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BASAL SAUROPODOMORPHA: HISTORICAL AND RECENT PHYLOGENETIC HYPOTHESES, WITH COMMENTS ON *AMMOSAURUS MAJOR* (MARSH, 1889)

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Abstract: Basal sauropodomorphs, historically referred to as 'prosauropods', include approximately 20 genera of Late Triassic–Early Jurassic age. Recent discoveries on several continents and taxonomic review of important species have brought to bear significant new taxon and character data. After review of the taxonomic status of *Anchisaurus polyzelus*, *Ammosaurus major* is recommended as the appropriate genus and species for basal sauropodomorph material from the Portland Formation of eastern North America. Traditional (precladistic) and cladistic interpretation of basal sauropodomorph phylogeny has varied between two extremes: a monophyletic clade of 'prosauropods' or a sequence of basal sauropodomorphs that increasingly approach the sauropod condition. Given new species that exhibit a range of derived features, future resolution will probably lie somewhere between these polar viewpoints. Conflicting results from recent analyses suggest that greater resolution of basal sauropodomorph phylogeny will come with continued clarification of anatomical details and a comparative methodology that focuses on character data rather than simply the most parsimonious tree.

Key words: Sauropodomorpha, prosauropod, dinosaur, *Anchisaurus*, *Ammosaurus*, phylogeny.

SAUROPODOMORPHS comprise the longest-lived, most speciose radiation of large-bodied, terrestrial vertebrate herbivores. The focus here is on basal sauropodomorphs, the non-sauropod portion of the radiation traditionally referred to as 'prosauropods'. This is an anatomically conservative assemblage of approximately 20 genera that flourished during a brief interval of approximately 30 million years from the Late Triassic (Late Carnian, *c.* 220 Ma) through the Early Jurassic (Hettangian–Sinemurian, *c.* 195 Ma). By the close of the Triassic, they had achieved a global distribution, extending their range east to west across Pangaea and toward each pole. They constitute the first morphologically closely knit, global radiation of dinosaurian herbivores (Sereno 1997; Galton and Upchurch 2004; Pol 2004).

In 1976, Peter Galton revived interest in basal sauropodomorphs with a seminal review of North American material, which includes some of the earliest dinosaur remains recovered on that continent. In the 30 years since, many discoveries and taxonomic studies have dramatically transformed the basis for understanding basal sauropodomorph phylogeny. The oldest basal sauropodomorph recorded to date, *Saturnalia tupiniquim*, was discovered recently in the Santa Maria Formation in southern Brazil (Langer *et al.* 1999, 2007; Langer 2003). Probably close to the Middle/Late Triassic boundary in age, the Santa Maria fauna is roughly coeval with the Ischigualasto fauna from Argentina, radiometrically dated to approximately 228 Ma (Rogers *et al.* 1993). *Saturnalia* provides tangible fossil evidence of the roots of the sauropodomorph radiation, which previously existed only as a ghost lineage generated by older members of their saurischian sister group, Theropoda (*Eoraptor*, Herrerasauridae).

By the close of the Triassic (*c.* 200 Ma), basal sauropodomorphs had diversified in southern Africa (*Antetonitrus*, *Melanorosaurus*, '*Euskelosaurus*', *Blikanasaurus*: Van Heerden 1979; Cooper 1981; Galton and Van Heerden 1998; Yates and Kitching 2003; Yates 2005), South America (*Coloradisaurus*, *Riojasaurus*, *Lessemsaurus*, *Mussaurus*, *Unayasaurus*: Bonaparte 1978, 1999; Casamiquela 1980; Leal *et al.* 2004; Pol 2004), Europe (*Efraasia*, *Plateosaurus*, *Ruehleia*, *Thecodontosaurus*: von Huene 1926; Galton 1984, 2001; Benton *et al.* 2000; Yates 2003*a*, *b*) and Greenland (cf. *Plateosaurus*: Jenkins *et al.* 1995).

Ten million years later, during the Early Jurassic (*c.* 190 Ma), basal sauropodomorphs had diversified in North America (*Ammosaurus*, *Anchisaurus*: Galton 1976; Yates 2004) and Asia (*Lufengosaurus*, *Jingshanosaurus*, *Yimenosaurus*, *Yunnanosaurus*: Young 1941, 1942; Bai *et al.* 1990; Zhang and Yang 1994; Barrett *et al.* 2005).

Well-preserved material from India is now known that is also probably Early Jurassic in age (Kutty 1969), and postcranial bones of similar age have been reported from Antarctica (Hammer and Hickerson 1994). Australia, a landmass with little exposure of fossiliferous terrestrial deposits of Mesozoic age, remains the only continent with no evidence of basal sauropodomorphs, the only record (*Agrosaurus*) now shown to be based on fossil material from England (Vickers-Rich *et al.* 1999).

This paper first briefly reviews the historical emergence of our current palaeontological record for basal sauropodomorphs. Second, a vexing taxonomic question is addressed: the proper assignment of material from eastern North America to either *Anchisaurus* or *Ammosaurus*. Third, traditional (precladistic) and cladistic hypotheses for basal sauropodomorphs are summarized and compared and several notable characters are discussed. Finally, a phylogenetic taxonomy is proposed that would accommodate alternative phylogenetic interpretations.

Institutional abbreviations: AM, Amherst College Museum, Amherst; AMNH, American Museum of Natural History, New York; IVPP, Institute for Vertebrate Paleontology and Paleoanthropology, Beijing; PVL, Paleontological Collection of the Fundación-Instituto Miguel Lillo, Tucumán; SMNS, Staatlichen Museums für Naturkunde, Stuttgart; UCR, University College of Rhodesia (Zimbabwe); YPM, Yale Peabody Museum, New Haven.

FOSSIL DISCOVERY

Early period (1836–1900)

Relatively complete skulls or skeletons of basal sauropodomorphs first came to light at the close of the 19th century, and so most of the early taxonomy was based on incomplete, disarticulated material. The first described genera, *Thecodontosaurus* from England and Wales (Riley and Stutchbury 1836), *Plateosaurus* from Germany (von Meyer 1837) and *Massospondylus* (Owen 1854; Seeley 1895) from southern Africa, survive to the present as valid taxa, although now represented by much more complete material (Cooper 1981; Galton 1984, 2001; Kermack 1984; Benton *et al.* 2000; Yates 2003*a*; Sues *et al.* 2004). The first reasonably complete skeleton pertained to the genus *Anchisaurus* and was discovered in a rock quarry near Manchester, Connecticut (Marsh 1891). Although most of the skull was preserved, preservational factors had complicated its interpretation. Marsh, for example, described *Anchisaurus* as a carnivorous theropod in a paper on its skeletal restoration (Marsh 1893). Just before the close of the 19th century, nonetheless, the general form of the skull and skeleton of a representative basal sauropodomorph had been realized.

Middle period (1900–1950)

In the first two decades of the 20th century, multiple articulated skeletons with skulls were discovered in rock quarries in Trossingen, Germany. Now collectively attributed to the genus *Plateosaurus* (Text-figs 4–8), this material formed the basis of von Huene's influential descriptive account of the skull and skeleton (von Huene 1926).

Trained in Germany, C. C. Young returned to China in the 1930s and directed the recovery of well-preserved remains of basal sauropodomorphs from the Lower Lufeng Formation in Yunnan Province. The majority of these pertain to the genera *Lufengosaurus* and *Yunnanosaurus*, which were described in a series of papers (Young 1941, 1942, 1947, 1951). Until recently, Young's reports constituted the only information available for basal sauropodomorphs from Asia.

Recent work (1970–present)

During the recent period, many new genera have been described, including: *Saturnalia* (Langer *et al.* 1999; Langer 2003) and *Unaysaurus* (Leal *et al.* 2004) from southern Brazil; *Coloradisaurus*, *Riojasaurus*, *Lessemsaurus* and *Mussaurus* from Argentina (Bonaparte 1969, 1978, 1999; Bonaparte and Vince 1979); *Yimenosaurus* and *Jingshanosaurus* from China (Bai *et al.* 1990; Zhang and Yang 1994); and *Efraasia* and *Ruehleia* from Germany (Galton 1973, 2001; Yates 2003*b*), and two unnamed genera from India (Kutty 1969).

Detailed taxonomic and descriptive studies have been undertaken, the most comprehensive of these involving reviews of *Anchisaurus* and *Ammosaurus* (Galton 1976; Yates 2004), *Efraasia* (Galton 1973; Yates 2003*b*), *Plateosaurus* (Galton 1984, 2000, 2001; Yates 2003*b*), *Massospondylus* (Cooper 1981; Gow *et al.* 1990; Sues *et al.* 2004), *Lufengosaurus* (Barrett *et al.* 2005), *Riojasaurus* (Bonaparte and Pumares 1995), *Mussaurus* and *Lessemsaurus* (Pol 2004), and *Thecodontosaurus* (Kermack 1984; Yates 2003*a*).

Finally, new material currently under study will better document *Saturnalia*, the Argentine genera *Mussaurus* and *Lessemsaurus* (Pol 2004; Pol and Powell 2005), and new remains from northern Argentina (R. Martinez, pers. comm. 2006). More information is needed for Asian genera, especially '*Gyposaurus*' *sinensis* (Young 1941, 1948), *Jingshanosaurus*, *Yunnanosaurus* and *Yimenosaurus*. New remains from North America and Greenland now under study will also impact future phylogenetic hypotheses. Well-preserved skull and postcranial material from the Kayenta Formation and Navajo Sandstone of western

North America, for example, represent new taxa (Attridge *et al.* 1985; Irmis 2005; Loewen *et al.* 2005), and specimens from the Newark Supergroup in Nova Scotia (Olsen *et al.* 1987) and from the Fleming Fjord Formation of eastern Greenland (Jenkins *et al.* 1995) are under study. Finally, a well-preserved skull and skeleton has recently been referred to the southern African genus *Melanorosaurus* (Yates 2005, 2007), which will strongly impact its phylogenetic interpretation.

AMMOSAURUS OR *ANCHISAURUS*?

Two genera, *Ammosaurus* and *Anchisaurus*, and their various species were described from the Lower Jurassic Portland Formation of Connecticut (Galton 1976). Sereno (1999*a*) regarded the Portland material as representing the single species *Ammosaurus major*, although no explanation was provided. Yates (2004), on the other hand, regarded *Anchisaurus polyzelus* as the appropriate name for this taxon. Galton and Upchurch (2004, p. 251), by contrast, maintained the generic separation of *Ammosaurus* and *Anchisaurus*, arguing that there are observable differences among the specimens. More recently, Fedak (2005) re-examined the same specimens. He regarded them as a single taxon and followed Yates by using the genus *Anchisaurus*. As detailed below, *Ammosaurus major* is regarded herein as the appropriate genus and species for diagnostic material from the Portland Formation. Referral of specimens to *Ammosaurus* from western North America (Navajo Formation of Arizona and southern Utah: Galton 1971, 1976) is not supported here, in agreement with Yates (2004) and Irmis (2005). *Ammosaurus major* will continue to play an important role in phylogenetic analysis, and so its taxonomic status should be carefully considered.

A single geographically disparate species from southern Africa, *Anchisaurus capensis*, was based on a small partial postcranial skeleton lacking much of the anterior half. Originally described by Broom (1906) and later named as a new genus and species, *Gyposaurus capensis* (Broom 1911), the taxon was initially placed within the Anchisauridae (Broom 1911). More recently, the genus was considered a junior synonym of *Anchisaurus*, based principally on the shared presence of an elongate iliac preacetabular process, the supposedly enlarged and ventrally incomplete obturator foramen, and a proportionately narrow foot (Galton and Cluver 1976). The larger size of the ungual of pedal digit I was the only diagnostic feature listed for *Anchisaurus capensis*; this relative proportion, however, is widespread among basal sauropodomorphs and may well be primitive within the clade.

Cooper (1981) listed *Gyposaurus capensis* as a junior synonym of *Massospondylus carinatus*, a conclusion followed by Galton (1990), and most recently the species was listed as a *nomen dubium* (Galton and Upchurch 2004). The elongate proportions of the iliac preacetabular process have long been recognized as distinctive of the North American material. Unfortunately, the dorsal margin of this process is incomplete in the holotype specimen of *Gyposaurus capensis*; it was reconstructed with deeper proportions (Galton and Cluver 1976, fig. 3). Although review of the holotype material in South Africa is necessary, the status of *Gyposaurus* and its type species (*G. capensis*) as doubtful names appears to be the most reasonable option at present.

Anchisaurus polyzelus

Hitchcock (1855) reported the discovery of a skeleton (AM 41/109) during a blasting operation at an armory in Springfield, Massachusetts. Initially described as *Megadactylus polyzelus* (Hitchcock 1865), preoccupation forced transfer first to the genus *Amphisaurus* (Marsh 1882) and then *Anchisaurus* (Marsh 1885). The holotype specimen consists of vertebral fragments, the proximal portion of a scapula, a partial right forelimb and manus, conjoined distal ischial shafts, and portions of the left hind limb (Galton 1976, figs 3, 5–10). The enlarged manual digit I, triangular cross-section of the conjoined ischial shafts at mid length and other features in the preserved material of the holotype clearly allow placement among basal sauropodomorphs. There are, however, no diagnostic features at generic or specific levels. None of the features listed by Galton (1976, p. 88) or Galton and Upchurch (2004, p. 251) is observable in the holotype. Galton and Upchurch, for example, cited the 'emarginated proximal portion of the pubis' when there is little, if any, of either pubis preserved in the holotype. These authors are surely referring to the much more complete referred specimen YPM 1883.

Galton (1976, p. 82) stated succinctly his reasoning, which attempts to salvage the taxon *Anchisaurus polyzelus* on the basis of the fragmentary holotype: 'It is apparent that the differences between AM 41/109 and YPM 1883 are minimal and can be attributed either to differences in preservation or to individual variation, a factor that tends to be overlooked. I conclude that YPM 1883 should be referred to *Anchisaurus polyzelus* because, on the basis of the available material, YPM 1883 cannot be distinguished from AM 41/109 by any characters of taxonomic significance'. The holotype specimen (AM 41/109), on which the validity of the generic and species name rests, must exhibit at least one diagnostic feature for referral of other specimens. Galton, by contrast, bases his referral of YPM 1883 only on the absence of differences.

Yates (2004, p. 5), aware of the need for the holotype to exhibit diagnostic traits, cited one feature in AM 41/109 as fulfilling this role: 'flattened coplanar ischial shafts'. Galton (1976, fig. 6I–J, p. 17) figured the ischial shafts of the holotype, and they have substantial dorsoventral depth in lateral and distal views. Galton described these shafts as 'subtriangular ischial rods'. Sereno (1999*a*) used the inverted subtriangular cross-section of conjoined ischial shafts as a prosauropod synapomorphy. This is the condition toward the distal end of the ischia in AM 41/109 (Galton 1976, fig. 6J), *Massospondylus carinatus* (Cooper 1981, fig. 55) and many other basal sauropodomorphs. There seems little basis for arguing that the form of the ischial shafts in AM 41/109 is diagnostic.

Yates (2004) also argued that the form of the ischial shafts is derived in other specimens, such as YPM 209. In this specimen, however, the proximal portion of the ischial shafts is angled at about 30 degrees to the horizontal (Galton 1976, figs 30A, 31D) as in *Massospondylus carinatus* (Cooper 1981, fig. 55). Galton (1976, p. 66) described the shafts as 'ischial rods', not as flattened and coplanar. Although he also remarked that they were 'horizontal' and 'oval' in cross-section, the critical distal portion of the shaft is broken away on both sides. The ischial shafts are not preserved in YPM 1883 and are broken at mid-length in YPM 208. The latter specimen comes closest to the cited condition of having coplanar ischial shafts (Yates 2004, fig. 2). However, only the proximal ends are preserved, and post-mortem dorsoventral compression cannot be ruled out. Should YPM 208 prove diagnostic in this regard, in any case, it is the holotype of *Ammosaurus major* not *Anchisaurus polyzelus*.

Other features listed by Yates (2004) as diagnostic for *Anchisaurus polyzelus* include a foramen at the base of the second sacral rib and an enlarged obturator fenestra on the pubis. The 'foramen' does not pass through the sacral rib but rather appears to be developed as a shallow depression, and the obturator opening appears to be artificially enlarged by loss of the thin bone margin around the foramen. In any case, these features are not observable on the holotype specimen (AM 41/109). The elongate proportions of the iliac preacetabular process, the final feature listed by Yates, has been recognized as diagnostic, but again is not preserved in the holotype specimen of *Anchisaurus polyzelus*.

In summary, evidence for diagnostic features in the holotypic specimen of *Anchisaurus polyzelus* is weak at best. AM 41/109, found in a Massachusetts quarry, may well be the same species as the sauropodomorph material recovered in Connecticut quarries to the south in the same river valley (East Windsor, Manchester) and perhaps the same as material collected recently in Nova Scotia (Olsen *et al.* 1987). However, it is imprudent to assume so without justification on the basis of diagnostic features, which, first and foremost, must be present in the holotype specimen. As such features are not apparent, *Anchisaurus polyzelus* is here regarded as a *nomen dubium*. Anchisauridae (Marsh 1885), furthermore, should not be employed as a higher taxon for species from the Portland Formation, because it is not clear that it would include the fragmentary holotype specimen on which the familial name is based. Although *Anchisaurus* has gained wider usage in the recent literature than *Ammosaurus*, both were listed as valid genera in recent taxonomic compilations (Galton 1990; Galton and Upchurch 2004). A special appeal to save the genus *Anchisaurus* and its type species *A. polyzelus* over *Ammosaurus major* does not seem warranted.

Ammosaurus major

The first fragmentary skeleton (YPM 2125) from the Connecticut River valley in Connecticut was discovered in 1818 during quarrying operations in the Upper Portland Formation near East Windsor. Three better-preserved specimens (YPM 208, 209, 1883) were collected in the 1880s from a single sandstone quarry some 20 km to the south near Manchester, Connecticut (Lull 1915, 1953; Galton 1976; Olsen *et al.* 1987). Sadly, the skull and anterior half of one of these specimens was incorporated into the abutments of a bridge, and only small fragments were later recovered (YPM 208: Ostrom 1969; Galton 1976).

These three specimens were initially allocated by Marsh (1889*a*, 1891, 1892) to three species of *Anchisaurus*, *A. solus* (YPM 209), *A. colurus* (YPM 1883), and *A. major* (YPM 208), the last of which he referred to a new genus as *Ammosaurus major* (Marsh 1891). Von Huene (1932) later assigned the most complete specimen (YPM 1883) to a new genus, *Yaleosaurus*. Galton (1976, pp. 82–83) subdivided these three specimens, assigning YPM 1883 to *Anchisaurus polyzelus* and referring YPM 208 and 209 to *Ammosaurus major*. Finally, Yates (2004) regarded *Ammosaurus major* as a junior synonym of *Anchisaurus polyzelus* as discussed above.

Galton's subdivision was based primarily on the proportions of the metatarsus. Because the metatarsus is not preserved in the holotype specimen (AM 41/109), *Anchisaurus polyzelus* was identified as 'narrow-footed' on the basis of a referred specimen (YPM 1883) and compared to the 'broad-footed' metatarsus in *Ammosaurus major* (YPM 208, 209). Cooper (1981), Yates (2004) and others have criticized this distinction as ontogenetic or as an artefact of preservation. The case is re-examined in the taxonomic revision presented below.

SYSTEMATIC PALAEONTOLOGY

SAUROPODOMORPHA von Huene, 1932

Genus AMMOSAURUS Marsh, 1891

1891 *Ammosaurus* Marsh, p. 267
1932 *Yaleosaurus* von Huene, p. 119.

Type species. *Ammosaurus major* (Marsh, 1889*a*).

Diagnosis. As for type and only species.

Ammosaurus major (Marsh, 1889*a*)

1889*a* *Anchisaurus major* Marsh, p. 331, text-fig. 1.
1891 *Ammosaurus major* (Marsh); Marsh, p. 267.
1891 *Anchisaurus colurus* Marsh, p. 267.
1892 *Anchisaurus solus* Marsh, p. 545.
1932 *Ammosaurus solus* (Marsh); von Huene, p. 27, pl. 49, fig. 1.
1932 *Yaleosaurus colurus* (Marsh); von Huene, p. 119, pl. 54, fig. 3.

Holotype. YPM 208, partial articulated skeleton in two blocks including several middle and posterior dorsal vertebrae and ribs, three sacral vertebrae, partial right scapula, pelvic girdle, and partial left and right hindlimbs.

Type locality and horizon. Manchester, Connecticut; Upper Portland Formation (Lower Jurassic).

Referred material. YPM 209, immature, partially articulated skeleton lacking the tail (originally described as *Anchisaurus solus* Marsh 1892); YPM 1883, well-preserved articulated adult skeleton lacking most of the cervical vertebrae and all caudal vertebrae (originally described as *Anchisaurus colurus* Marsh, 1891).

Diagnosis. Basal sauropodomorph with spool-shaped dorsal vertebrae with length approximately twice the dorsoventral diameter of the centrum face and an elongate preacetabular process on the ilium (length twice basal depth) that extends as far anteriorly as the pubic peduncle.

Remarks. Both of the diagnostic features are present in the holotype and referred specimens. The spool-shaped dorsal vertebrae, present in the holotype but better exposed in YPM 209 and 1883, have unusually elongate proportions (Galton 1976, figs 15I–J, 30). The preacetabular process is unusually long compared with that in other basal sauropodomorphs, as measured with ischial and pubic peduncles positioned along a horizontal (Galton and Cluver 1976; Yates 2004). The process, however, has been figured as slightly longer than preserved relative to the remainder of the ilium (Galton 1976, figs 19A, 26E). The preacetabular process does not extend beyond the distal end of the pubic peduncle. The process in YPM 208, which is identical to that in YPM 1883, was also shown as more pointed than preserved.

Galton (1976) did not figure the carpus and manus accurately in *Ammosaurus major*. Misinformation has arisen, as a result, regarding the inset of metacarpal 1 into the carpus (Yates 2004; Irmis 2005). In YPM 1883 the enlarged distal carpal 1, the only carpal preserved, is not positioned directly over metacarpal 1 (Galton 1976, fig. 17C) but rather is inset from the medial edge of metacarpal 1 so that its lateral margin would overlap metacarpal 2. The proximal end of metacarpal 1 is not aligned with the bases of the other metacarpals (Galton 1976, fig. 17C) but rather is inset approximately 4 mm into the carpus relative to metacarpal 2 (Galton 1976, fig. 18). The strong overlap of metacarpals 2 and 3 and metacarpals 4 and 5 as preserved is lost in the flattened reconstruction of the metacarpus. The specimens clearly suggest that *Ammosaurus major* had a carpus and manus of similar design to that found in other basal sauropodomorphs in which these parts have been preserved in natural articulation (Cooper 1981, fig. 35); distal carpal 1 overlaps distal carpal 2, metacarpal 1 is inset into the carpus relative to metacarpal 2, and metacarpal 1 articulates laterally with distal carpal 2.

The shallow dorsoventral height of the ischium had been used to distinguish YPM 208 (Galton 1976, pp. 56, 82), but a comparable portion of the ischium is not preserved in any other specimen from the Manchester quarry. In YPM 208 the ventral margins of both ischia are eroded and have broken edges. The shallow subacetabular depth of the ischia and the supposed presence of an ischial obturator process appear to be artefacts of preservation (Galton 1976, fig. 26E–F). Reconstructions of the pubis differ markedly in YPM 208 and 1883. The former was shown with a broad margin under the acetabulum and an unusually large obturator foramen (Galton 1976, figs 19A, 20A, 26E–F). The margins of the foramen, however, are poorly preserved, bringing into question the true size of the opening. The latter specimen was reconstructed with a narrow margin under the acetabulum with an open obturator notch. Although Galton remarked that the margin of the foramen is preserved, it appears broken like adjacent areas of the pubic blade (Galton 1976, fig. 12).

Galton's description of the pes in YPM 1883 as 'narrow-footed' and that in YPM 208 as 'broad-footed' is not supported by re-examination of the specimens. First, the metatarsals in both specimens have been distorted post-mortem, severely so in YPM 208. In both specimens the broad medial side of the shaft of metatarsal 1 faces dorsally, rather than medially, as a result of dorsoventral flattening. Second, it is difficult to compare the degree of metatarsal overlap in each specimen, because the metatarsus is exposed only in dorsal view in YPM 208 and ventral view in YPM 1883. Third, YPM 1883 is approximately 25 per cent smaller than YPM 208, leaving open the possibility that proportional differences may reflect this differential in body size.

Despite these caveats, it is possible to measure the metatarsals in these specimens to assess the qualitative claim long held in the literature that one (YPM 1883) is discordantly more slender than the other (YPM 208: Galton 1976, 1990; Galton and Cluver 1976; Galton and Upchurch 2004). The maximum width across the metatarsus (metatarsals 1–5) and the maximum length of metatarsal 3 are, respectively, 60 mm and 98 mm in YPM 1883 (right side) and 81 mm and 135 mm in YPM 208 (left side). The width of the metatarsus relative to the length of metatarsal 3, thus, is 61 per cent in YPM 1883 and 60 per cent in YPM 208. They have virtually identical metatarsal proportions as noted previously by Yates (2004).

An identical pair of comparative measurements taken on the reconstruction of the metatarsus of these two specimens (Galton 1976, figs 22E, 29D), however, yields different results. Using the associated scale bar for determining the length and width of the metatarsus, YPM 1883 (37, 49 mm) and YPM 208 (23, 41 mm) yield relative widths of 56 per cent (YPM 1883) and 76 per cent (YPM 208). Thus, a 20 per cent difference in width was generated in the process of reconstructing specimens that appear very similar and were found in the same quarry. Post-mortem distortion has also played a role, generating an 11 per cent difference in length between right and left third metatarsals in a single individual (Galton 1976, table 4; YPM 208, 120 vs. 135 mm).

PHYLOGENY: TRADITIONAL INTERPRETATIONS

Prosauropods as 'carnosaurs', ornithischians or more distant archosauromorphs

When the first partial skeletons of basal sauropodomorphs came to light, they were placed among theropods (Marsh 1884). Genera now regarded as basal sauropodomorphs have since been linked to, or placed within, the two remaining dinosaurian clades, Ornithischia and Sauropoda (von Huene 1914*a*, 1932; Romer 1956; Colbert 1964; Charig *et al.* 1965; Bakker and Galton 1974; Paul 1984; Gauthier 1986). The early history of these disparate taxonomic assignments can be traced to an erroneous association with jaw fragments and teeth of rauisuchian archosaurs. The mix-up first occurred among fossils collected in the Middle Stubensandstein (Norian, Late Triassic) of Germany. Von Huene (1908, 1914*a*, 1932) referred articulated and disarticulated remains now identified as *Plateosaurus gracilis* (=*Sellosaurus*) to *Teratosaurus suevicus*, now regarded as a poposaurid (Galton 1985; Benton 1986). Young (1951) repeated von Huene's spurious association in his work with fossils from the Lower Lufeng Formation, assigning basal sauropodomorph material to a taxon (*Sinosaurus triassicus*) based on jaw fragments with carnivorous teeth. Finally, Raath (1972) described isolated carnivorous teeth found near the pelvis of the holotype specimen of the basal sauropod *Vulcanodon karibaensis*, an association that continued to haunt the more recent detailed revision of this important taxon (Cooper 1984).

These apparently carnivorous forms had to be reconciled with other basal sauropodomorphs characterized by lightweight skulls with herbivorous teeth, a group von Huene (1920) collectively called Prosauropoda. At the time, all of these forms were regarded as Late Triassic in age. The view that emerged and remained dominant until the mid 1960s regarded 'prosauropods' as the central stock of saurischian phylogeny, with a herbivorous subgroup (Plateosauria) more closely related to sauropods and a carnivorous subgroup (Palaeosauria) more closely related to theropods (Text-fig. 1A; von Huene 1914*a*, 1932, 1956; Romer 1956; Colbert 1964).

Several basal sauropodomorphs, often very immature specimens, were initially attributed to other clades, such as the 'ornithischian' *Tawasaurus* (Young 1982) and the 'lepidosaurian' *Fulengia* (Carroll and Galton 1977) from the Lower Lufeng Formation of China (Evans and Milner 1989; Sereno 1991). On the other hand, jaws of disparate archosauromorphs have been regarded as basal sauropodomorphs. 'Two new prosauropods' were briefly described from rocks of probable Late Triassic age in Madagascar (Flynn *et al.* 1999, p. 763), although only one feature was cited that is currently regarded as a basal sauropodomorph synapomorphy (ventral deflection of the anterior alveolar margin of the dentary). The presence of low triangular crowns, some apparently with wear facets (Flynn *et al.* 1999, fig. 1), raises questions about the affinity of this material as well as similar jaw material described previously under the genus *Azendohsaurus* (Dutuit 1972; Gauffre 1993). More complete material recently recovered from Madagascar is expected to clarify the non-dinosaurian status of these specimens, which continue to lurk around basal nodes within Sauropodomorpha even in the most recent analyses (Pol 2004).

Prosauropods as ancestors or side-branch?

Ancestors. As the name implies, Prosauropoda has long been viewed as the ancestral group that gave rise to sauropods. Prosauropoda, in other words, is paraphyletic with some basal sauropodomorphs, in particular the ‘melanorosaurids’, more closely related to Sauropoda than others. Colbert (1964) crystallized this view (Text-fig. 1A), versions of which were presented long before and after his timely review (von Huene 1929; Romer 1968; Cooper 1981; Bonaparte 1986; Bonaparte and Pumares 1995).

Supporting evidence to link ‘melanorosaurids’ and sauropods has always been meagre at best and typically based on femoral morphology or assumptions about quadrupedal posture. As summarized by Romer (1966, p. 150): ‘Even as regards *Plateosaurus* and its relatives, most, at least, seem to have left no descendants. But in the case of such a form as *Melanorosaurus* of South Africa, in which little of a trend toward bipedalism is present, we may be dealing with forms close to the ancestry of later sauropods.’

Stocky long bones, a more columnar femoral shaft and fourth trochanter positioned closer to mid shaft are features that were used to group together forms such as South American *Riojasaurus incertus* (Bonaparte 1972), European *Camelotia borealis* (Galton 1998), and South African *Melanorosaurus readi* as Melanorosauridae (Galton 1985; Van Heerden and Galton 1997) in close proximity to Sauropoda. A more complete skeleton including a skull with a surprising combination of features has recently been referred to *Melanorosaurus readi* (Yates 2005, 2007). When described it will doubtless shed much light on the affinities of at least the nominotypical genus.

Side-branch. Another traditional interpretation is that Prosauropoda constitutes a side-branch, or monophyletic sister taxon, to Sauropoda. Cruickshank (1975) was the first to clearly depict this alternative hypothesis in graphical form (Text-fig. 1B). There were two principal lines of evidence driving this view, both of which are now regarded as unsatisfactory: (1) the overlapping temporal range of prosauropods and early sauropods suggesting their independent evolution (Charig *et al.* 1965); (2) reduction patterns in metatarsals or phalanges that preclude bipedal precursors or are irreversible (Charig *et al.* 1965; Cruickshank 1975). Surprisingly, traditional arguments for the monophyly of prosauropods were not based on shared derived features, such as the twisted pollex.

Basal sauropodomorphs and sauropods were initially regarded as Late Triassic and Jurassic–Cretaceous in age, respectively. It soon became clear from associations in the field as well as re-dating of various formations that these two groups broadly overlapped each other during the Early Jurassic (Charig *et al.* 1965). That begged the question as to which basal sauropodomorphs were more closely related to sauropods, as a simple linear progression was clearly an inadequate hypothesis. Temporal relations alone, however, cannot provide the basis for phylogenetic relationships, and so this argument ultimately fails to clarify relations at the base of Sauropodomorpha.

The morphology of the manus and pes in sauropodomorphs has been used to posit separate origins for prosauropods. Charig *et al.* (1965) argued that prosauropods and sauropods evolved along separate lineages because sauropods showed no evidence in their manus or pes that their forebears were bipedal. They argued further that facultative bipedalism in prosauropods was probably a derived condition. Cruickshank (1975) and Van Heerden (1978) focused on the fifth pedal digit, contrasting the reduced paddle-shaped fifth metatarsal in prosauropods as compared with the strong weight-bearing fifth metatarsal in sauropods. Cruickshank (1975, p. 90) posited that ‘This character must indicate that the lineage leading to *Vulcanodon* separated from the typical prosauropod at a time, when their common ancestor had a “normal” [unreduced] fifth metatarsal.’ Reduction of the fifth pedal digit, in other words, was a condition that seemed irreversible to Cruickshank. Van Heerden (1978) provided a hypothesis to suit this argument; he set prosauropods aside, linking the early dinosaur *Herrerasaurus*, with its proportionately longer fifth metatarsal, to later sauropods.

Although it is true that strong digital reduction or loss of phalanges most often does not reverse in descendants in dinosaurs and other tetrapods, such reversal cannot be excluded *a priori*. Character reversal must be entertained if the preponderance of phylogenetic data favours that interpretation. Furthermore, Cooper (1984) and others have noted the transitional form of the fifth metatarsal in the basal sauropod *Vulcanodon*. In the time since these arguments were forwarded, a similar remarkable reversal in the reduction of pedal digit I has been shown to have occurred within therizinosauroid theropods (Kirkland *et al.* 2005) that involves proximal relocation and renewed articular contact of metatarsal 1 with the astragalus.

Narrow-footed vs. broad-footed prosauropods

Galton (1971, 1973, 1976) and Galton and Cluver (1976) subdivided basal sauropodomorphs into ‘narrow-footed’ species placed in Anchisauridae and ‘broad-footed’ species placed in Plateosauridae and Melanorosauridae. The narrow condition was alleged to be present in both the manus and the pes. Furthermore, it was defended as being unrelated to size (Galton and Cluver 1976, p. 132). Galton and Upchurch (2004, p. 251) recently have reiterated the importance of metatarsal proportions, citing Galton (1976) and referring to the original distinctions that were made among materials from the Manchester quarry in Connecticut: '*Ammosaurus major* has a broad metatarsus, while it is slender in the larger *Anchisaurus.*'

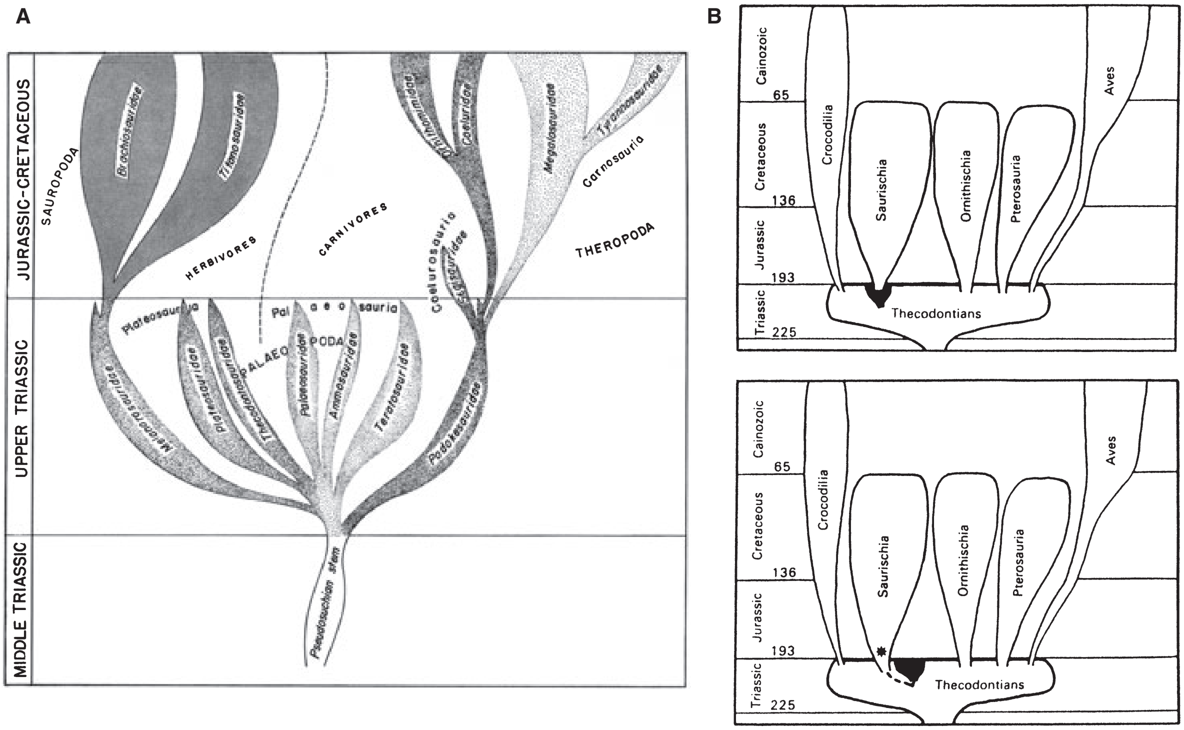
Cooper (1981, p. 696) was first to strongly criticize the distinction between narrow- and broad-footed sauropodomorphs. He argued that all of the differences were size related and could be found in a growth series for the species *Massospondylus carinatus*. Yates (2004) concurred and provided a critique using measurements. I have extended this critique to the influential pedal reconstructions for *Anchisaurus* and *Ammosaurus* (see above). The distinction clearly lacks justification and is based on specimens here referred to the same species (*Ammosaurus major*). The classificatory scheme that separated narrow- from broad-footed genera has not been supported by any subsequent cladistic analysis.

PHYLOGENY: CLADISTIC INTERPRETATIONS

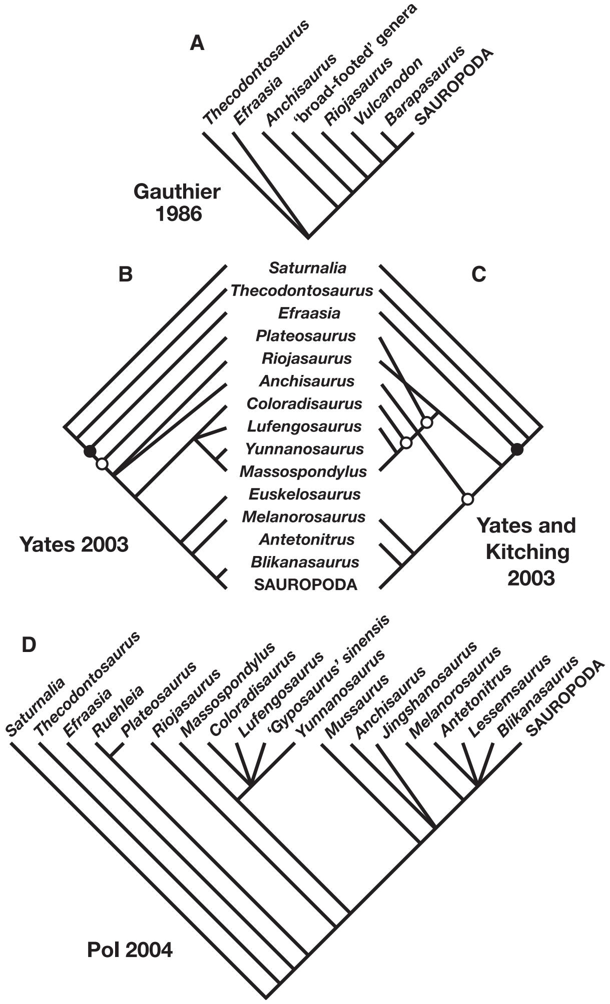
Cladistic interpretation of basal sauropodomorph phylogeny, similar to traditional interpretation, has varied between two extremes: a sequence of basal sauropodomorphs that increasingly approach the sauropod condition or a monophyletic clade of 'prosauropods' (Text-figs 2–3). The first analyses were qualitative. Subsequent quantitative analyses incorporated new characters, specimens and taxa (Table 1). The large increase to more than 100 characters in analyses after 2000 represents, in large part, an increase in the taxonomic scope of the phylogenetic problem under consideration. Whereas the character data in Sereno (1999*a*) focused on non-sauropod sauropodomorphs (traditional 'prosauropods'), later analyses include character data relevant to adjacent portions of the tree (Sauropodomorpha and or more basal nodes; nodes within Sauropoda). Although this has advantages regarding character sampling, one of the disadvantages is that the data relevant to a particular portion of the tree (basal Sauropodomorpha) are admixed with data relevant only to distant nodes.

Prosauropod paraphyly

Prosauropod paraphyly (Text-fig. 2) was first framed in a cladistic context by Gauthier (1986) and later argued in more detailed analyses by Yates (2003*a*, 2004), Yates and Kitching (2003) and Pol (2004).



TEXT-FIG. 1. Traditional (precladistic) phylogenetic hypotheses for basal sauropodomorphs. A, spindle diagram showing families of herbivorous and carnivorous basal sauropodomorphs collected together in the paraphyletic taxon Palaeopoda (from Colbert 1964). B, earliest clear distinction of paraphyletic (upper) vs. monophyletic (lower) hypotheses for basal sauropodomorph dinosaurs (from Cruickshank 1975). Asterisk indicates the position of the basal sauropod *Vulcanodon karibaensis*.



TEXT-FIG. 2. Qualitative (A) and quantitative (B–D) phylogenetic hypotheses for basal Sauropodomorpha that support 'prosauropod' paraphyly. For ease of comparison, terminal taxa outside Sauropodomorpha are excluded and sauropods are collapsed to a single taxon. A, cladogram as indicated by text and character lists in Gauthier (1986). B, reduced consensus cladogram (after Yates 2003*a*, fig. 23). C, consensus cladogram from analysis of 212 characters (after Yates and Kitching 2003). D, consensus hypothesis from analysis of 212 characters (Pol 2004). Unmarked branch points = 1–4 unambiguous synapomorphies; circled branch points = 5–9 unambiguous synapomorphies; solid nodes = 10 or more unambiguous synapomorphies.

Gauthier (1986). Gauthier (1986) was first to outline a cladistic hypothesis for basal sauropodomorphs, citing several genera and listing associated synapomorphies. I have translated his text into a cladogram (Text-fig. 2A). The 'narrow-footed' *Thecodontosaurus* and *Efraasia* are set aside as basal taxa. He identified two nested clades among basal sauropodomorphs: *Anchisaurus* plus more derived sauropodomorphs and unnamed 'broad-footed' genera plus more derived sauropodomorphs, listing four synapomorphies for the first clade and ten for the second (Table 2). 'Broad-footed' prosauropods, in his view, 'are more closely related to sauropods, thus demonstrating the paraphyly of Prosauropoda' (Gauthier 1986, p. 44). Although he followed traditionalists by suggesting that *Riojasaurus* was even more closely linked to Sauropoda, no supporting evidence was cited, and his less inclusive use of Sauropoda (camarasaurids plus titanosaurians) was not followed by later authors (Text-fig. 2A).

Later authors have set aside most of Gauthier's synapomorphies, presumably because some are plesiomorphic, others no longer apply to basal sauropodomorph nodes, and several are size comparisons without comparative ratios. At most five (or 25 per cent) of these synapomorphies (Table 2: 1, 3, 5, 10, 13) are present in modified form in the matrix of Yates (2004). In summary, Gauthier (1986) provided a valuable initial cladistic interpretation of the traditional argument for prosauropod paraphyly, and a few of the synapomorphies he articulated have remained relevant to subsequent analyses.

Yates (2003a, 2004). Yates (2003*a*) scored 164 characters in 18 ingroups, 14 of which are non-sauropod sauropodomorphs ('prosauropods') (Text-fig. 2B). Other ingroups include the basal sauropod *Vulcanodon*, Eusauropoda and two theropod taxa. The taxonomic scope of the analysis therefore is more inclusive than analyses limited to basal sauropodomorph relationships (e.g. Galton 1990; Sereno 1999*a*; Benton *et al.* 2000) and includes character data for Sauropodomorpha and Saurischia (Text-fig. 2B–C). Additive binary coding was used to eliminate all but one multistate character, and only opposing character states were listed rather than the character followed by its character states (Table 1).

Re-analysis of Yates' dataset yields results similar to those reported (Text-fig. 2B). There are five minimum-length trees of 350 steps (351 reported) with very limited branch support for nodes within Sauropodomorpha. To collapse basal nodes linking *Saturnalia*, *Thecodontosaurus* and *Efraasia* with all other sauropodomorphs, six (seven reported), four and two additional steps are needed, respectively. All other nodes within Sauropodomorpha collapse with a single additional step. The dataset supports 'prosauropod' paraphyly, especially if all basal sauropodomorphs are considered; Yates reported that 24 extra steps were needed to place all non-sauropod basal sauropodomorphs within a single clade. If one imposes less severe constraints to include only what are here called 'core prosauropods' (*Plateosaurus*, *Massospondylus*, *Lufengosaurus*, *Yunnanosaurus* and *Riojasaurus*), only ten steps are required. Ten steps, nevertheless, constitute a very significant difference. Yates (2003*a*) further pointed

TABLE 1. Profile of phylogenetic analyses that consider relationships at the base of Sauropodomorpha. When synapomorphies alone are given as character evidence (e.g. Gauthier 1986), the characters themselves and their primitive states are missing and thus are tallied below as absent (–).

Authors		Matrix				Character documentation				
No.	Analysis	Printed	e-Archived	No. ingroups	No. characters	Character listed	Character states listed	Original author cited	Character description (%)	Character figured (%)
1	Gauthier (1986)	–	–	5	20	–	+, –	–	0	0
2	Sereno (1989)	–	–	3	13	–	+, –	–	0	0
3	Galton (1989)	–	–	13	19	–	+, –	–	0	50
4	Galton (1990)	–	–	13	49	–	+, –	–	0	50
5	Sereno (1999*a*)	–	+	9	32	+	+	–	0	0
6	Benton *et al.* (2000)	+	–	12	49	+	+	–	0	0
7	Yates (2003*a*)	+	+	15	164	–	+	+	19	12
8	Yates and Kitching (2003)	–	+	18	212	+	+	–	–	0
9	Yates (2004)	+	–	17	205	+	+	+	19	5
10	Galton and Upchurch (2004)	–	+	23	137	+	+	+	–	5
11	Pol (2004)	+	–	47	277	+	+	–	–	0

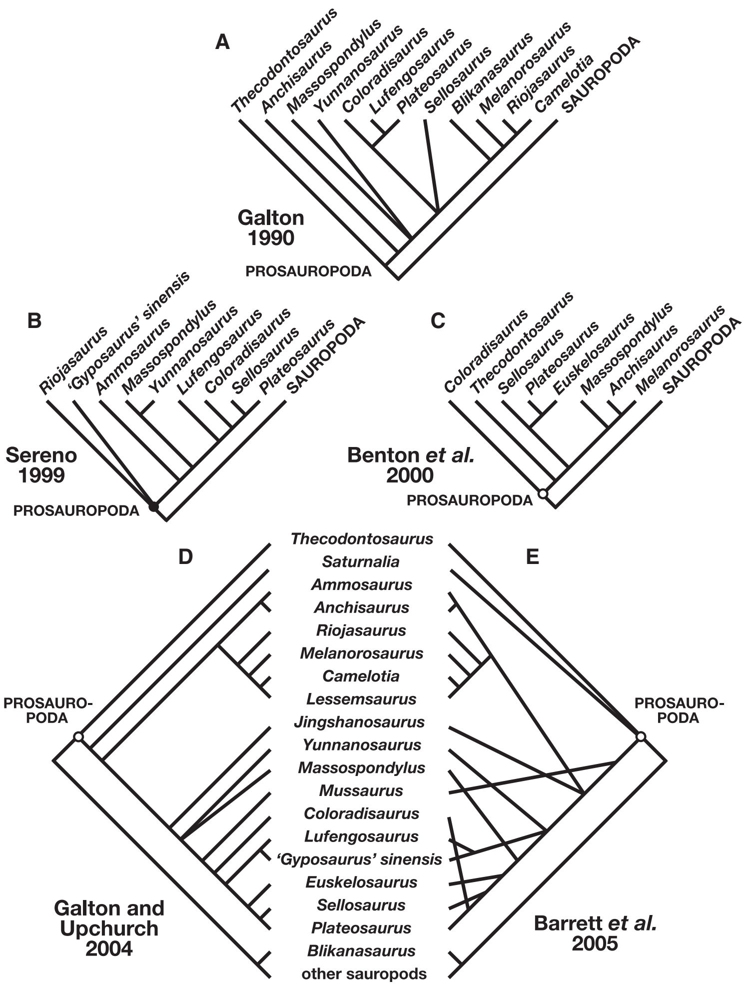
out that a prosauropod clade reappears if basal taxa (*Saturnalia*, *Thecodontosaurus*) and derived taxa (‘*Euskelosaurus*’, *Melanorosaurus*, *Blikanasaurus*) are removed. Branch support for this clade (three steps), however, is not substantial even under pruned circumstances. In summary, Yates (2003*a*) made a strong case for prosauropod paraphyly, if one accepts his dataset.

Yates (2003*a*) provided a critique of the 19 ‘prosauropod’ synapomorphies identified by Sereno (1999*a*; Table 3), reporting the following results: three were omitted; six could not be scored in ‘prosauropod’ outgroups; seven were diagnosed as more-inclusive or less-inclusive clades; and only three ‘unambiguously support “prosauropod” monophyly’ (2003*a*, p. 30). His phylogenetic results depend to a large extent on how this set of characters was rescored, recoded or discarded. Using the original numbering scheme for these characters (Table 3), Yates’ evaluation is reconsidered below. The term ‘core prosauropods’ will be used for the following five genera: *Plateosaurus*, *Massospondylus*, *Lufengosaurus*, *Yunnanosaurus* and *Riojasaurus*.

Although Yates claimed to have omitted characters 1, 3 and 9 from his analysis, character 3 was included (numbered 12) with a citation to Sereno (1999*a*). Yates modified character 3 to read ‘Development of a secondary *internal* wall of the antorbital fossa’ (emphasis added) and scored it as a saurischian synapomorphy. The character, however, involves the *external*, or secondary, wall of the antorbital fossa rather than the primitive internal wall. Several archosaur clades partially enclose the antorbital cavity with a lateral (external) secondary wall. Among dinosaurs this occurs notably in ornithischians and core prosauropods, in which a secondary vertical wall encloses the ventral margin of the fossa (Text-fig. 4). This appears to be poorly developed in the fragmentary maxilla available for *Thecodontosaurus* (Yates 2003*a*, fig. 3) and in *Ammosaurus* (= *Anchisaurus*; YPM 1883). In the latter, differences between opposing sides suggests that some plastic deformation might have flattened the left maxilla. The secondary wall is well developed in ‘core prosauropods’ but entirely absent in sauropods (e.g. *Riojasaurus*, Wilson and Sereno 1998; *Shunosaurus*, Chatterjee and Zheng 2002).

Yates noted correctly that he omitted characters 1 and 9, but he also omitted characters 13 and 16. Character 1 involves the presence of a keratinous beak covering the anterior margin of the premaxilla. Without doubt, this character is difficult to observe in most taxa, is possibly correlated with character 6, and was scored as present by Sereno (1999*a*) only in several taxa examined closely (*Plateosaurus*, *Massospondylus* and *Riojasaurus*). Yates (2003*a*, p. 27) described the feature as ‘parasagittal ridges’: I had described it as a raised platform (Sereno 1997, pp. 451–452). The derived condition was first observed in *Riojasaurus* (Wilson and Sereno 1998, fig. 36A) and later in mature individuals of other core prosauropods. The details supporting this inference are presented below. Although there are various neurovascular foramina on the premaxillae of basal sauropods, no comparable premaxillary attachment area has been described.

Character 9, the degree of deflection of the deltopectoral crest, was discarded by Yates because of the potential for correlation with body size, difficulty in measuring the angle when the crest is reduced and ease of post-mortem distortion. Without specific justification or evidence, it



TEXT-FIG. 3. Qualitative (A) and quantitative (B–E) phylogenetic hypotheses for basal Sauropodomorpha that support 'prosauropod' monophyly. For ease of comparison, terminal taxa outside Sauropodomorpha are excluded and sauropods are collapsed to a single taxon. A, cladogram from Galton (1990). B, consensus cladogram from analysis of 32 characters (after Sereno 1999*a*). C, single most-parsimonious cladogram from analysis of 49 characters (after Benton *et al.* 2000). D, consensus cladogram from analysis of 137 characters (after Galton and Upchurch 2004). E, consensus cladogram from analysis of the same dataset but with modified scores for *Lufengosaurus huenei* (after Barrett *et al.* 2005). Unmarked branch points = 1–4 unambiguous synapomorphies; circled branch points = 5–9 unambiguous synapomorphies; solid nodes = 10 or more unambiguous synapomorphies.

seems these criteria could be applied to any character. *Saturnalia* (Langer *et al.* 2007) and *Thecodontosaurus* (Benton *et al.* 2000) are both small sauropodomorphs, the former clearly showing the derived condition present as in core prosauropods and the latter the primitive condition (60 degree deflection or less). In both cases, the authors had more than a single specimen to observe and did not express concern regarding their estimated angle of deflection. *Omeisaurus* is an example of a basal sauropod with a weakly developed crest but one that clearly is not strongly deflected as seen in proximal view (He *et al.* 1988, pl. 14).

Character 13, the presence of a protruding proximal heel, or ventral intercondylar process, on the first phalanx of manual digit I characterizes core prosauropods, even when immature (Text-fig. 9D–E), as well as heavier-bodied genera, such as *Jingshanosaurus* (Zhang and Yang 1994, fig. 32A). The heel is associated with a well-developed intercondylar crest that gives the proximal end of the phalanx a rounded apex in ventral view rather than a broadly concave margin (Text-fig. 9E). Contrary to Yates, all of these features are present in the smaller-bodied *Efraasia* (Galton 1973, fig. 10G–L). Sauropods do not have this process (e.g. *Camarasaurus*; Ostrom and McIntosh 1999, pl. 62). Among dinosaurian herbivores, only in the grasping hand of heterodontosaurids is there comparable development of this articular surface. Even in basal theropods, such as *Herrerasaurus*, the ventral heel is not as well developed; it protrudes proximally but the intercondylar crest is incomplete and the proximoventral margin is broadly convex without a distinct apex (Sereno 1993, figs 14–15). Yates correctly observed that a heel of equivalent prominence is present in *Allosaurus* and other neotheropods, tentatively ascribed the apomorphy to Saurischia, and then omitted it from the analysis. 'Given that the difference between a large and a small protrusion is slight, I prefer not to draw a distinction and simply regard the presence of the protrusion as a derived character that is probably diagnostic of the Saurischia' (Yates 2003*a*, p. 29).

Character 16 identifies a swollen rugose welt on the lateral aspect of the iliac preacetabular process. Yates

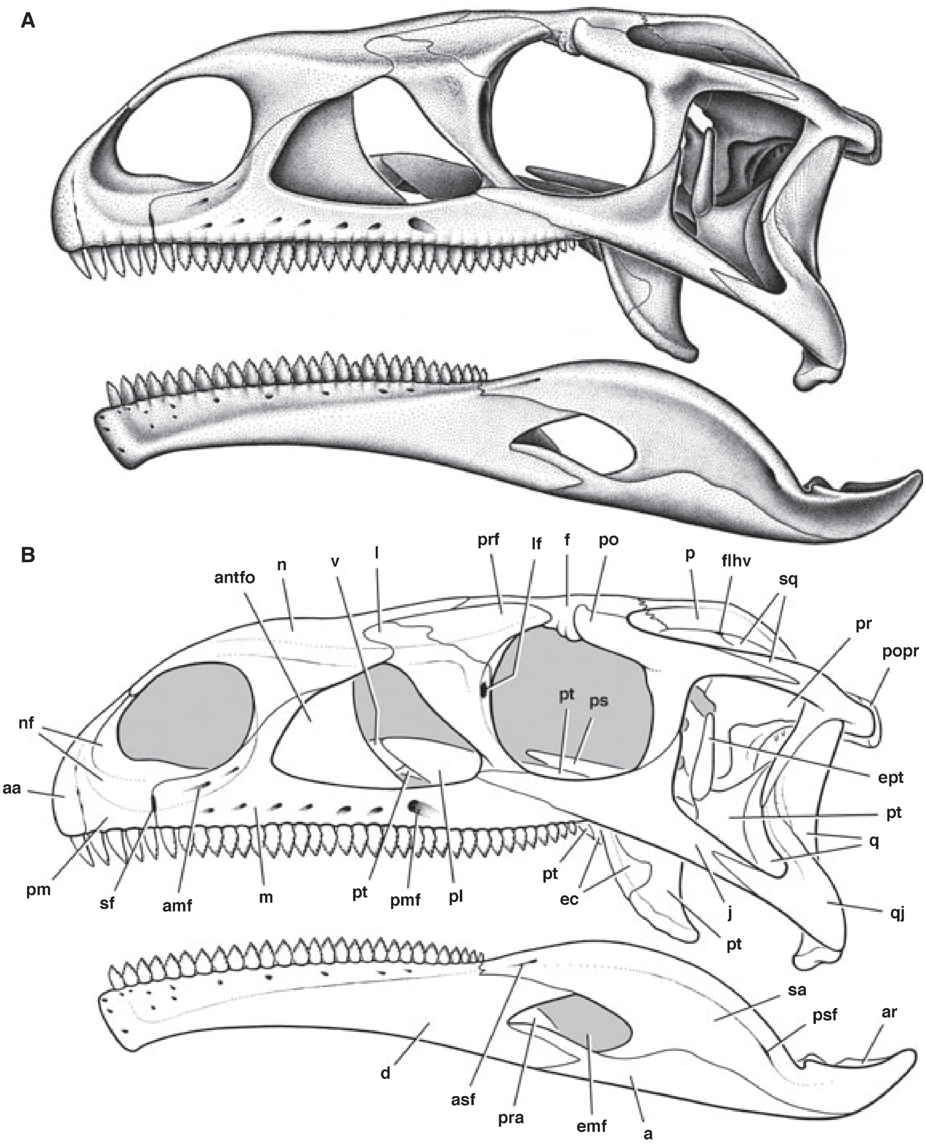
TABLE 2. Initial synapomorphies listed for basal nodes within Sauropodomorpha (Gauthier 1986).

Sauropodomorpha	
1	Manual digit I robust with enlarged claw
2	Lanceolate teeth with coarsely serrated crowns
3	Skull small on long neck of ten cervical vertebrae
4	Cervical vertebrae longer than most trunk vertebrae
5	Hind limb subequal to, or shorter than, the trunk
6	Tibia shorter than the femur
Anchisaurus plus more derived sauropodomorphs	
7	More robust digit I and metacarpal 1
8	Anterior caudal vertebrae with wider-based neural spines
9	Ilium with arched dorsal margin
10	Acetabulum completely open
'Broad-footed' genera plus more derived sauropodomorphs	
11	Quadrate condyle set below tooth row
12	Premaxillary internasal process compressed
13	Nares very large
14	Teeth increase in size anteriorly in upper tooth row
15	Proximal caudal centra compressed anteroposteriorly; broad-based neural spines
16	Robust forelimbs with short, broad, stout manus (same for pes to a lesser extent)
17	Manual digit I greatly enlarged
18	Proximal carpals absent (unossified)
19	Acetabulum much larger than femoral head
20	Tibial posterolateral flange rudiment present

TABLE 3. Synapomorphies (unambiguous in bold type) listed for core prosauropods by Sereno (1999*a*). This analysis did not consider *Thecodontosaurus*, and *Saturnalia* had yet to be described.

1	Premaxillary beak: absent (0); present (1).
2	Premaxilla-maxilla external suture: oblique (0); L-shaped (1).
3	Secondary antorbital fossa wall: absent (0); present (1).
4	Maxillary vascular foramina, form: irregular (0); one directed posteriorly, 5–6 anterior (1).
5	Squamosal ventral process, shape: tab-shaped (0); strap-shaped (1).
6	Dentary tooth 1, position: terminal (0); inset (1).
7	Axial postzygapophyses, length: overhang (0), or flush with (1), the posterior centrum face.
8	Deltopectoral crest, length: less (0), or equal to or more (1), than 50 per cent of the length of the humerus (1).
9	Deltopectoral crest, deflection: 45–60 degrees (0), or 90 degrees (1), to the transverse axis of the distal condyles.
10	Distal carpal 1, size: small (0); large (1).
11	Metacarpal 1, basal articulation: flush with other metacarpals (0); inset into the carpus (1).
12	Metacarpal 1, basal width: less than 50 per cent (0), or more than 65 per cent (1), maximum length.
13	Manual digit I, phalanx 1, proximal heel: absent (0); present (1).
14	Manual digit I-phalanx 1, rotation of axis through distal condyles: rotated slightly ventromedially (0); rotated 45 degrees ventrolaterally (1); rotated 60 degrees ventrolaterally (2).
15	Iliac preacetabular process, shape: blade-shaped (0); subtriangular (1).
16	Iliac preacetabular process, scar: absent (0); present (1).
17	Ischial distal shaft cross-section: ovate (0); subtriangular (1).
18	Metatarsal 2 proximal articular surface: subtriangular or subquadrate (0); hourglass-shaped (1).
19	Metatarsal 4 proximal end, transverse width: subequal (0), three times broader than (1), dorsoventral depth.

misunderstood this character as referring to the dorsal margin or blunt end of the preacetabular process, describing the scar as the site of attachment for a 'cartilaginous cap' (Yates 2003*a*, p. 30). The character was then omitted from the analysis. This attachment welt is a subtle textural feature, comparable in scale with the ambiens process on the pubis or anterior trochanter of the fibula. Drawings of basal



TEXT-FIG. 4. A–B, reconstruction of the skull of *Plateosaurus longiceps* in lateral view, based especially on SMNS 12949, 12950, 13200 and AMNH 6810. Abbreviations: a, angular; aa, attachment area for keratinous upper bill; amf, anterior maxillary foramen; antfo, antorbital fossa; ar, articular; asf, anterior surangular foramen; d, dentary; ec, ectopterygoid; emf, external mandibular fenestra; ept, epipterygoid; f, frontal; flhv, foramen for the lateral head vein; j, jugal; l, lachrymal; lf, lachrymal foramen; m, maxilla; n, nasal; nf, narial fossa; p, parietal; pl, palatine; pm, premaxilla; pmf, posterior maxillary foramen; po, postorbital; popr, paroccipital process; pr, prootic; pra, prearticular; prf, prefrontal; ps, parasphenoid; psf, posterior surangular foramen; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sf, subnarial foramen; sq, squamosal; v, vomer.

sauropodomorph ilia in the literature often do not distinguish the feature well. A similar swelling and rugosity has been described in *Saturnalia* (Langer *et al.* 2007) and attributed to the origin of the iliofemoralis cranialis. A swelling is present in a similar position in the herrerasaurid *Staurikosaurus* but absent in its close cousin *Herrerasaurus*. The attachment welt is widespread among basal sauropodomorphs but absent in *Ammosaurus* and sauropods.

Character 19, which identified the extreme relative width of the proximal end of metatarsal 4 in core prosauropods as derived, was modified by Yates to allow other saurischians to be scored with the derived condition. The original character identified a width three times dorsoventral depth as the derived condition; Yates suggested that such a dimension only characterized *Riojasaurus* and reduced the ratio to twice dorsoventral depth. The base of metacarpal 4 in core prosauropods, nevertheless, is proportionately very broad as originally coded (e.g. *Massospondylus*, Cooper 1981, fig. 76; *Plateosaurus*, von Huene 1926, pl. 6).

Characters 2, 4, 7 and 12 were scored as polymorphic in Sauropoda or present in Ornithischia, reducing or eliminating unambiguous support for the monophyly of core prosauropods. Character 4 identifies a stereotypical pattern of neurovascular foramina on the maxilla, the posteriormost of which is largest and exits posterolaterally. Basal sauropods, such as *Shunosaurus* and *Omeisaurus*, have an irregular pattern of foramina and do not have a noticeable posterolaterally directed neurovascular foramen. Many neosauropods have a pneumatic opening on the maxilla identified as the preantorbital fenestra (Wilson and Sereno 1998). Typically developed as a slit-shaped opening or larger fenestra, it opens anterolaterally. To eliminate character 4 as a factor favouring core prosauropod monophyly, Yates ignored the absence of the derived condition in basal sauropods, likened the posterior neurovascular foramen to the preantorbital fenestra, and scored the condition for Sauropoda as polymorphic.

Character 12 highlights the broad proximal width of metacarpal 1 in core prosauropods (proximal width greater than 65 per cent metacarpal length). Yates remarked, 'The only basal sauropods with well-preserved forefeet are those of euhelopodids, most of which have stout, "prosauropod"-like first metacarpals', citing *Shunosaurus* and *Hudeisaurus* (Yates 2003*a*, p. 29). *Shunosaurus*, does have the proportionately shortest hand of any basal (non-neosauropod) sauropod (proximal width approximately 60–80 per cent metacarpal length). *Hudeisaurus*, however, has a much longer metacarpal 1 (proximal width less than 30 per cent metacarpal length), as does *Omeisaurus* (proximal width about 50 per cent metacarpal length), which was included among 'euhelopodids' (Upchurch 1995). If *Shunosaurus* is situated alone as the most basal sauropod with data available for the manus, then the character state for Sauropoda would be ambiguous (or polymorphic).

Characters 10 and 11 also illustrate selective scoring that effectively undermines these and several of the remaining characters as synapomorphies for a larger group of core prosauropods. Character 10 highlights the size of distal carpal 1 (Table 3). No specific relative measure was originally given; this carpal is by far the largest in the carpus, equalling or exceeding the width of the base of the broadened first metacarpal (Text-fig. 10). Yates recoded the character (number 88) relative to distal carpal 2 (greater than 120 per cent of distal carpal 2). *Ammosaurus* (= *Anchisaurus*, YPM 1883) is an important taxon, but only the posterior aspect of the carpal of interest is exposed. Although it would have been larger if fully exposed in anterior view, even as exposed it is nearly as broad as the base of the enlarged metacarpal 1 as in other core prosauropods (Text-fig. 10). Also like these basal sauropodomorphs, distal carpal 1 is inset medially from the medial margin of metacarpal 1 (Text-fig. 9). In Galton's figure of the manus and carpal, however, an outline of the posterior contour of this carpal is centred directly over metacarpal 1 with no medial inset (1976, figs 17–18). In another specimen from the same region, an enlarged, medially inset distal carpal 1 is visible overlapping a small distal carpal 2 (erroneously figured as a single carpal; YPM 2125; Galton 1976, fig. 32). Yates, nonetheless, scored the condition in *Ammosaurus* (= *Anchisaurus*) as unknown, presumably because the enlarged distal carpal 1 in YPM 1883 is the only carpal exposed. Yates then scored both Neotheropoda and Sauropoda as derived, the former apparently based mainly on *Allosaurus* (rather than several other theropods with unfused equal-sized distal carpals 1 and 2) and the latter based on *Shunosaurus*. Three disc-shaped carpals are preserved in *Shunosaurus*, the first slightly larger than the second. Neither closely resembles the condition in core prosauropods (Zhang 1988, fig. 48). A few small carpal bones were reported in *Omeisaurus* as well, another basal sauropod. As a result of the character state scores outlined above, the distinctive enlarged, medially inset, distal carpal 1 of core prosauropods was optimized on Yates' tree as a synapomorphy uniting Neotheropoda and Sauropodomorpha (excluding Herrerasauridae).

Regarding the proximal inset of metacarapal 1 into the carpus (character 11), Yates scored several basal sauropodomorphs as primitive (with flush metacarpal bases), including *Thecodontosaurus*, *Ammosaurus* (= *Anchisaurus*), *Efraasia* and *Riojasaurus*. Earlier in this paper I described the inset position of metacarpal 1 in *Ammosaurus*. Well-preserved specimens of metacarpal 1 in *Riojasaurus* also strongly suggest this bone was inset into the carpus. The single specimen referred to *Thecodontosaurus* that preserves the carpus and metacarpus, on the other hand, is partially disarticulated and not particularly well preserved (Benton *et al.* 2000). It was scored as having the primitive condition with metacarpal bases flush against the distal carpals. As a result of the character state scores outlined above, an inset metacarpal 1 was optimized on Yates' trees as an autapomorphy of *Plateosaurus* and a synapomorphy for *Lufengosaurus*, *Yunnanosaurus* and *Massospondylus*.

Yates and Kitching (2003) and Yates (2004) performed additional analyses (Text-fig. 2D). Yates (2004) scored 205 characters in 17 ingroups, only ten of which are commonly understood as 'prosauropods'. Other ingroups include the basal sauropods *Vulcanodon*, *Kotasaurus*, *Shunosaurus*, *Barapasaurus*, *Omeisaurus* and Neosauropoda. Compared with Yates (2003*a*), the taxonomic scope of ingroups is both trimmed and extended; two basal sauropodomorphs ('*Euskelosaurus*', *Yunnanosaurus*) and all ingroups outside Sauropodomorpha have been trimmed, whereas Eusauropoda is split into five terminal taxa. Building on the dataset in Yates (2004), Yates and Kitching (2003) employed 212 characters in 19 ingroups, two of which were new to the analysis (*Antetonitrus*, *Isanosaurus*). Compared with Yates (2004), one character was removed and eight added for a total of 212 characters (Text-fig. 2C).

How this dataset corresponds to that in Yates (2003*a*) is not clear, because the character data now includes ordered and unordered multistate characters, and the results are quite different (Text-fig. 2B–C). Substantial character support is now present for a clade of core prosauropods that in the previous dataset required ten additional steps to compose. This major phylogenetic difference is presumably a byproduct of variation in character selection, coding and scoring. Several additional characters were added, some of which link *Anchisaurus* and Sauropoda (Yates 2004), such as wrinkled enamel. Interpretation of the cranial morphology of this taxon, however, remains controversial (Fedak 2005).

Pol (2004). Pol (2004) and Pol and Powell (2005) have recently presented a broad-scale phylogenetic analysis of basal Sauropodomorpha, with 24 non-sauropod sauropodomorphs, 13 sauropods and 16 taxa outside Sauropodomorpha scored for 277 characters (Text-fig. 2C). The results are broadly consistent with Yates and Kitching (2003) and Yates (2003*a*, 2004) insofar as *Saturnalia*, *Thecodontosaurus* and *Efraasia* are in successively less inclusive basal positions and *Anchisaurus*, *Antetonitrus*, *Melanorosaurus* and *Blikanasaurus* are most closely related to Sauropoda. Several genera in between these extremes, which include the five core prosauropods, are depicted as successive stem taxa, more closely resembling the results of Yates (2003*a*). Branch support is less than five for all of the depicted nodes, even when the most poorly known, unstable taxa are removed.

How the data of Pol (2004) and Yates (2004) compare in terms of characters used and how those characters are coded and scored is not known. Pol (2004) compiled 469 characters from the literature. He rejected 192 (41 per cent) and modified most of the remaining 277 characters (59 per cent). Character selection is as important as character scoring in the evaluation of data, especially when considering cladistic hypotheses like these with relatively with low levels of branch support. Further commentary awaits formal publication of Pol's dataset.

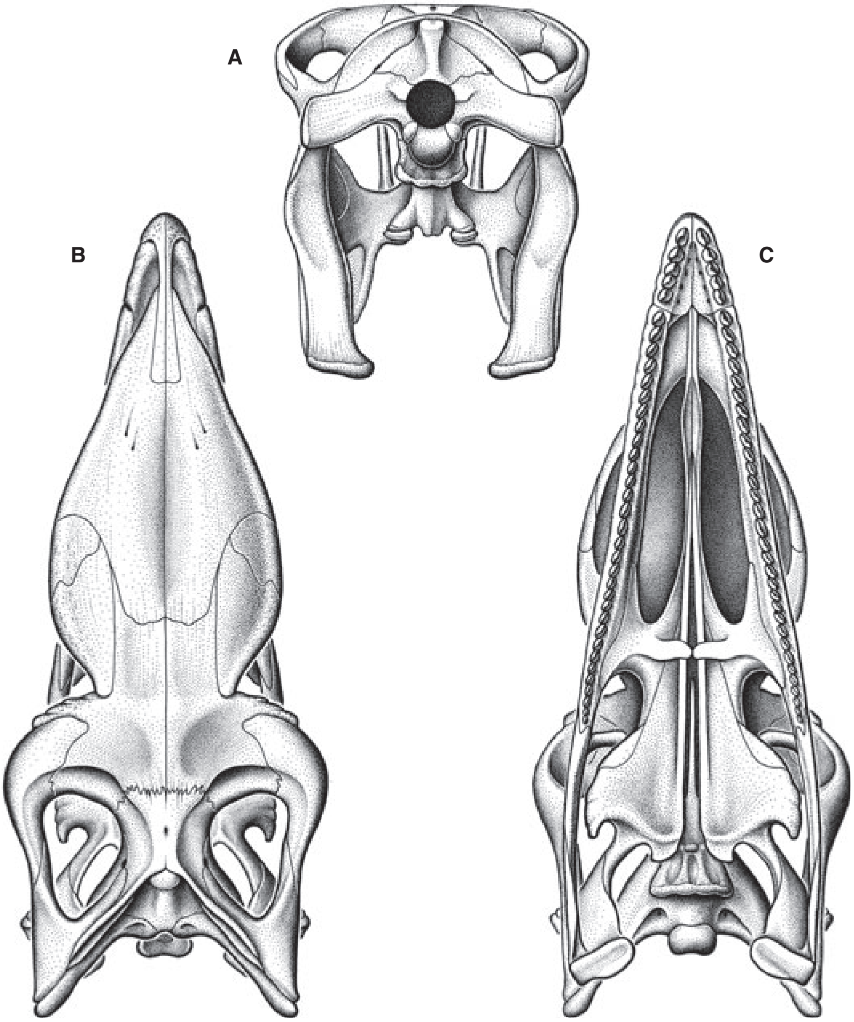
Prosauropod monophyly

Prosauropod monophyly (Text-fig. 3) was proposed independently in the same year in qualitative analyses by Sereno (1989) and Galton (1989, 1990). Quantitative versions of these analyses eventually would appear (Sereno 1999*a*; Galton and Upchurch 2004). In addition, Benton *et al.* (2000) drew the same conclusions in considering the phylogenetic placement of *Thecodontosaurus*.

Sereno (1989, 1999). Sereno (1989) listed 11 synapomorphies to unite prosauropods or a larger clade composed of prosauropods plus 'segnosaurs' (now referred to as therizinosauroids and clearly situated among coelurosaurian theropods). Nine of the 11 features were later coded in the first quantitative analysis of basal sauropodomorphs (Sereno 1999*a*). Using Sauropoda and Theropoda as successive outgroups, Sereno (1999*a*) scored 32 characters in nine of the best-known 'prosauropod' genera (Tables 1, 3). Nineteen characters, or approximately 60 per cent of the character data, supported a 'prosauropod' clade without any homoplasy. The consensus of six minimum-length trees (34 steps, CI = 0·97, RI = 0·98, character 27 ordered) shows *Riojasaurus* as the most basal taxon and *Plateosaurus* the most nested (Text-fig. 3B). The published cladogram simplified these results, showing only six of nine ingroup genera (Sereno 1999*a*, fig. 2). The remaining 13 characters provided little branch support among prosauropods; fewer than five supported any particular node, and all nodes except *Efraasia* + *Plateosaurus* collapse with two additional steps. Furthermore, this last node actually unites two species of the genus *Plateosaurus*, as the material upon which *Efraasia* was scored has more recently been referred to *Plateosaurus gracilis* (Yates, 2003b).

Other less complete taxa, such as *Thecodontosaurus*, *Melanorosaurus*, *Mussaurus* or *Blikanasaurus*, were excluded because few, if any, of the characters included in the analysis could be scored. Interpretation of the morphology of *Thecodontosaurus*, the most complete specimen of which is now referred to a new species, *T. caducus* (Yates 2003*a*), is complicated by its immaturity and small size, raising some concern over whether primitive features are merely growth related or allometric correlates of small body size, such as the proportionately smaller deltopectoral crest. The partial preservation and disarticulation of available skull elements has also complicated their interpretation and reconstruction (Kermack 1984; Yates 2003*a*). There is little chance that this situation will change, as the best material was recovered long ago from fissure-fill deposits. *Melanorosaurus readi*, on the other hand, may soon be represented by a much better skeleton with a skull (Yates 2005, 2007).

Although the 1999 dataset strongly favoured prosauropod monophyly, many less complete taxa were not considered, besides those described recently (*Saturnalia*, *Antetonitrus*). Sauropoda, in fact, was originally logged as an outgroup, although the results are the same if

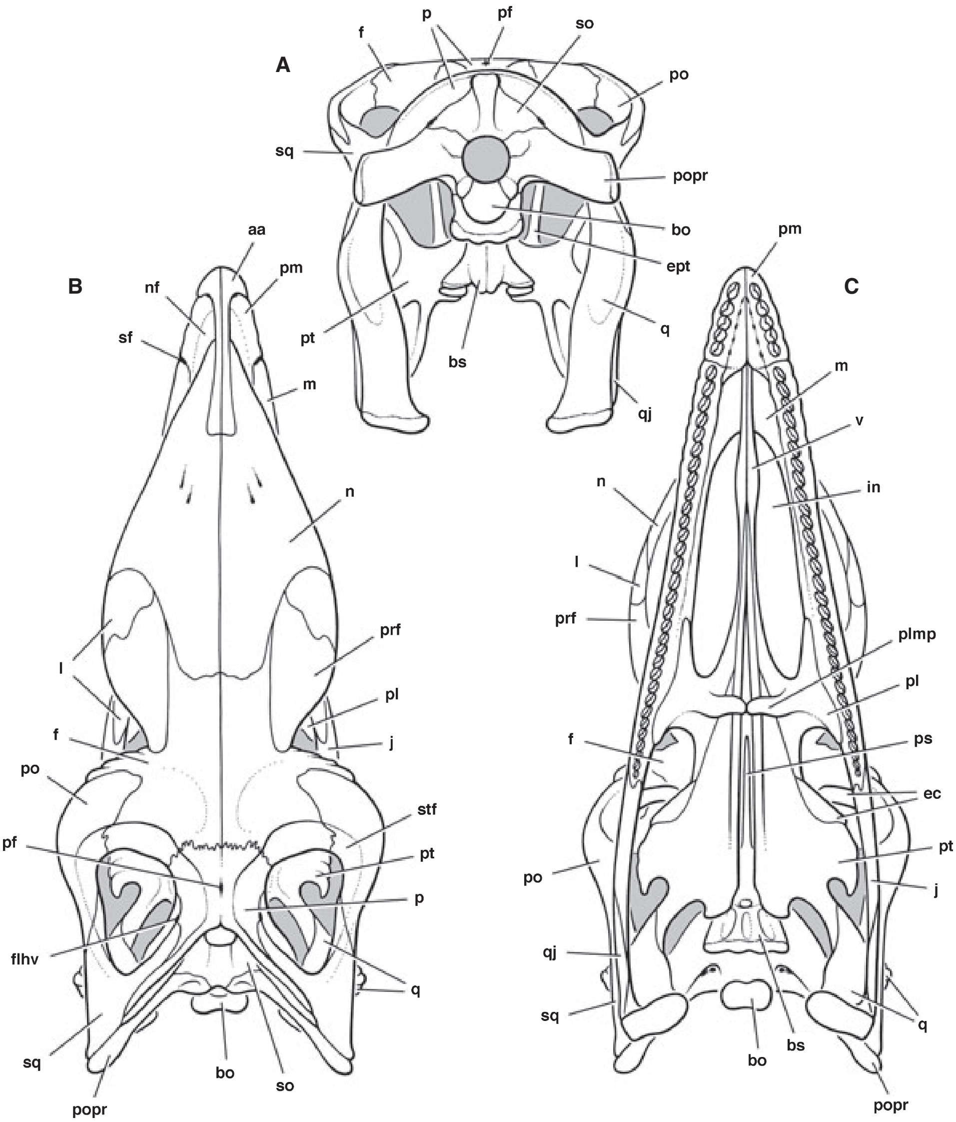


TEXT-FIG. 5. Reconstruction of the skull of *Plateosaurus longiceps* in A, posterior, B, dorsal, and C, ventral views. Based especially on SMNS 12949, 12950, 13200 and AMNH 6810. See Text-figure 6 for labelling.

Sauropoda is transferred to the ingroup. To imply on the basis of this analysis therefore that all, or nearly all, taxa commonly considered 'prosauropods' comprise a monophyletic clade is an overstatement (Sereno 1997, 1999*a*). The analysis provided some initial evidence in support of the monophyly of a core of prosauropod genera.

Galton (1989, 1990) and Galton and Upchurch (2004). Galton (1989, p. 82; 1990, p. 321) listed eight derived features in support of 'prosauropod' monophyly (Text-fig. 2A). Only one of these characters, the 'twisted' phalanx 1 of manual digit I, was used in support of prosauropod monophyly by Sereno (1989, 1999*a*) or the subsequent analysis by Galton and Upchurch (2004: Text-fig. 3D). The remaining features originally listed by Galton are either present in sauropodomorph outgroups (e.g. diminutive size of manual digits IV and V) or were relocated to less inclusive nodes within Sauropodomorpha by later authors.

Galton and Upchurch scored 137 binary characters (ten of which are uninformative) in 18 'prosauropod' genera as well as in *Blikanasaurus* and four sauropods (Table 1). The data yield two minimum-length trees of 260 steps (279 reported) that include a monophyletic Prosauropoda that excludes only the stocky-limbed genus *Blikanasaurus* (Text-fig. 3D). The dramatic increase in character number is due in part to the incorporation of data for the nodes Sauropodomorpha and Sauropoda and nodes within Sauropoda, which account for approximately 40 unique synapomorphies on minimum-length trees. Character data in Galton and Upchurch (2004) broadly overlap that in Sereno (1999*a*), and the resulting support at basal nodes is very similar. Seventeen of 19 synapomorphies



TEXT-FIG. 6. Reconstruction of the skull of *Plateosaurus longiceps* in A, posterior, B, dorsal, and C, ventral views. Abbreviations: aa, attachment area for keratinous upper bill; bo, basioccipital; bs, basisphenoid; ec, ectopterygoid; ept, epipterygoid; f, frontal; flhv, foramen for the lateral head vein; in, internal nares; j, jugal; l, lachrymal; m, maxilla; n, nasal; nf, narial fossa; p, parietal; pf, parietal foramen; pl, palatine; pm, premaxilla; plmp, palatine medial process; po, postorbital; popr, paroccipital process; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sf, subnarial foramen; so, supraoccipital; sq, squamosal; stf, supratemporal fossa; v, vomer.

that supported prosauropod monophyly in Sereno (1999*a*) are present at similar basal nodes in Galton and Upchurch (2004). A single additional step is sufficient to collapse all structure outside Sauropoda, because several terminal taxa are very poorly known taxa. If ingroups are limited to those considered by Sereno (1999*a*: Text-fig. 3B), however, there are two strongly supported nodes (more than ten synapomorphies) within Sauropodomorpha: Prosauropoda and Sauropoda. This is not an artefact arising after removal of homoplastic taxa; these synapomorphies are present at basal nodes in minimum-length trees with all taxa included. There is very little structure within Prosauropoda, in contrast, which is clearly revealed by the range of relationships that were altered after adjusting character state scores for *Lufengosaurus* (Barrett *et al.* 2005: Text-fig. 3E).

Benton et al. *(2000).* Benton *et al.* (2000) scored 49 characters in nine ‘prosauropods’ and four sauropods. The dataset, which includes four uninformative characters, yields 42 minimum-length trees of 84 steps (83 reported) with no resolution of relationships among basal sauropodomorphs. By removing *Riojasaurus*, Benton *et al.* (2000) were able to obtain a single tree of

78 steps (77 reported), now with five uninformative characters. Prosauropod monophyly was weakly supported. Yates (2003*a*) remarked that this monophyletic clade collapses when a single character state for sauropods is corrected. One additional step, in fact, collapses all resolution except a subclade of three well-known sauropods. There are two fundamental reasons for this. First, fully one-half of the characters are not informative for 'prosauropod' relationships (five are uninformative and 20 constitute unique synapomorphies for Sauropodomorpha, Sauropoda or nodes within Sauropoda). Second, approximately 70 per cent of character state scores are unknown for several 'prosauropod' genera, namely *Coloradisaurus*, '*Euskelosaurus*' and *Melanorosaurus*, leaving them poorly constrained. With this degree of missing data, it is difficult to justify the removal of *Riojasaurus* with the aim of obtaining meaningful resolution; *Riojasaurus* is scored for 98 per cent of the character data (all but 1 character).

The character that was rendered uninformative by removal of *Riojasaurus* involves the large size of distal carpal 1 (character 25). Besides *Massospondylus*, *Riojasaurus* was the only ingroup taxon scored with the derived condition (size twice that of other distal carpals), despite the fact that elsewhere in the paper *Thecodontosaurus* was clearly shown with the derived condition (Benton *et al.* 2000, fig. 12A). *Plateosaurus* was also shown with a large distal carpal 1 in a paper by one of the coauthors (Galton and Cluver 1976, fig. 7M). This character was one of five that appeared as prosauropod synapomorphies in the analysis of Sereno (1999*a*). Only two of these (manual phalanx I-1 twisted, subtriangular preacetabular process) continue to support 'prosauropod' monophyly in Benton *et al.* (2000), given differences in how they were scored. Although Benton *et al.* (2000) might have gone to press before Sereno (1999*a*) was available, they cited his use of the inset position of metacarpal 1, a character used for the first time in the 1999 analysis.

KEY QUESTIONS

Morphology

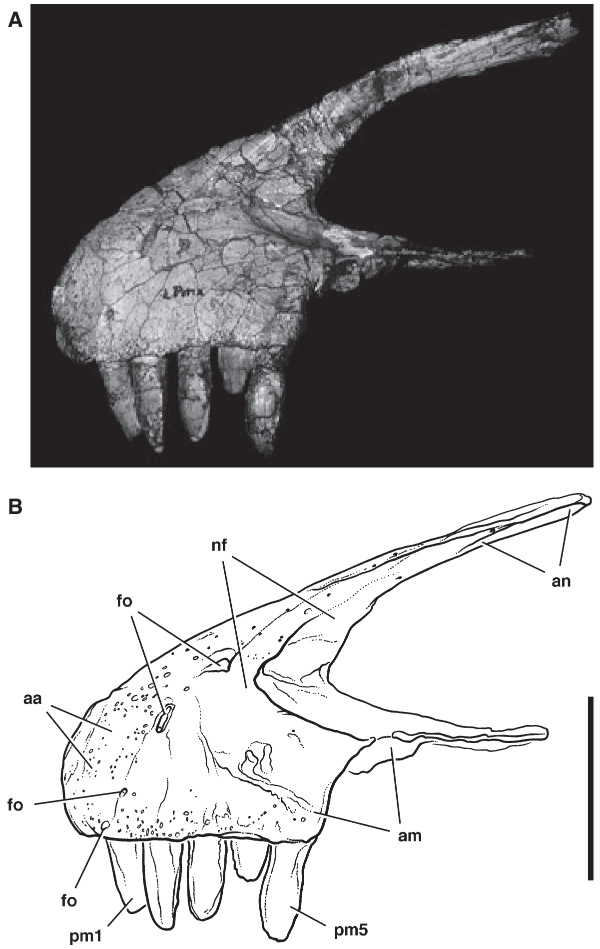
The most parsimonious scheme has ramifications for morphology. Some notable features will either be verified as unique 'prosauropod' synapomorphies or viewed as outstanding instances of characters that evolved and then were reversed in the line leading to sauropods. Two are discussed below.

Keratinous beak, tooth retraction. Sereno (1999*a*) cited as two separate characters the presence of a keratinous sheath on the anterior end of the premaxilla and the retraction of the first dentary tooth from the anterior end of the dentary (Table 3; Text-figs 4–8). Here I describe them together as possibly associated with the presence of a narrow keratinous beak on upper and lower jaws.

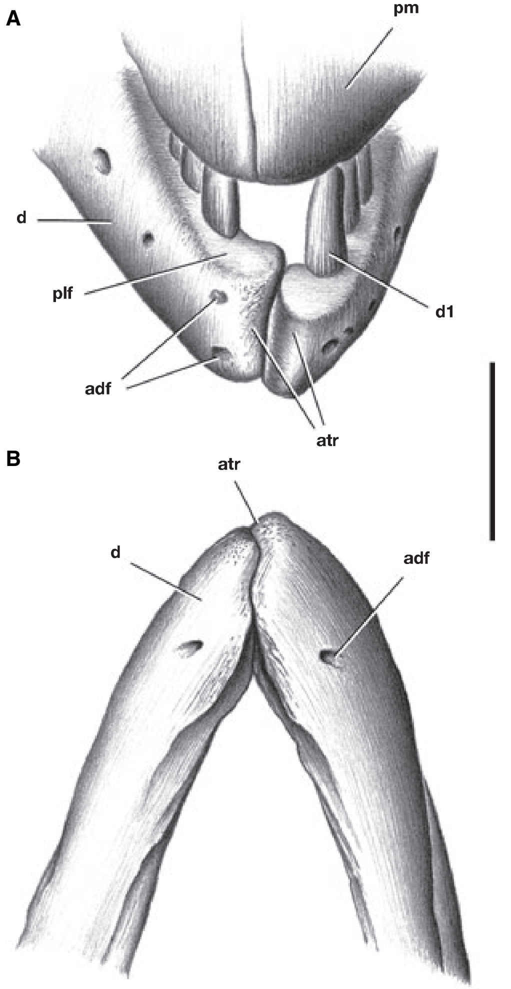
I became aware of the derived morphology of the premaxilla while examining the skull of *Riojasaurus*, in which the attachment area on the premaxilla is raised as a distinct platform (Wilson and Sereno 1998, fig. 36A). A similar raised platform is now known in another undescribed specimen from Argentina pertaining to a different genus (R. Martinez, pers. comm. 2006). More subtle expression of the character is present in other basal sauropodomorphs, such as *Massospondylus* (Gow *et al.* 1990, fig. 9) and a basal sauropod from the Kayenta Formation (Crompton and Attridge 1986). As in *Plateosaurus* the attachment surface is covered with fine pores much like the surface of other keratin-covered jaw bones among dinosaurs, such as the predentary or rostral (Text-figs 4–7). One to three nutrient foramina enter the premaxilla along the posterior border of this region, which is located above the first premaxillary crown or between first and second crowns. It appears from these features that a keratinous sheath covered the anterior end of the premaxillae, which was scored only in these few taxa with exceptional preservation (Sereno 1999*a*). Although there are various pits and neurovascular foramina on the premaxillae of basal sauropods, no comparable premaxillary attachment area has been described.

Retraction of the first dentary tooth is easier to verify than fine points of premaxillary form. The retraction of the position of the first dentary tooth may well be related to a keratinous lower beak. The condition in *Saturnalia* has not been described in detail and may not be determinable (scored as absent by Yates 2003*a*), whereas in *Thecodontosaurus* some retraction is present (Benton *et al.* 2000). In *Plateosaurus* a flat platform is located in the position usually occupied by the first tooth (Text-fig. 8A). A shallow trough is present between the dentaries anterior to the symphysis, which also may have functioned for attachment, and a sizeable pair of nutrient foramina always seems to be present and inset a short distance from the leading edge of the dentary (*Plateosaurus*, *Massospondylus*, *Thecodontosaurus*; Text-fig. 8).

A platform of similar form and position is present in other basal sauropodomorphs, such as a basal sauropodomorph from the Kayenta Formation. A keratinous beak shaped like an ornithischian predentary was previously inferred to have been present in this specimen (Crompton and Attridge 1986, fig. 17.6). Based in large part on a preservational artefact that misaligned upper and lower jaws, they suggested that the lower jaw in this specimen is unusually short, that the tips of maxillary crowns inserted into neurovascular foramina on the dentary, and that a



TEXT-FIG. 7. Left premaxilla of *Plateosaurus longiceps* (AMNH 6810) in lateral view. Abbreviations: aa, attachment area for keratinous upper bill; am, articular surface for the maxilla; an, articular surface for the nasal; fo, foramen; pm1–5, premaxillary teeth; nf, narial fossa. Scale bar in B represents 3 cm.



TEXT-FIG. 8. Anterior end of the skull of *Plateosaurus longiceps* (SMNS 12949) in A, anterodorsal, and B ventral views. Abbreviations: adf, anterior dentary foramen; atr, attachment trough; d, dentary; d1, dentary tooth 1; plf, platform; pm, premaxilla. Scale bar represents 2 cm.

keratinous sheath covered other neurovascular foramina and projected anteriorly to complete the lower jaw. Although I cannot support these conclusions for several reasons, Crompton and Attridge (1986) also reported the presence of a high-angle wear facet on a premaxillary crown. Wear facets are unknown elsewhere among basal sauropodomorphs. They have been reported thus far only in isolated teeth referred without justification to *Yunnanosaurus* (Galton 1985) and in fragmentary material improperly referred to Sauropodomorpha (Flynn *et al.* 1999).

In the Kayenta skull, all four premaxillary crowns are preserved on the right side and the second and third are preserved on the left side. A high-angle wear facet is present on the first crown on the right side and second crown on the left side. The facet cuts through the thin enamel that covers the anteromedial edge of the crown. The crowns are canted anteromedially, so the wear facets were made by a structure passing inside the anterior end of the premaxillary tooth rows. The anteriormost dentary crowns do not have compensatory wear and were not positioned far enough anteriorly to account for the premaxillary facets. The reduced denticulation of the anterior premaxillary teeth also resemble ornithischian premaxillary teeth that oppose a lower keratinous bill.

The inference of an anterior beak in basal sauropodomorphs, thus, is based on the form of the anterior ends of the premaxilla and dentary and the presence of high-angle wear facets on the inside of the anteriormost premaxillary crowns. Sauropods show no indication of this morphology. The lower tooth row in sauropods extends to the midline and the muzzle is often squared. Tooth retraction is a common phenomenon within Tetrapoda, but with rare exception it is progressive and irreversible. These features at the anterior end of the snout either characterize a basal sauropodomorph clade or were reversed without trace in the line leading to Sauropoda.

Carpal-metacarpal complex. Distal carpal 1 is enlarged and overlaps distal carpal 2 in an arrangement unique to basal sauropodomorphs as originally described by Broom (1911: Text-fig. 9A–C). Metacarpal 1 is inset into the carpus and develops a synovial joint on the lateral side of its base, against which rests the smaller distal carpal 2 (Text-figs 9B–C, 10B). In this configuration, distal carpal 1 completely overlaps the proximal surface of distal carpal 2, which effectively separates distal carpal 1 and metacarpal 2. The distal carpals and metacarpals of basal sauropodomorphs show very little variation in form and arrangement, the telltale clues for which are present in synovial joints on the base of metacarpal 1 (Text-fig. 9B–C). The presence of this configuration, in other words, seems possible to infer with only metacarpal 1 at hand (e.g. *Antetonitrus*: Yates and Kitching 2003). The complex is well preserved in articulation in *Massospondylus*, which documents the dramatic size decrease from distal carpal 1 to distal carpal 3 and concomitant change in shape from flattened hemispheroid to elongate hemispheroid to small pyramid, respectively (Broom 1911; Cooper 1981). *Lufengosaurus* shows exactly this condition (Young 1947, figs 4–8). Other basal sauropodomorphs with carpus and metacarpus in natural articulation show the derived configuration, including cf. *Ammosaurus* (YPM 1225), an unnamed taxon from the Navajo Sandstone in western North America (Galton 1976; Irmis 2005), *Plateosaurus* from Europe (von Huene 1932) and Greenland (Galton 2001), *Lufengosaurus* (Young 1941), and *Mussaurus* (Casamiquela 1980; Pol 2004). Whether this is also the case in *Saturnalia* (Langer 2003), *Thecodontosaurus* (Benton *et al.* 2000) or in the more derived *Jingshanosaurus* (Zhang and Yang 1994) remains uncertain.

Misinformation is present in the literature for several taxa. In *Lufengosaurus*, for example, Young (1947) described all of the distal carpals and metacarpals but reassembled the manus with proximal ends of the metacarpals aligned. Young described a pair of distal articular fossae on the enlarged distal carpal 1 as accommodating metacarpals 1 and 2, a condition common among theropods. These fossae, to the contrary, are fitted to metacarpal 1 and distal carpal 2, as has long been documented in *Massospondylus* (Text-fig. 9B–C). This configuration is also present in YPM 1225 from the Connecticut River valley (cf. *Ammosaurus major*), but distal carpals 1 and 2 were drawn as a single element (Galton 1976, fig. 32). Casamiquela (1980) documented and Pol (2004) described this configuration in *Mussaurus*, but the character was omitted in his phylogenetic analysis (Pol 2004). Santa Luca (1980, fig. 15) figured a similar condition in *Heterodontosaurus* and this has been refigured elsewhere (Langer and Benton 2006, fig. 8). His interpretation was based on the right manus, in which digit I is slightly disarticulated distally. The fully articulated left manus shows the base of the metacarpals in alignment. The inset position of metacarpal 1 and its lateral articulation with distal carpal 2 appears to constitute a unique configuration among dinosaurs.

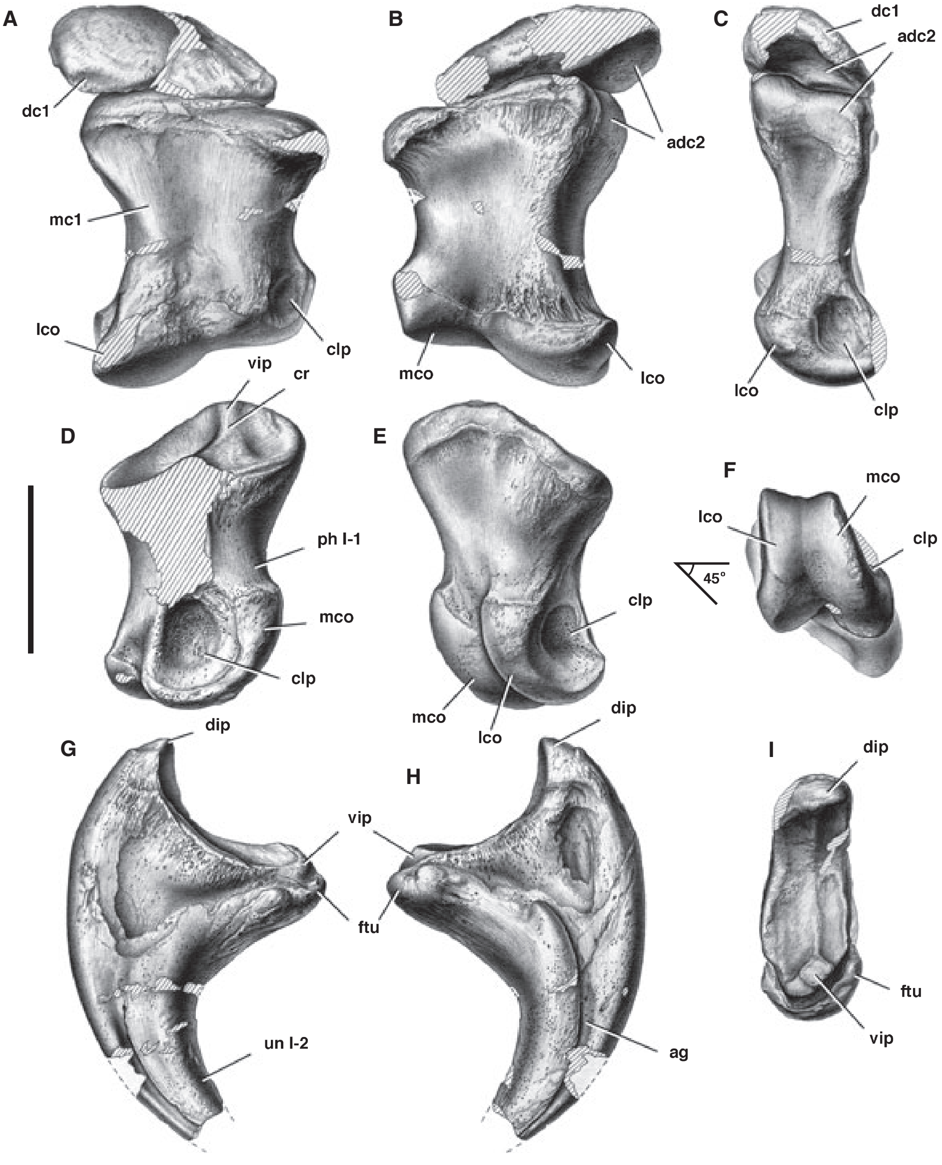
Sauropods do not exhibit any aspect of this carpal-metacarpal complex. That absence is difficult to discount as a necessary correlative of using the hand in obligate quadrupedal locomotion, not least because some basal sauropodomorphs of considerable size have been interpreted as facultative quadrupeds. *Antetonitrus*, which appears to have maintained this complex within a particularly stout manus, has long front limbs (humerus 90 per cent femoral length) and may well have been a facultative quadruped (Yates and Kitching 2003). To discount all evidence from sauropods as too transformed to score is problematic, when many basal species retain an ossified distal carpus as well as five metacarpals. The unusual configuration of carpus and metacarpus and rotated manual digit I either characterizes a basal sauropodomorph clade or, as now appears more likely, evolved only to be lost without trace in the line leading to Sauropoda.

Phylogeny

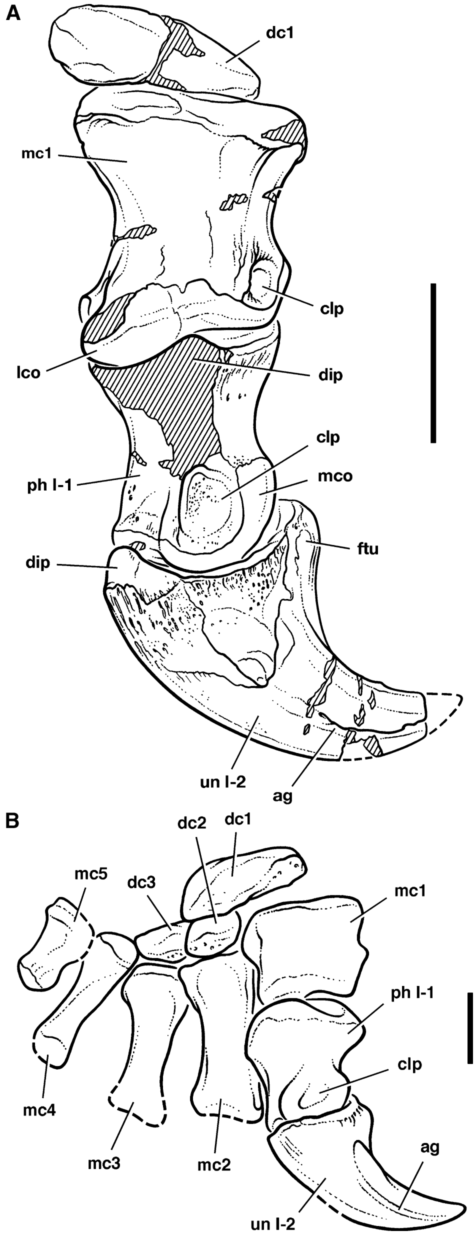
New fossil remains described in the last decade, especially *Saturnalia tupiniquim* (Langer 2003; Langer *et al.* 2007), *Mussaurus* (Pol 2004), *Jingshanosaurus xinwaensis* (Zhang and Yang 1995) and *Antetonitrus ingenipes* (Yates and Kitching 2003), have broadened the morphologically narrow core of basal sauropodomorphs that had been central to early phylogenetic hypotheses. In recent years broader sampling of taxa and characters have generated hypotheses for basal sauropodomorphs that are both monophyletic (Galton and Upchurch 2004) and paraphyletic (Yates 2003*a*, 2004; Yates and Kitching 2003; Pol 2004). The nodes in these hypotheses en route to Sauropoda typically have branch support of only one or two steps. Only one node in one analysis is supported by as many as five unambiguous synapomorphies (Text-fig. 2C), a node uniting sauropodomorphs above *Thecodontosaurus*. I try to frame below what seems reasonable to conclude at this juncture about the phylogenetic relationships of basal sauropodomorphs and where major questions remain.

New basal and derived species. Saturnalia is clearly basal to other known sauropodomorphs, given the primitive morphology of its ilium, ischium, pubis, femur and metatarsus, the description of which has only recently become available (Langer 2003) (Text-fig. 11A). In *Saturnalia* these bones are easily distinguished from comparable bones in *Thecodontosaurus*, *Efraasia* and core prosauropods. The ilium, for example, has a broad flange backing the acetabulum (Langer 2003), the femur has a trochanteric shelf, and the proximal end of metatarsal 4 is not strongly compressed. These are primitive conditions unknown elsewhere among basal sauropodomorphs. *Thecodontosaurus* is more derived but only positioned tentatively here, given some uncertainty in the association of disparate and often immature specimens (Benton *et al.* 2000; Yates 2003*a*).

Mussaurus patagonicus (Casamiquela 1980; Pol 2004; Pol and Powell 2005) and *Jingshanosaurus xinwaensis* (Zhang and Yang 1994) exhibit notable derived features in the skull. One or both exhibit a skull with anteroposteriorly short proportions, external nares retracted relative to the antorbital opening, a dentary that expands



TEXT-FIG. 9. Right distal carpal 1 and manual digit I of *Massospondylus carinatus* (AMNH 5624). A–C, right distal carpal 1 and metacarpal 1 in dorsal, ventral, and lateral views. D–F, right phalanx 1 of manual digit I in dorsal, ventral and distal views. G–I, right ungual of manual digit I in dorsal, ventral and proximal views. Abbreviations: adc2, articular surface for distal carpal 2; ag, attachment groove; clp, collateral ligament pit; cr, crest; dc1, distal carpal 1; dip, dorsal intercondylar process; ftu, flexor tubercle; lco, lateral condyle; mc1, metacarpal 1; mco, medial condyle; ph I-1, phalanx 1 of manual digit I; un I-2, ungual of manual digit II; vip, ventral intercondylar process. Angle in F is a measurement of the degree of torsion in the shaft of the phalanx. Scale bar represents 2 cm.



TEXT-FIG. 10. Right carpus and manus of *Massospondylus carinatus*. A, right distal carpal 1 and manual digit I in dorsal view (AMNH 5624). B, right carpus and manus in dorsal view (UCR9558: after Cooper 1981, fig. 35). Abbreviations: ag, attachment groove; clp, collateral ligament pit; dc1–3, distal carpal 1–3; dip, dorsal intercondylar process; ftu, flexor tubercle; lco, lateral condyle; mc1–5, metacarpal 1–5; mco, medial condyle; ph I-1, phalanx 1 of manual digit I; un I-2, ungual of manual digit II. Scale bars represent 2 cm.

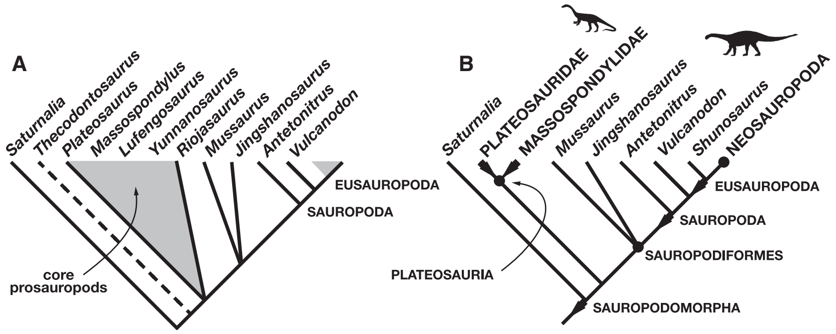
anteriorly and textured enamel on some crowns. Their postcranial skeleton, however, is similar to that in other basal sauropodomorphs and characterized by robust short forelimbs, an inset metacarpal 1 and relatively slender metatarsals. They may occupy a position more advanced than core prosauropods, although more detailed information on each is needed.

Antetonitrus is clearly more derived than other basal sauropodomorphs (Yates and Kitching 2003: Text-fig. 11A). Based on a partial disarticulated skeleton, *Antetonitrus* has a broadened scapular blade, unusually long forelimbs relative to its hind limbs, proportionately short manus and pes, and especially robust metatarsal 1. *Blikanasaurus* (Galton and Van Heerden 1998), represented by the distal portion of a hind limb, has been recognized by many as a sister group to sauropods, but such fragmentary material severely limits confidence in such phylogenetic conclusions. *Antetonitrus*, on the other hand, is represented by several key axial and appendicular elements that help paint a picture of an intermediate form between better known 'core prosauropods' and basal sauropods like *Vulcanodon*.

'Core prosauropods'. These basal sauropodomorphs have been known for some time from near complete skeletons and include *Plateosaurus longiceps*, *Massospondylus carinatus*, *Lufengosaurus huenei*, *Yunnanosaurus huangi* and *Riojasaurus incertus*. I exclude *Thecodontosaurus caducus*, *Efraasia diagnostica* and *Ammosaurus major* on the grounds that their skeletal remains are either relatively incomplete, immature, variously interpreted, poorly preserved, or some combination of the foregoing. Furthermore, given the geological setting where they were discovered, it is unlikely that more complete specimens will be found. I also exclude *Melanorosaurus readi* because of the extremely limited material that has, until recently, limited its interpretation.

The aim here is not to demote the importance of the four species cited above, but rather to highlight a core group of five well-documented species on which to rest the traditional taxon Prosauropoda. Yates and Kitching (2003) revised Prosauropoda in a very similar manner, uniting four of the five taxa listed above (they did not consider *Yunnanosaurus*). Some taxonomists, to be sure, have continued to list every single non-sauropod sauropodomorph under Prosauropoda, even the most derived (e.g. *Blikanasaurus*: Galton and Van Heerden 1998). Yet, if it is possible to unite the five species cited above as a monophyletic clade, salvaging the name Prosauropoda seems appropriate.

Data documentation and comparison. Phylogeneticists increasingly realize the need to document characters and character states better with supporting information. Explanatory notes, specimen documentation and images, for example, are likely to be increasingly attached to the cells of a taxon-character matrix (Pol 2004). The maturity of specimens must also be more carefully considered, because some characters change with age. Yates and Kitching (2003, p. 1755) downplayed growth as a con-



TEXT-FIG. 11. A, summary cladogram depicting a conservative interpretation of the current status of basal sauropodomorph phylogeny. Relations among core prosauropods and between them and other basal sauropodomorphs remain unresolved. B, summary cladogram of suggested phylogenetic taxonomy. Should core prosauropods be united as a clade to the exclusion of Sauropodiformes, the taxon Prosauropoda would be available (see Table 4 for definitions). Dots indicate node-based taxa and arrows indicate stem-based taxa.

founding factor, suggesting that the 'appendicular skeleton of sauropodomorphs experiences little, if any, allometric changes with growth.' The proportions of metacarpal 1 and degree of torsion in phalanx I-1, nevertheless, are good examples (Table 3, character 14). The basal width of metacarpal 1 changes in proportion to length by at least 25 per cent from subadult to adult, from a width considerably less than length to one that exceeds length (Text-fig. 10). Torsion in phalanx I-1 measures approximately 45 degrees in subadult *Massospondylus* (Text-fig. 9F) but apparently increases to 60 degrees in adults (Text-fig. 10B; Broom 1911; Cooper 1981). Sereno (1999*a*) and Yates (2003*a*) scored *Massospondylus* as derived (60 degrees or more). Yates (2003*a*) scored *Thecodontosaurus* as primitive (torsion of less than 50 degrees), although the degree of torsion so far has been described only as similar to that 'in all other prosauropods' (Benton *et al.* 2000, p. 92). Documenting the maturity of specimens and age-related variation may well be an important factor to consider for the many proportional characters in basal sauropodomorph data.

Although increased data documentation will constitute a significant improvement, other challenges rank as more important to achieve a measure of synthesis in phylogenetic resolution. We must attempt to compose morphological characters with more uniformity and then compare character data in more rigorous ways (Sereno, in manuscript). As outlined above, each major analysis of basal sauropodomorph relationships has assembled a unique dataset that is then analysed and compared *a posteriori* to the results obtained from previous datasets. Character comparisons were done selectively, rather than systematically. In this way, we understand the similarities and differences of results, but often have little idea regarding the underlying root causes. The datasets themselves must be compared. Root causes for differing phylogenetic results are few in number and include most importantly (1) character selection and (2) character scoring. As discussed above, there are striking differences in the characters used and how similar characters have been scored in different analyses. These differences can be logged and quantified with indices as intuitive as the consistency index is to better understand *a posteriori* results.

PHYLOGENETIC TAXONOMY

The phylogenetic definitions listed in Table 4 are summarized below. The aim is to provide heuristic definitions that are historically consistent and maximize stability of taxonomic content in the face of known phylogenetic uncertainty (Sereno 2005*a*). Further historical information regarding previous definitions and usage is available online (http://www.taxonsearch.org; Sereno 2005b, in manuscript).

Sauropodomorpha

Sauropodomorpha was coined as both a node- and stem-based group by Salgado *et al.* (1997) and Upchurch (1997), respectively. Sereno (1998) used a node-based definition, because it allowed the formation of a node-stem triplet for what was regarded as a basal split of Sauropodomorpha into Prosauropoda and Sauropoda (Galton 1989; Sereno 1989, 1997, 1999*a*, *b*). Support for this dichotomy, nevertheless, has been seriously eroded by the discovery of basal and derived genera that have relocated synapomorphies and increased homoplasy as outlined above. Given the phylogenetic uncertainty that currently exists, there is no sense in erecting a node-stem triplet at the base of Sauropodomorpha. The taxonomy of basal dinosaurs, in my opinion, is better served by adopting a stem-based definition of Sauropodomorpha as

TABLE 4. Phylogenetic definitions for basal Sauropodomorpha as recommended in this paper. For background, see Sereno (in manuscript; also http://www.taxonsearch.org).

Taxon	Phylogenetic definition	Definitional type
SAUROPODOMORPHA von Huene, 1932	The most inclusive clade containing *Saltasaurus loricatus* Bonaparte and Powell, 1980 but not *Passer domesticus* (Linnaeus, 1758), *Triceratops horridus* Marsh,1889*b*	stem
SAUROPODIFORMES Sereno, 2005b	The least inclusive clade containing *Mussaurus patagonicus* Bonaparte and Vince, 1979 and *Saltasaurus loricatus* Bonaparte and Powell, 1980	node
SAUROPODA Marsh, 1878	The most inclusive clade containing *Saltasaurus loricatus* Bonaparte and Powell, 1980 but not *Jingshanosaurus xinwaensis* Zhang and Yang, 1994, *Mussaurus patagonicus* Bonaparte and Vince, 1979	stem
EUSAUROPODA Upchurch, 1995	The most inclusive clade containing *Saltasaurus loricatus* Bonaparte and Powell, 1980 but not *Vulcanodon karibaensis* Raath, 1972	stem
PROSAUROPODA von Huene, 1920	The most inclusive clade containing *Plateosaurus engelhardti* Meyer, 1837, *Massospondylus carinatus* Owen, 1854, *Lufengosaurus hunei* Young, 1941, *Yunnanosaurus huangi* Young, 1942, and *Riojasaurus incertus* Bonaparte, 1969 but not *Saltasaurus loricatus* Bonaparte and Powell, 1980	stem
PLATEOSAURIA Tornier, 1913	The least inclusive clade containing *Massospondylus carinatus* Owen, 1854 and *Plateosaurus engelhardti* Meyer, 1837 but excluding *Saltasaurus loricatus* Bonaparte and Powell, 1980	node
PLATEOSAURIDAE Marsh, 1895	The most inclusive clade containing *Plateosaurus engelhardti* Meyer, 1837 but not *Massospondylus carinatus* Owen, 1854, *Saltasaurus loricatus* Bonaparte and Powell, 1980	stem
MASSOSPONDYLIDAE von Huene, 1914*b*	The most inclusive clade containing *Massospondylus carinatus* Owen, 1854 but not *Plateosaurus engelhardti* Meyer, 1837, *Saltasaurus loricatus* Bonaparte and Powell, 1980	stem

initially proposed by Upchurch (1997) and later modified by Upchurch *et al.* (2004). The definition recommended here, thus, is a first-order revision of that in Upchurch (1997) using more deeply nested specifiers (Table 4). In this way, the taxonomic content of the clade is stabilized under any arrangement of basal taxa.

Sauropodiformes

Description of the emerging phylogenetic pattern leading to Sauropoda would benefit by having an appropriate taxon name for a clade that unties basal sauropodomorphs more advanced than ‘core prosauropods’ but less advanced than taxa that might be regarded as basal sauropods. *Mussaurus patagonicus* and *Jingshanosaurus xinwaensis* are known from very complete material including skulls and share several significant synapomorphies with sauropods (Casamiquela 1980; Zhang and Yang 1994; Pol 2004; Pol and Powell 2005). They are destined to become two of the better-known advanced basal sauropodomorphs. Sauropodiformes Sereno, 2005*b* (‘in the form of a sauropod’) therefore has been proposed as a node-based taxon anchored by definition to *Mussaurus patagonicus*, *Jingshanosaurus xinwaensis* and the derived sauropod *Saltasaurus loricatus*. A node-based Sauropodiformes is more useful as an anchor outside Sauropoda than a stem-based definition, which for stability would require citation of a broad range of basal sauropodomorphs as external specifiers.

Sauropoda

Sauropoda was initially defined as both node- and stem-based by Salgado *et al.* (1997) and McIntosh (1997), respectively. The node-based definition focused on the basal sauropod *Vulcanodon*. The stem-based definition was initially constructed when at least ‘core prosauropods’ were regarded as monophyletic. A stem-based Sauropoda has been adopted by several subsequent authors (e.g. Sereno 1998; Wilson and Sereno 1998; Upchurch *et al.* 2004) but should be retooled to exclude the most derived of basal sauropodomorphs. Otherwise, as Yates and others have observed, Sauropoda will incorporate many taxa formerly considered prosauropods, a marked departure from its traditional taxonomic content. The active definition, thus, is a first-order revision of the stem-based definition of McIntosh (1997), Wilson and Sereno (1998) and Sereno (1998). Two external specifiers were selected (*Mussaurus patagonicus*, *Jingshanosaurus xinwaensis*) for their completeness and efficacy in limiting the taxonomic content of Sauropoda to a less inclusive clade than Sauropodiformes.

Prosauropoda, Plateosauria, Plateosauridae and Massospondylidae

The definition recommended here for Prosauropoda, a first-order revision of the original definition (Upchurch 1997), includes five species viewed as 'core prosauropods' as internal specifiers and *Saltasaurus loricatus* as an external specifier. Should 'core prosauropods' prove to be paraphyletic, the taxon Prosauropoda would not be applicable. Other taxa, such as Plateosauria, Plateosauridae and Massospondylidae (Table 4), are available for less inclusive clades that include the well-known genera *Plateosaurus* and *Massospondylus*. Although the content of these clades would not be particularly stable in some current analyses, the definitions are an attempt to provide a useful taxonomic framework based on pre-existing taxa that is anchored upon well-known species.

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NOTE ADDED IN PROOF

Yates (2006) has recently published another analysis of basal sauropodomorphs based on 353 characters in 41 ingroup taxa, 19 of which are traditional basal (non-sauropod) sauropodomorphs. How these character data differ from those in previous analyses (Yates 2003*a*, 2004; Yates and Kitching 2003; Text-fig. 2B–C) is not indicated, although the results exhibit significant differences. *Yunnanosaurus* is positioned closer to sauropods than other core prosauropods, unlike the most parsimonious hypothesis in Yates (2003*a*), and *Plateosaurus* and *Riojasaurus* are positioned basal to many other core prosauropods, unlike the shortest trees in Yates and Kitching (2003) and Yates (2004).

Two new suprageneric taxa of questionable utility were coined and defined. Riojasauridae was erected to include *Riojasaurus incertus* and *Eucnemasaurus fortis*, a new genus and species based on fragmentary postcranial bones; Massopoda was erected for all basal sauropodomorphs that are closer to sauropods than to *Plateosaurus engelhardti*. Plateosauria was used without any qualifying conditions, unlike the present recommendation (Table 4; Sereno *et al.* 2005); as a result many taxa including Sauropoda are subsumed, and the taxon bears little resemblance to its historical usage (Text-fig. 1A). Finally, Sauropoda was redefined using *Melanorosaurus readi* as an external specifier rather than *Jingshanosaurus xinwaensis* and *Mussaurus patagonicus* (Sereno *et al.* 2005; Table 4). Although a reasonable alternative definition, the positioning of *Melanorosaurus readi* may depend in good measure on the status of newly referred material.

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