Mike Coates, Giovanni Galizia, Michael Lee, Ken Joysey, Laura Canning, Paul Barrett and Elizabeth Pringle. Kim Graham and Michael Lee gave some assistance with the preparation of the figures presented in this paper. I thank David Norman (Department

of Earth Sciences, Cambridge) for directing me into this fruitful area of research.

REFERENCES

- Barrett, P. M. & Upchurch, P. 1995 Feeding mechanisms of *Diplodocus*. *GAEA: Revista Geoscienc., Mus. nacional Hist. natl.* (In the press.)
- Berman, D. S. & McIntosh, J. S. 1978 Skull and relationships of the Upper Jurassic sauropod *Apatosaurus* (Reptilia, Saurischia). *Bull. Carnegie Mus. nat. Hist.* **8**, 1–35.
- Bonaparte, J. F. 1979 Dinosaurs: a Jurassic assemblage from Patagonia. *Science, Wash.* **205**, 1377–1379.
- Bonaparte, J. F. 1984 Late Cretaceous faunal interchange of terrestrial vertebrates between the Americas. In *Third symposium on Mesozoic terrestrial ecosystems* (ed. W.-E. Reif & F. Westphal), pp. 19–24. Tübingen: Attempto Verlag.
- Bonaparte, J. F. 1986 The early radiation and phylogenetic relationships of Jurassic sauropod dinosaurs, based on vertebral anatomy. In *The beginning of the age of dinosaurs* (ed. K. Padian), pp. 247–258. Cambridge: Cambridge University Press.
- Bonaparte, J. F. & Powell, J. E. 1980 A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda–Coelurosauria–Carnosauria–Aves). *Mém. Soc. géol. Fr.* **139**, 19–28.
- Borsuk-Bialynicka, M. 1977 A new camarasaurid *Opisthocoeleicaudia* gen. n. sp. n. from the Upper Cretaceous of Mongolia. *Palaeont. Polonica* **37**, 5–64.
- Calvo, J. O. & Bonaparte, J. F. 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.
- Carpenter, K. & Currie, P. J. 1990 *Dinosaur systematics: approaches and perspectives*. Cambridge: Cambridge University Press.
- Chao, S. 1985 The reptilian fauna of Jurassic in China. In *The Jurassic system of China. An outline of stratigraphy in China* (ed. S. Wang, Z. Cheng & N. Wang), pp. 286–289. Beijing: Geological Publishing House.
- Charig, A. J. 1980 A diplodocid sauropod from the Lower Cretaceous of England. In *Aspects of vertebrate history. Essays in honour of Edwin Harris Colbert* (ed. L. L. Jacobs), pp. 231–244. Flagstaff: Museum of Northern Arizona Press.
- Colbert, E. H. 1989 The Triassic dinosaur *Coelophysis*. *Mus. northern Arizona Bull.* **57**, 1–160.
- Cooper, M. R. 1984 A reassessment of *Vulcanodon karibaensis* Raath (Dinosauria: Saurischia) and the origin of the Sauropoda. *Palaeont. Afr.* **25**, 203–231.
- Corro, G. del 1975 Un nuevo saurópodo del Cretácico superior. *Chubutisaurus insignis* gen. et sp. nov. (Saurischia–Chubutisauridae nov.) del Cretácico superior (Chubutiano), Chubut, Argentina. *Actas Congr. Argent. Paleont. Bioestrat.* **2**, 229–240.
- Dong, Z. M. 1990 On remains of the sauropods from Kelamaili region, Junggar Basin, Xinjiang, China. *Vertebrata Palasiatica* **28**, 43–58. (In Chinese with English summary.)
- Dong, Z. M. 1992 *Dinosaurian faunas of China*. Berlin: Springer-Verlag.
- Dong, Z. M., Peng, G. & Huang, D. 1989 The discovery of the bony tail club in sauropods. *Vertebrata Palasiatica* **27**, 219–224. (In Chinese with English summary.)
- Dong, Z. M. & Tang, Z. L. 1984 Note on a mid-Jurassic sauropod (*Datousaurus bashanensis* gen. et sp. nov.) from the Sichuan Basin, China. *Vertebrata Palasiatica* **22**, 69–75. (In Chinese with English summary.)
- Dong, Z. M., Zhou, S. & Zhang, Y. 1983 The dinosaurian remains from Sichuan Basin, China. *Palaeont. Sinica* **23**, 1–145. (In Chinese with English summary.)
- Dorlodot, J. de 1934 L'exploration du gîte à dinosauriens Jurassiques de Damparis. *Terre Vie* **4**, 563–586.
- Enkin, R. J., Zhentu, Y., Yan, C. & Courtillot, V. 1992 Paleomagnetic constraints on the geodynamic history of the major blocks of China from the Permian to the present. *J. geophys. Res.* **97**(B10), 13953–13989.
- Galton, P. M. 1977 The ornithopod dinosaur *Dryosaurus* and a Laurasia–Gondwanaland connection in the Upper Jurassic. *Nature, Lond.* **268**, 230–232.
- Galton, P. M. 1990 Basal Sauropodomorpha–Prosauropods. In *The Dinosauria* (ed. D. B. Weishampel, P. Dodson & H. Osmolska), pp. 320–344. Berkeley and Los Angeles: University of California Press.
- Galton, P. M. & Heerden, J. van 1985 Partial hindlimb of *Blikanasaurus cromptoni* n. gen. and n. sp. representing a new family of prosauropod dinosaurs from the Upper Triassic of South Africa. *Geobios* **18**, 509–516.
- Gauffre, F.-X. 1994 The prosauropod dinosaur *Azendohsaurus laaroussii* from the Upper Triassic of Morocco. *Palaeontology* **36**(4), 897–908.
- Gauthier, J. 1986 Saurischian monophyly and the origin of birds. In *The origin of birds and the evolution of flight* (ed. K. Padian). *Mem. Calif. Acad. Sci.* **8**, pp. 1–55.
- Gillette, D. D. 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. *J. Vert. Paleont.* **11**(4), 417–433.
- Gilmore, C. W. 1925 A nearly complete articulated skeleton of *Camarasaurus*, a saurischian dinosaur from The Dinosaur National Monument. *Mem. Carnegie Mus.* **10**, 347–384.
- Gilmore, C. W. 1933 Two new dinosaurian reptiles from Mongolia with notes on some fragmentary specimens. *Am. Mus. Novit.* **679**, 1–20.
- Gilmore, C. W. 1936 Osteology of *Apatosaurus* with special reference to specimens in the Carnegie Museum. *Mem. Carnegie Mus.* **11**, 175–300.
- Hallett, M. 1987 Bringing dinosaurs to life. In *Dinosaurs past and present* (ed. S. J. Czerkas & E. C. Olson), vol. I, pp. 96–113. Natural History Museum Los Angeles County.
- Harland, W. B., Armstrong, R. L., Cox, A. V., Craig, L. E., Smith, A. G. & Smith, D. G. 1990 *A geologic time scale*. Cambridge: Cambridge University Press.
- Hatcher, J. B. 1903 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. *Mem. Carnegie Mus.* **2**, 1–72.
- Huene, F. von 1926 Vollständige Osteologie eines Plateosauriden aus dem Schwäbischen Trias. *Geol. Palaeont. Abhandl.* **15**, 129–179.
- Huene, F. von 1927 Short reviews of the present knowledge of the Sauropoda. *Mem. Queensland Mus.* **8**, 121–126.
- Huene, F. von 1929 Los Saurisquios y Ornithisquios de Cretacéo Argentino. *An. Mus. La Plata* (ser. 2) **3**, 1–196.
- Hunt, A. P., Lockley, M. G., Lucas, S. G. & Meyer, C. A. 1995 The global sauropod fossil record. *GAEA: Revista Geocienc. Mus. nacional Hist. natl.* (In the press.)
- Jacobs, L. L., Winkler, D. A., Downs, W. R. & Gomani, E. M. 1993 New material of an early Cretaceous sauropod dinosaur from Africa. *Palaeontology* **36**(3), 523–534.
- Jain, S. L., Kutty, T. S., Roy-Chowdhury, T. & Chatterjee, S. 1975 The sauropod dinosaur from the Lower Jurassic Kota Formation of India. *Proc. R. Soc. Lond. B* **188**, 221–228.
- Jain, S. L., Kutty, T. S., 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)*, vol. 1, pp. 204–216.
- Janensch, W. 1929 Die Wirbelsäule der Gattung *Dicraeosaurus*. *Palaeontographica* no. 1, part 2, pp. 37–133.
- Janensch, W. 1935–36 Die Schädel der Sauropoden *Brachiosaurus*, *Barosaurus* und *Dicraeosaurus*, aus den Tendaguru-Schichten Deutsch-Ostafrikas. *Palaeontographica* part 2, pp. 147–298.
- Janensch, W. 1950 Die Wirbelsäule von *Brachiosaurus brancai*. *Palaeontographica* part 3, pp. 27–93.
- Janensch, W. 1961 Die Gliedmassen und Gliedmaszengürtel der Sauropoden der Tendaguru-Schichten. *Palaeontographica* suppl. 7, pp. 177–235.
- Jensen, J. A. 1985 Three new sauropod dinosaurs from the Upper Jurassic of Colorado. *Great Basin Natur. Mem.* **45**, 697–709.
- Jensen, J. A. 1988 A fourth new sauropod dinosaur from the Upper Jurassic of the Colorado plateau and sauropod bipedalism. *Great Basin Natur. mem.* **48**, 121–145.
- Kurzanov, S. M. & Bannikov, A. F. 1983 A new sauropod from the Upper Cretaceous of Mongolia. *Paleont. Zh.* **1983**, 91–97. (In Russian.)
- Langston, W. 1974 Nonmammalian Comanchean tetrapods. *Geosci. Man.* **8**, 77–102.
- Lapparent, A. F. de 1943 Les dinosauriens Jurassiques de Damparis (Jura). *Mém. Soc. Géol. Fr.* **47**, 5–20.
- Lapparent, A. F. de 1960 Los dos dinosaurios de Galve (provincia de Teruel, Espana). *Teruel* **24**, 177–197.
- Lapparent, A. F. de & Zbysewski, G. (1957) Les dinosauriens du Portugal. *Mem. Serv. Geol. Portugal* **2**, 1–63.
- Longman, H. A. 1926 A giant dinosaur from Durham Downs, Queensland. *Mem. Queensland Mus.* **8**, 183–194.
- Longman, H. A. 1927 The giant dinosaur *Rhoetosaurus browni*. *Mem. Queensland Mus.* **9**, 1–18.
- Lucas, S. G. & Hunt, A. P. 1989 *Alamosaurus* and the sauropod hiatus in the Cretaceous of the North American Western Interior. In *Paleobiology of the dinosaurs* (ed. J. O. Farlow), pp. 75–85. Boulder: Geological Society of America.
- Lydekker, R. 1888 *Catalogue of the fossil Reptilia and Amphibia of the British Museum (Natural History)*, part I. London: Taylor and Francis.
- Lydekker, R. 1890 *Catalogue of the fossil Reptilia and Amphibia of the British Museum (Natural History)*, part IV. London: Taylor and Francis.
- Lydekker, R. 1895 On bones of a sauropod dinosaur from Madagascar. *Q. Jl geol. Soc. Lond.* **51**, 328–336.
- Mantell, G. A. 1852 On the structure of the *Iguanodon* and on the fauna and flora of the Wealden Formation. *Not. Proc. R. Inst. Gr. Br.* **1**, 141–146.
- Marsh, O. C. 1896 The dinosaurs of North America. *Sixteenth A. Rep. U.S. geol. Surv.*, part I.
- Mateer, N. J. & McIntosh, J. S. 1985 A new reconstruction of the skull of *Euhelopus zdanskyi* (Saurischia, Sauropoda). *Bull. geol. Inst. Univ. Uppsala* **11**, 125–132.
- McIntosh, J. S. 1989 The sauropod dinosaurs: a brief survey. In *The age of dinosaurs* (ed. S. J. Culver), *Short courses in paleontology*, no. 2, pp. 85–99. Knoxville: The Paleontological Society.
- McIntosh, J. S. 1990a Species determination in sauropod dinosaurs with tentative suggestions for their classification. In *Dinosaur systematics: approaches and perspectives* (ed. K. Carpenter & P. J. Currie), pp. 53–70. Cambridge: Cambridge University Press.
- McIntosh, J. S. 1990b Sauropoda. In *The Dinosauria* (ed. D. B. Weishampel, P. Dodson & H. Osmolska), pp. 345–401. Berkeley and Los Angeles: University of California Press.
- Nowinski, A. 1971 *Nemegtosaurus mongoliensis* n. gen., n. sp., (Sauropoda) from the uppermost Cretaceous of Mongolia. *Palaeont. Polonica* **25**, 57–81.
- Ogier, A. 1975 Étude de nouveaux ossements de *Bothriospondylus* d'un gisement du Bathonien de Madagascar. Doctoral thesis (3^e cycle), Université Paris VI.
- Ostrom, J. H. 1970 Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana. *Bull. Peabody Mus. nat. Hist.* **35**, 1–234.
- 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. *Proc. geol. Soc. Lond.* **3**, 457–462.
- Owen, R. 1875 British fossil reptiles of the Mesozoic formation (part II). *Palaeontogr. Soc. Monogr.* **29**, 15–93.
- Owen, R. 1876 Fossil reptiles of the Wealden and Purbeck formations. *Palaeontogr. Soc. Monogr.* (suppl. VII) **30**, 1–7.
- Raath, M. A. 1972 Fossil vertebrate studies in Rhodesia: a new dinosaur (Reptilia, Saurischia) from near the Triassic–Jurassic boundary. *Arnoldia* **5**, 1–37.
- Rawson, P. F., Curry, D., Dilley, F. C., Hancock, J. M., Kennedy, W. J., Neale, J. W., Wood, C. J. & Worssam, B. C. 1978 Cretaceous. *Geol. Soc. Lond., spec. Rep.* **9**, 1–70.
- Romer, A. S. 1956 *Osteology of the reptiles*. Chicago: University of Chicago Press.
- Russell, D. A. 1993 The role of Central Asia in dinosaurian biogeography. *Can. J. Earth Sci.* **39**(10–11), 2002–2012.
- Russell, D. A. & Zheng, Z. 1993 A large mamenchisaurid from the Junggar Basin, Xinjiang, People's Republic of China. *Can. J. Earth Sci.* **30**(10–11), 2082–2095.
- Salgado, L. & Bonaparte, J. F. 1991 Un nuevo sauropodo Dicraeosauridae, *Amargasaurus cazau* 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, J. O. 1992 Cranial osteology of *Amargasaurus cazau* Salgado & Bonaparte (Sauropoda, Dicraeosauridae) from the Neocomian of Patagonia. *Ameghiniana* **29**(4), 337–346.
- Sanz, J. L., Buscalioni, A. D., Casanovas, M. L. & Santafe, J. V. 1987 Dinosaurios del Cretacico inferior de Galve (Teruel, Espana). *Estud. Geol. Vol. extraord. Galve-Tremp.*, pp. 45–64.
- Sereno, P. C. 1989 Prosauropod monophyly and basal sauropodomorph phylogeny. *J. Vert. Paleont.* **9** (suppl.), 38A.
- Sereno, P. C. & Arcucci, A. B. 1994a Dinosaurian precursors from the Middle Triassic of Argentina: *Lagerpeton chanarensis*. *J. Vert. Paleont.* **13**(4), 385–399.
- Sereno, P. C. & Arcucci, A. B. 1994b Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, gen. nov. *J. Vert. Paleont.* **14**(1), 53–73.
- Sereno, P. C., Wilson, J. A., Larsson, H. C. E., Duthiel, D. B. & Sues, H.-D. 1994 Early Cretaceous dinosaurs from the Sahara. *Science, Wash.* **266**, 267–271.
- Smith, A. G., Smith, D. G. & Funnell, B. M. 1994 *Atlas of Mesozoic and Cenozoic coastlines*. Cambridge: Cambridge University Press.
- Sues, H.-D. 1990 *Staurikosaurus* and Herrerasauridae. In *The Dinosauria* (ed. D. B. Weishampel, P. Dodson & H. Osmolska), pp. 143–147. Berkeley and Los Angeles: University of California Press.
- Thévenin, A. 1907 Paléontologie de Madagascar. IV. Dinosauriens. *Ann. Paléontol.* **2**, 121–136.
- Upchurch, P. 1993 The anatomy, phylogeny and systematics of sauropod dinosaurs. Ph.D. dissertation, University of Cambridge.
- Weishampel, D. B. 1990 Dinosaurian distribution. In *The Dinosauria* (ed. D. B. Weishampel, P. Dodson & H. Osmol-

- ska), pp. 63–139. Berkeley and Los Angeles: University of California Press.
- Weishampel, D. B., Dodson, P. & Osmolska, H. (eds) 1990 *The Dinosauria*. Berkeley and Los Angeles: University of California Press.
- White, T. E. 1958 The braincase of *Camarasaurus lentus* Marsh. *J. Paleont.* **32**, 477–494.
- Wild, R. 1978 Ein Sauropoden-Rest (Reptilia, Saurischia) aus dem Posidonienschiefer (Lias, Toarcium) von Holzmaden. *Stuttgart Beitr. Naturk.* **B 41**, 1–15.
- Wild, R. 1991 *Janenschia* n. g. *robusta* (E. Fraas 1908) pro *Tornieria robusta* (E. Fraas 1908) (Reptilia, Saurischia, Sauropodomorpha). *Stuttgart Beitr. Naturk.* **B 173**, 1–4.
- Wilson, J. A. & Sereno, P. C. 1994 Higher-level phylogeny of sauropod dinosaurs. *J. Vert. Paleont.* **14** (3, suppl.), 52A.
- Young, C. C. 1937 A new dinosaurian from Sinkiang. *Palaontologica Sinica C* **2**, 1–25.
- Young, C. C. & Chao, H. C. 1972 *Mamenchisaurus hochuanensis* sp. nov. *Szechuan Academica Sinica, Inst. Vert. Paleont. Paleanthrop.*, ser. A, spec. Publ. no. 8, pp. 1–30. (In Chinese.)
- Yu, C. 1990 Sauropod phylogeny: a preliminary cladistic analysis. *J. Vert. Paleont.* **10** (suppl.), 51A.
- Zhao, X. 1993 A new mid-Jurassic sauropod (*Klamelisaurus gobiensis* gen. et sp. nov.) from Xinjiang, China. *Vertebrata Palasiatica* **31**, 132–138. (In Chinese with English summary.)

Received 4 January 1995; accepted 22 February 1995