The skull of *Yunnanosaurus huangi* Young, 1942 (Dinosauria: Prosauropoda) from the Lower Lufeng Formation (Lower Jurassic) of Yunnan, China

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The Lower Lufeng Formation (Lower Jurassic: ?Hettangian–?Sinemurian) of Yunnan Province, China, has yielded an important and diverse fauna of terrestrial vertebrates that is dominated by early sauropodomorph dinosaurs (prosauropods and basal sauropods). Nevertheless, few of these animals have been studied in detail, undermining their potential significance in understanding sauropodomorph phylogeny, palaeobiology, and palaeoecology. Here, we present a detailed re-description of the cranial osteology of *Yunnanosaurus huangi* Young, 1942 and propose an emended diagnosis for this taxon on the basis of numerous autapomorphic characters (including an expanded internarial bar, unusual midline cranial bosses, and the possession of elongate maxillary tooth crowns lacking marginal serrations). Incorporation of these novel anatomical data into existing phylogenetic analyses of sauropodomorph interrelationships substantially affects the resolution, length, and topologies of the trees recovered. Although the phylogenetic position of *Yunnanosaurus* remains labile, these new analyses undermine previous suggestions that the former was the sister taxon of the southern African prosauropod *Massospondylus*. Several features of the skull of *Yunnanosaurus* (small external nares, cranial bosses, tooth crown morphology, and the lack of maxillary foramina) indicate that the palaeobiology of *Yunnanosaurus* may have been rather different from that of other prosauropods and basal sauropods, although more detailed functional studies and better material are needed to confirm this suggestion.   © 2007 Natural History Museum, London. Journal compilation © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, **150**, 319–341.

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INTRODUCTION

Late Triassic and Early Jurassic terrestrial biomes hosted a diverse array of sauropodomorph dinosaurs, including basal sauropods (e.g. *Isanosaurus* and *Vulcanodon*), prosauropods (e.g. *Plateosaurus* and *Lufengosaurus*), and basal forms that lie outside of the prosauropod/sauropod clade (e.g. *Saturnalia* and *Thecodontosaurus*). Sauropodomorphs were the dominant large animals in these ecosystems, accounting for up to 95% of the standing vertebrate biomass (Galton, 1985a, 1986), and achieved a global distribution (with the exception of Australia; Weishampel *et al.*, 2004).

Recent reviews of the group recognize around 30 provisionally valid taxa in the Late Triassic–Early Jurassic interval (e.g. Galton & Upchurch, 2004; Upchurch, Barrett & Dodson, 2004). Early sauropodomorphs ranged in size from small bipeds (1.5–2 m in length, e.g. *Thecodontosaurus*) to large quadrupeds (10–14 m in length, e.g. *Riojasaurus* and *Gongxianosaurus*). Some taxa were probably omnivorous (Barrett, 2000), whereas others were obligate high-fibre herbivores representing the first major radiation of herbivorous dinosaurs (Bakker, 1978; Galton, 1985a, 1986; Crompton & Attridge, 1986; Barrett & Upchurch, 2007). Several species (e.g. *Plateosaurus*, *Massospondylus*, and *Thecodontosaurus*) are known from multiple specimens, including complete skulls and skeletons, and

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material is often well preserved and locally abundant (Galton & Upchurch, 2004).

Although it is generally accepted that prosauropods and Sauropoda constitute the monophyletic clade Sauropodomorpha (e.g. Gauthier, 1986; Sereno, 1999), the interrelationships of prosauropods and basal sauropods are controversial. Pre-cladistic studies generally concluded that at least some prosauropods were ancestral to sauropods, with the latter exhibiting trends towards increased body size, quadrupedality, and neck elongation (e.g. Romer, 1956; Charig, Attridge & Crompton, 1965). Prosauropod paraphyly was supported by the first cladistic analysis of the group (Gauthier, 1986), but since that time various authors have argued that prosauropods form the monophyletic sister group of sauropods (e.g. Galton, 1990; Gauffre, 1993; Sereno, 1999). Recent discoveries of new Late Triassic sauropodomorph taxa, including the early sauropod *Isanosaurus* (Buffetaut *et al*., 2000) and the basal sauropodomorph *Saturnalia* (Langer *et al*., 1999), have contributed significantly to this debate. Re-interpretations of previously described taxa, including the recognition that at least some 'prosauropods' are probably early sauropods (e.g. *Anchisaurus*, *Antetonitrus*, and *Blikanasaurus*), have also had a major effect on our understanding of character evolution in the group, and on the topology of sauropodomorph cladograms (Benton *et al*., 2000; Yates, 2003a, 2004; Yates & Kitching, 2003; Galton & Upchurch, 2004; Upchurch, Barrett & Galton, 2007; Yates 2007). Nevertheless, controversy still surrounds the precise interrelationships of many basal sauropodomorph taxa: some authors suggest that the majority of prosauropods form a pectinate array of taxa with respect to sauropods (e.g. Yates, 2003a, 2004; Yates & Kitching, 2003; Yates 2007), whereas others place most prosauropods within a monophyletic clade (e.g. Benton *et al*., 2000; Galton & Upchurch, 2004; Upchurch *et al*., 2007). Part of this conflict stems from the fact that many basal sauropodomorph taxa are known from incomplete material or have not yet been fully described.

One such taxon is *Yunnanosaurus huangi* Young, 1942 from the Lower Lufeng Formation (Lower Jurassic) of Yunnan, south-western China. Although the holotype of *Y. huangi* consists of an almost complete skull and postcranial skeleton, it has not been studied in detail since the initial, rather brief, description was published over 60 years ago. Nevertheless, *Yunnanosaurus* has been discussed in a number of taxonomic and systematic publications during this interval, although few authors have had the opportunity to examine the material first-hand. Rozhdestvensky (1965) regarded *Yunnanosaurus* as a junior subjective synonym of *Lufengosaurus huenei* Young, 1941, a second basal sauropodomorph from the Lower Lufeng

Formation (a conclusion followed by Galton, 1976), whereas Cooper (1981) proposed that *Yunnanosaurus* was synonymous with *Massospondylus*, a prosauropod from the Lower Jurassic of southern Africa. In contrast, most other authors have retained *Yunnanosaurus* as a distinct taxon (Steel, 1970; Galton, 1990; Galton & Upchurch, 2004; Barrett, Upchurch & Wang, 2005). *Yunnanosaurus* has been included in several cladistic analyses of sauropodomorph interrelationships (Sereno, 1999; Yates, 2003a; Galton & Upchurch, 2004; Upchurch *et al*., 2007; Yates, 2007), but was omitted from the analysis of Benton *et al*. (2000) because these authors questioned the validity of the genus. Here, we present a detailed re-description of the skull of *Y. huangi* and use these new anatomical data to address the phylogenetic position of the taxon.

A list of institutional abbreviations is given in Appendix 1, and a list of abbreviations used in the figures is given in Appendix 2.

SYSTEMATIC PALAEONTOLOGY

DINOSAURIA OWEN, 1842
SAURISCHIA SEELEY, 1887
SAUROPODOMORPHA VON HUENE, 1932
PROSAUROPODA VON HUENE, 1920
YUNNANOSAURUS YOUNG, 1942
TYPE SPECIES. *YUNNANOSAURUS HUANGI*
YOUNG (1942)

Emended diagnosis: As for type species (see below).

Distribution: Dark Red Beds of the Lower Lufeng Formation (Lower Jurassic), Lufeng County, Yunnan Province, China.

Comments: Young (1951) erected a second species, *Yunnanosaurus robustus*, based on a partial skeleton including cranial remains (IVPP V94). Although Steel (1970) regarded *Y. huangi* and *Y. robustus* as separate valid species, most authors have regarded the latter as either a junior subjective synonym of *Y. huangi* (e.g. Galton, 1990; Galton & Upchurch, 2004) or *L. huenei* (e.g. Rozhdestvensky, 1965). In order to stabilize the genus, we base our diagnosis of *Yunnanosaurus* on the type species only. The validity of *Y. robustus* and its referral to *Yunnanosaurus* will be addressed elsewhere.

YUNNANOSAURUS HUANGI YOUNG, 1942

1942 *Y. huangi* (Young, 1942: 64, figs 1–17).
1965 *L. huenei* Young, 1941 (Rozhdestvensky, 1965: 103).
1970 *Y. huangi* (Steel, 1970: 52).
1981 *Massospondylus huenei*, Young, 1941 (Cooper, 1981: 804).
1990 *Y. huangi* (Galton, 1990: 335).

2004   *Y. huangi* (Galton & Upchurch, 2004: 236).

Holotype: NGMJ 004546, an almost complete skeleton consisting of the following: the skull, atlas, and axis; three other cervical vertebrae; nine dorsal vertebrate and dorsal rib fragments; sacrum; eight caudal vertebrae and six haemal arches; left scapula; sternum; right and left humeri; right ulna; partial left manus; right and left ilia, pubes, and ischia; right and left femora, tibiae, fibulae, astragali, and calcanea; and two metatarsals.

Locality and horizon: Huangchiatien village, Lufeng County, Yunnan Province, China. Dark Red Beds of the Lower Lufeng Formation, Lower Jurassic (Sinemurian: Luo & Wu, 1994, 1995).

Emended diagnosis (cranial features only): Small external naris (~10% of maximum skull length); robust, rostrocaudally expanded nasal process of the premaxilla; presence of a ventral projection from the caudal margin of ascending maxillary process; lack of nutritive foramina on lateral surface of maxilla; shallow, subcircular fossa present on lateral surface of ventral lachrymal process; presence of a midline boss near to the rostral end of the frontals; prominent midline boss present on the parietals; rostrolateral process of the parietal rostrocaudally expanded relative to the width of the caudolateral process; maxillary teeth are mesiodistally narrow and lack denticles.

Comments: Young (1942) designated this specimen with the catalogue number V20. This number was later changed to NGMJ V0116 (as indicated on the label within the display case), but the correct accession number is now NGMJ 004546. The postcranial skeleton of *Yunnanosaurus* will be described elsewhere.

The original diagnosis of *Y. huangi* incorporated a large number of cranial characteristics (Young, 1942: 64–65; see also Young, 1951: 56): skull elongate, with width to length ratio of 3.8; skull equivalent in length to four anterior caudal vertebrae; external nostril small; antorbital fenestra large; orbit circular and largest skull opening; supratemporal fenestra 'bean-shaped' in dorsal view and partly visible in lateral view (i.e. the upper temporal bar is ventrally displaced with respect to the skull roof); lower jaw slender; small external mandibular fenestra; 15 maxillary and 13 dentary teeth; teeth slender, rounded, and pointed; teeth generally lacking denticles. Some of these characters do appear to be unique to *Yunnanosaurus* and have been modified for inclusion in the emended diagnosis given above (e.g. tooth morphology). However, many of the other features listed do not differ substantially from those seen in other basal sauropodomorphs (e.g. tooth counts, orbit size, and shape, ventral deflection of the upper temporal bar and size of the external mandibular fenestra) and cannot be regarded as diagnostic for *Yunnanosaurus* (see below for further details).

DESCRIPTION & COMPARISON

GENERAL COMMENTS

The following description extends and augments that provided by Young (1942). Comparisons are provided with those animals traditionally regarded as 'prosauropods' (e.g. Galton & Upchurch, 2004), although we note that some of these taxa may either represent basal sauropods (e.g. *Anchisaurus*; Yates, 2004) or basal taxa that lie outside a prosauropod/sauropod clade (e.g. *Thecodontosaurus*; see Yates & Kitching, 2003; Yates, 2003a). Sources of comparative data (both published and from personal observations) are listed in Table 1.

Table 1. Sources of comparative data used in this study. Accession numbers denote those specimens examined by the authors first-hand: other data were gathered from the literature. Species taxonomy of the Upper Triassic German prosauropods follows Yates (2003b)

Taxon	Source(s)
Anchisaurus polyzelus	YPM 1883; Galton (1976); Yates (2004).
Coloradisaurus brevis	Bonaparte (1978).
Efraasia minor	Galton (1985c); Galton & Bakker (1985); Yates (2003b).
Jingshanosaurus xinwaensis	Zhang & Yang (1994).
Lufengosaurus huenei	IVPP V15; Young (1941); Barrett *et al*. (2005).
Massospondylus carinatus	BP/1/4376; BP/1/4779; BP/1/4934; BP/1/5241; SAM-PK-K1314; Gow (1990); Gow, Kitching & Raath, (1990); Sues *et al*. (2004).
Mussaurus patagonicus	Bonaparte & Vince (1979).
Plateosaurus spp.	AMNH 6810; MB XXIV; Galton (1984, 1985b); Yates (2003b).
Riojasaurus incertus	ULR 56; Bonaparte & Pumares (1995).
Thecodontosaurus caducus	BMNH RU P24; Kermack (1984); Yates (2003a).
Unaysaurus tolentinoi	Leal *et al*. (2004).

The skull is three-dimensionally preserved and many elements of the skull roof and suspensorium are preserved in life position (Figs 1–6). The skull has been crushed transversely, particularly in its rostral part, resulting in some dislocation of the cheek elements on both sides and extensive damage to the palate. Many small cracks are present on the bone surfaces, which may have been caused by surface weathering. Ventral surfaces of the skull roof bones are not visible because of the presence of matrix and plaster. The left-hand side of the skull is not as well preserved, or as fully prepared, as the right-hand side: the left lachrymal and jugal are missing and the left postorbital, squamosal, quadrate, and quadratojugal are all damaged to some extent. Comparison with the original figure of the skull in left lateral view (Young, 1942: fig. 1) indicates that at least some of this damage occurred subsequent to Young's description. Both lower jaws are present and substantially complete, but they are closely adhered to the rest of the skull and their medial surfaces, and those of the tooth-bearing and other suspensorial bones, are partially obscured as a consequence. The atlas-axis complex is also preserved in articulation with the rear of the skull, almost completely obscuring the ventral part of the occiput. The palate is not visible in ventral view because of the presence of the lower jaws and matrix, but sections can be observed through the orbit and lower temporal fenestra. Nevertheless, those portions of the palate that are accessible are crushed and difficult to interpret. Although substantially complete, the individual skull elements are rather poorly preserved and it is often difficult to identify individual sutures. Most of the braincase is also obscured by matrix and crushing.

In lateral view, the skull is low, elongate, and subtrapezoidal in outline (Figs 1–3). It is more than twice as long (as measured from the tip of the snout to the caudal margin of the distal quadrate) as it is high (as measured from the dorsal margin of the parietals to the base of the quadrate). The region of the skull roof dorsal and caudal to the orbit lies in an approximately horizontal plane, but rostral to the orbit the snout slopes gradually ventrally to its termination. In dorsal view, the skull is triangular, and tapers gradually from its widest point, at the occiput, to the tip of the snout (Fig. 4). The snout is extremely narrow transversely, a feature that has been accentuated by crushing. Although Young (1942) suggested that the elongate skull, with a width : length ratio of 3.8 was diagnostic, similar values are also obtained for skulls of *Plateosaurus*, *Massospondylus* and *Riojasaurus*.

The cranial openings are relatively large, giving the skull an open appearance (Figs 1–3). The supratemporal fenestrae are approximately kidney-shaped in dorsal view and are bordered by the parietal (rostrally, medially and caudomedially), squamosal (caudolaterally), and postorbital (laterally). At least one specimen of *Massospondylus* (BP/1/5241) has supratemporal fenestrae with a similar outline, and in both the latter and *Yunnanosaurus* this appears to have been accentuated by deformation and medial bowing of the upper temporal bar. Consequently, it is unlikely to be a useful diagnostic character for *Yunnanosaurus* (*contra* Young, 1942). The supratemporal fenestrae are visible in lateral view, as the upper temporal bar is positioned ventrally with respect to the postorbital/skull roof contact (Figs 1–3): a similar condition also occurs in *Massospondylus*, *Mussaurus*, and *Thecodontosaurus*. In lateral view, the infratemporal fenestra has an irregular quadrilateral outline (visible on the right-hand side only). The infratemporal fenestra is bounded by the postorbital (rostrodorsally), jugal (rostroventrally), quadratojugal (caudoventrally), and squamosal (caudodorsally). The rostroventral corner of the infratemporal fenestra extends beneath the orbit for a short distance, but does not reach orbital mid-length.

The orbit is the largest opening in the skull (as in all other early sauropodomorphs) with a diameter equivalent to ~30% of the total skull length. It has a subcircular outline and is bounded by the postorbital, jugal, lachrymal, frontal, and prefrontal. Although the ascending process of the right maxilla and the left lachrymal are missing, it is possible to use the remaining skull elements to determine the outline and boundaries of the antorbital fossa. The antorbital fossa is subtriangular in outline, with an almost horizontal ventral margin formed by the maxilla, a rostrodorsally orientated caudal margin formed by the lachrymal, and a caudodorsally extending rostral margin composed of the ascending process of the maxilla. It is possible that the nasal made a small contribution to the dorsal part of the fossa, but poor preservation does not permit confirmation or refutation of this suggestion. Young (1942) suggested that the large size of the fossa (reaching ~18% of the total skull length) may be diagnostic for the genus, but the majority of basal sauropodomorphs have relatively larger antorbital fossae (e.g. *Massospondylus*, 19–21%; *Plateosaurus*, 25–27%; *Riojasaurus*, 24%): smaller fossae are found only in *Mussaurus* (~16%) and *Anchisaurus* (~13%). The external nares were small, with a maximum rostrocaudal length equivalent to only ~10% of the total skull length (measured on the right-hand side of the skull): the small size appears to be a genuine feature, as the rostral part of the snout has not been affected by significant dorsoventral compression (*contra* Young, 1942). The right external naris is approximately teardrop-shaped in lateral view. In the majority of other early sauropodomorphs (*Massospondylus*, *Plateosaurus*, *Mussaurus*, *Riojasaurus*, *Coloradisaurus*, and *Jingshanosaurus*), the external nares are
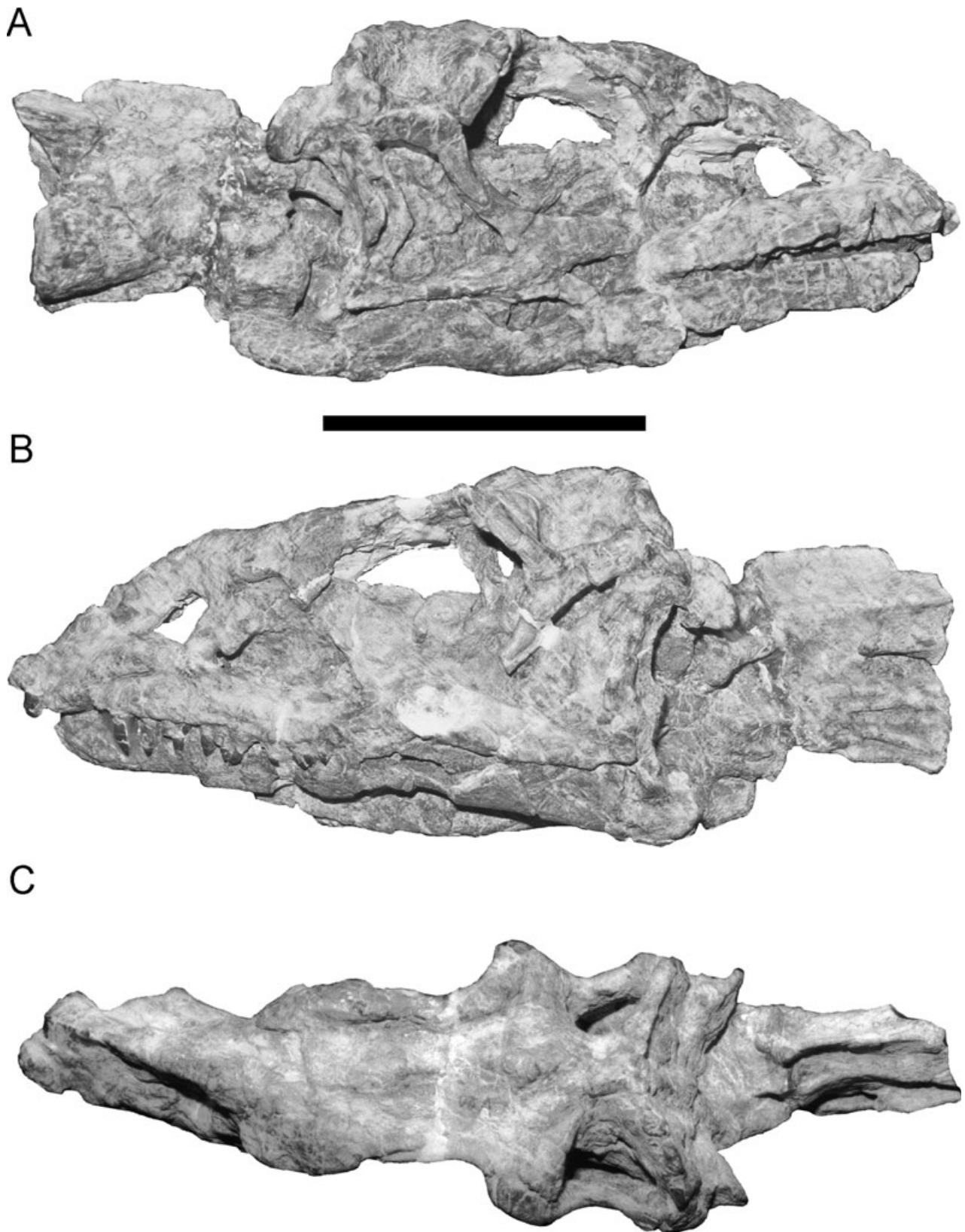
Figure 1. Skull and atlas-axis complex of *Yunnanosaurus huangi* (NGMJ 004546). A, right lateral view. B, left lateral view. C, dorsal view. Scale bar equals 100 mm.
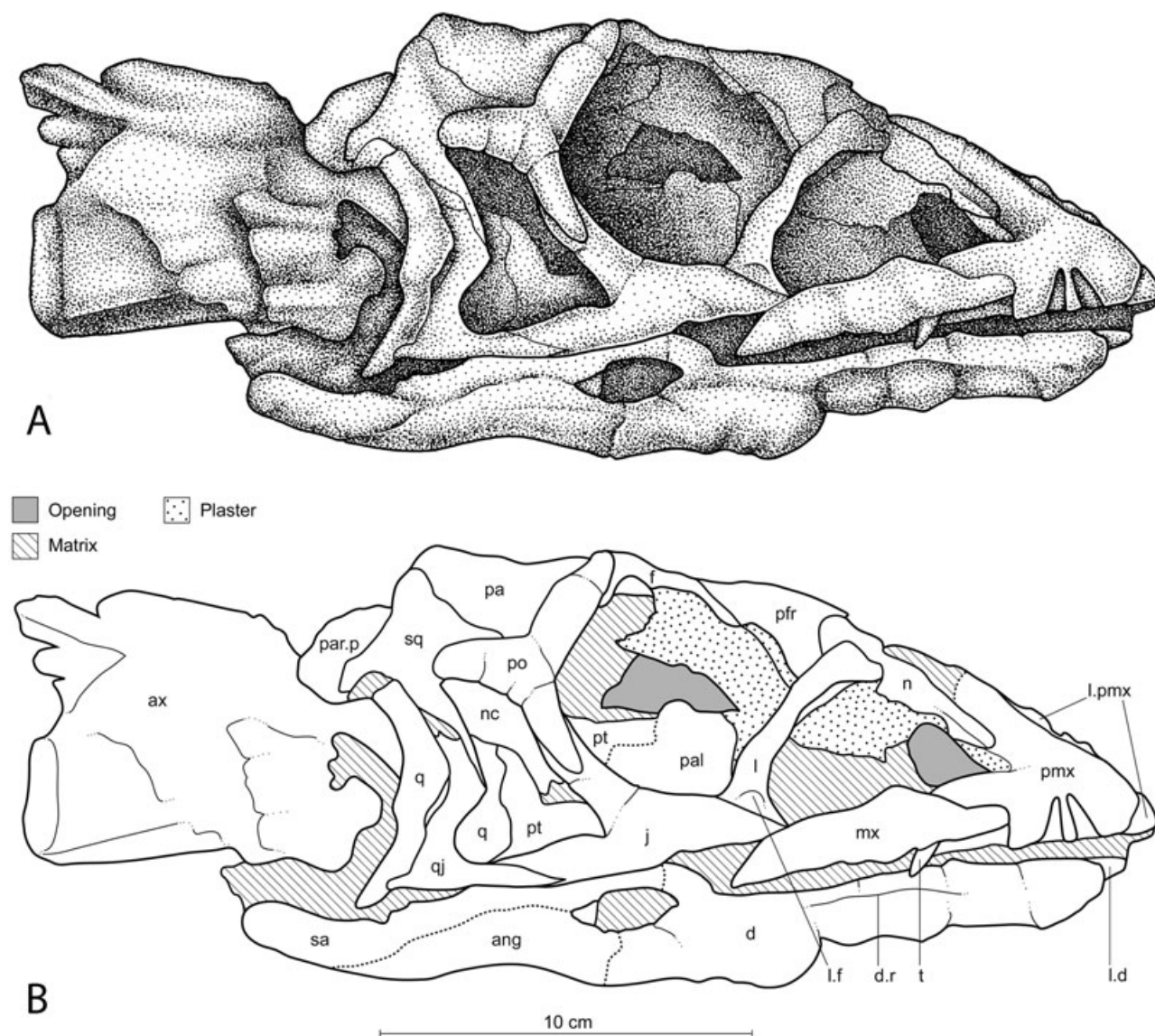
Figure 2. Skull and atlas-axis complex of *Yunnanosaurus huangi* (NGMJ 004546) in right lateral view. A, drawing of skull as preserved. B, interpretative line drawing of the skull showing damaged areas, reconstruction, and areas obscured by matrix. See Appendix 2 for abbreviations.

relatively larger, with diameters that range from 14 to 18% of the total skull length. A recent reconstruction of *Thecodontosaurus caducus* indicates that this taxon may have had a small external naris, the maximum diameter of which reached ~11% of the total skull length; however, as no articulated snout is known for *Thecodontosaurus* this figure should be viewed with caution. Moreover, a growth series of *Massospondylus* indicates that relative external narial diameter increases through ontogeny (from 14 to 17% of the skull length), so the small nostril of *T. caducus* may reflect the juvenile status of the holotype material (Kermack, 1984; Yates, 2003a). As the holotype of *Y. huangi* is from a large, presumably subadult or

adult individual (as evidenced by the lack of open sutures/articulations between many cranial elements; see below), we regard the very small external naris as a provisional autapomorphy of this taxon.

DERMAL SKULL AND PALATAL COMPLEX

Premaxilla
The lateral surfaces are extensively cracked, making interpretation of some areas difficult. The midline junction between the premaxillae is acute and sharp, but this may have been exaggerated by transverse crushing of the snout.

The premaxilla consists of a robust, rostrocaudally short, tooth-bearing main body and an elongate nar-
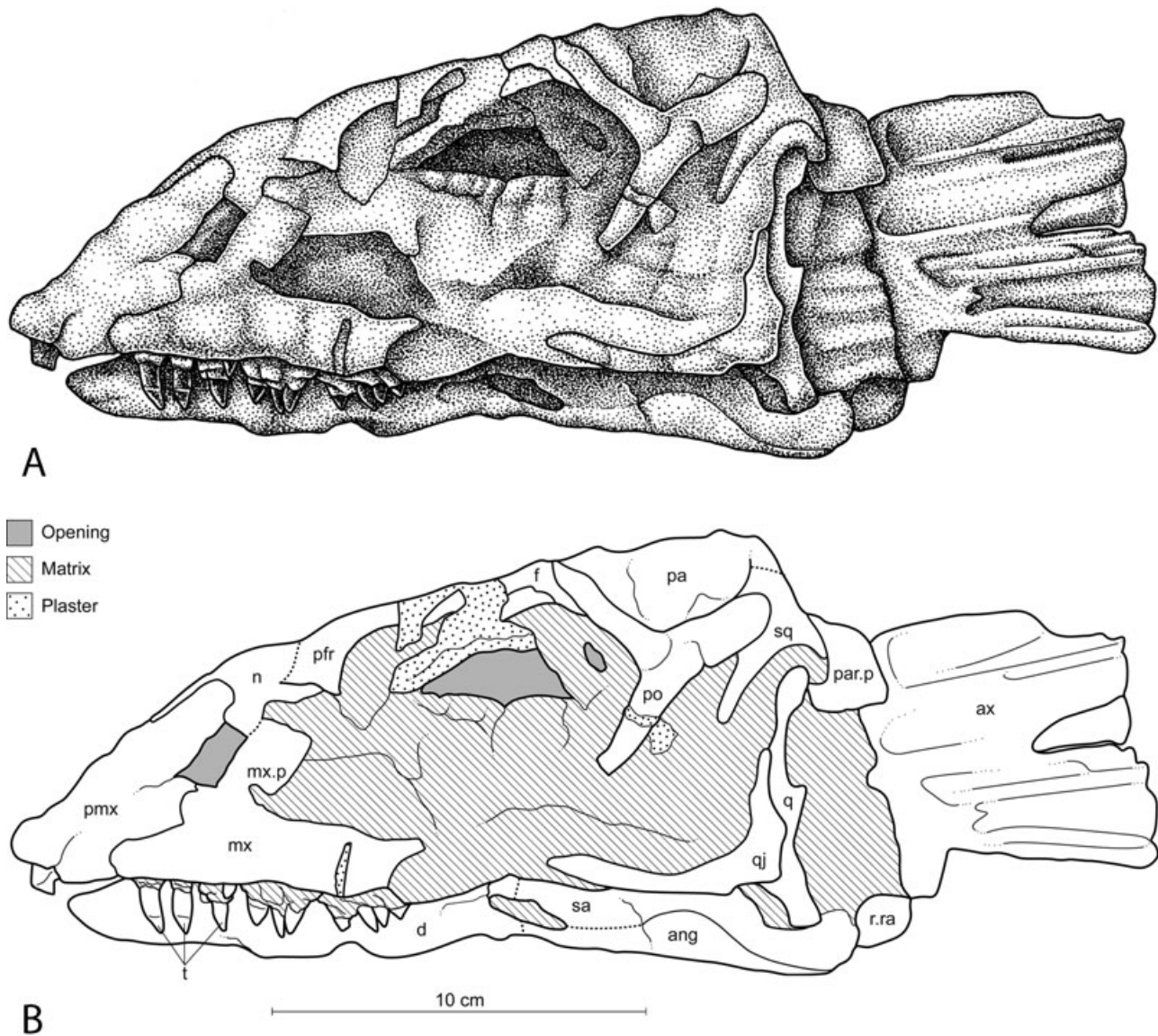
Figure 3. Skull and atlas-axis complex of *Yunnanosaurus huangi* (NGMJ 004546) in left lateral view. A, drawing of skull as preserved. B, interpretative line drawing of the skull showing damaged areas, reconstruction, and areas obscured by matrix. See Appendix 2 for abbreviations.

ial process. The lateral surface of the main body is dorsoventrally convex and slightly convex rostrocaudally. It is not possible to determine the number of tooth positions, as the ventral borders of both premaxillae are broken and partially obscured by matrix, although it seems likely that either three or four teeth were present (Young, 1942). No nutrient foramina can be identified on the lateral surface. The ventral margin of the premaxillary main body is level with that of the maxilla. A stout maxillary process extends caudally from the caudodorsal part of the main body to overlap the rostrodorsal part of the maxilla, although it does not extend to the level of

the maxillary ascending process, caudally. The maxillary process is relatively deep dorsoventrally and does not taper significantly towards its distal termination, giving its tip a blunt, almost square-ended appearance (Figs 1–3). Rostrodorsally, the surface of the main premaxillary body bears a shallow excavation (immediately caudal to the base of the narial process), which forms part of a shallow external narial fossa. The dorsal surface of the premaxilla forms approximately 50% of the ventral margin of the external naris.

The narial process extends caudodorsally, at an angle of approximately 45° to the main premaxillary
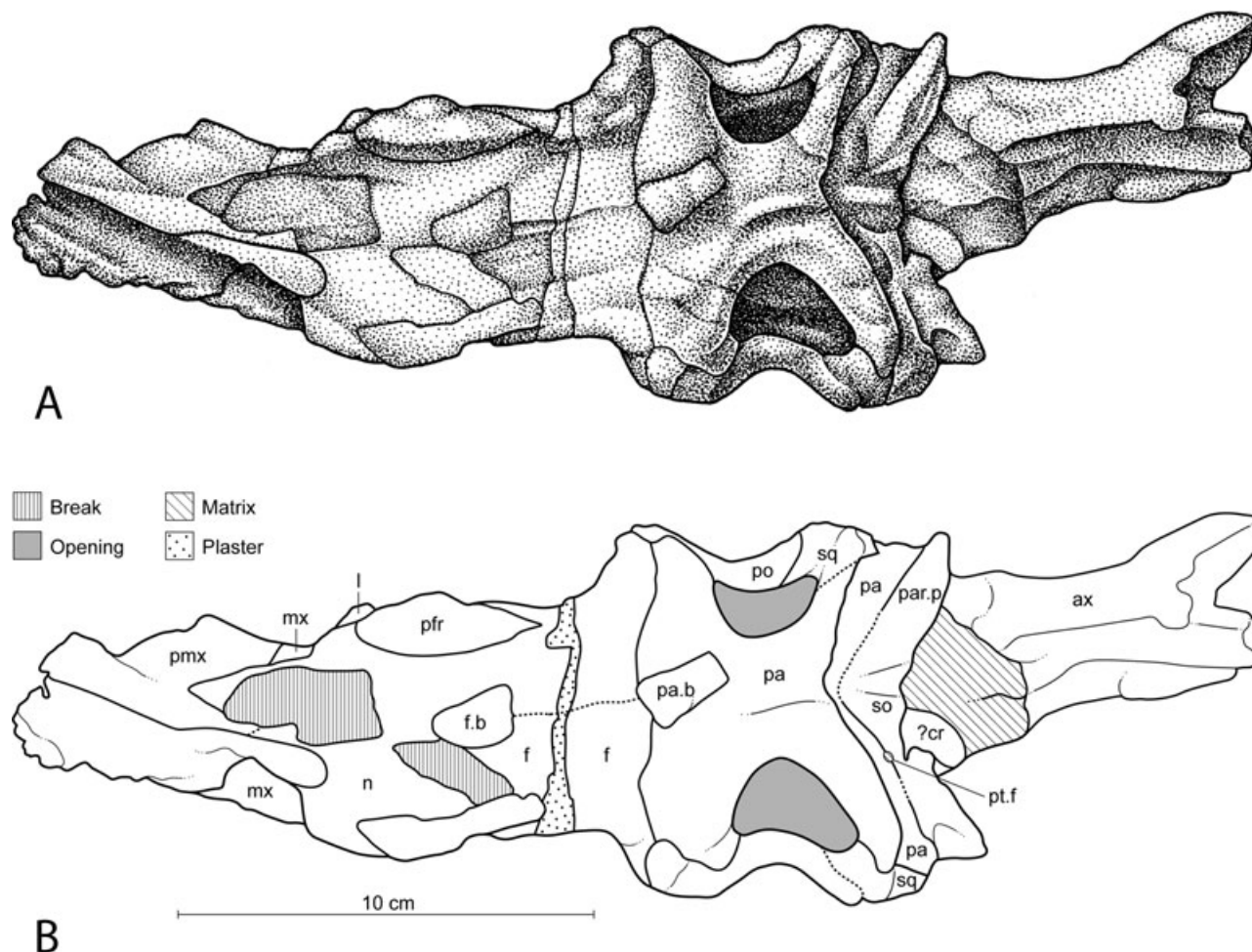
Figure 4. Skull and atlas-axis complex of *Yunnanosaurus huangi* (NGMJ 004546) in dorsal view. A, drawing of skull as preserved. B, interpretative line drawing of the skull showing damaged areas, reconstruction, and areas obscured by matrix. See Appendix 2 for abbreviations.

body. Its ventral surface forms the rostrodorsal margin of the external naris. The base of the narial process is rostrocaudally expanded: this expansion is maintained along almost the entire length of the process, which terminates dorsally in a broadly rounded apex. This apex is clasped between the medial and rostrolateral processes of the nasal. The rostrocaudal expansion of the narial process is largely responsible for the robust nature of the internarial bar and the small size of the external naris (Fig. 3). An expanded internarial bar appears to be autapomorphic for *Yunnanosaurus*: the narial process is much more gracile in other early sauropodomorphs, where appropriate material is known, including *Efraasia*, *Massospondylus*, *Plateosaurus*, *Unaysaurus*, and *Coloradisaurus*.

Young (1942: 72, fig. 1) suggested that the premaxilla formed most of the rostral external narial margin: however, his figure of the right-hand side of the skull (ibid. fig. 2) shows the nasal forming the majority of

the internarial bar. The former interpretation is confirmed herein. *Yunnanosaurus* appears to lack the subnarial foramen that is present in *Efraasia*, *Massospondylus*, and some individuals of *Plateosaurus*.

Maxilla

The maxilla consists of two main portions – a horizontally directed tooth-bearing ramus and a caudodorsally directed ascending process (although the latter has been broken in the left maxilla; Fig. 3). Laterally, the surface of the maxilla is smoothly convex dorsoventrally and almost straight rostrocaudally. No nutritive foramina appear to be present on the lateral surface of the maxilla: this is a potential autapomorphy of *Yunnanosaurus*, as the majority of other basal sauropodomorphs [*Plateosaurus*, *Massospondylus*, *Lufengosaurus*, *Riojasaurus*, *Unaysaurus*, *Thecodontosaurus*, *Anchisaurus* (P. M. Galton, pers.
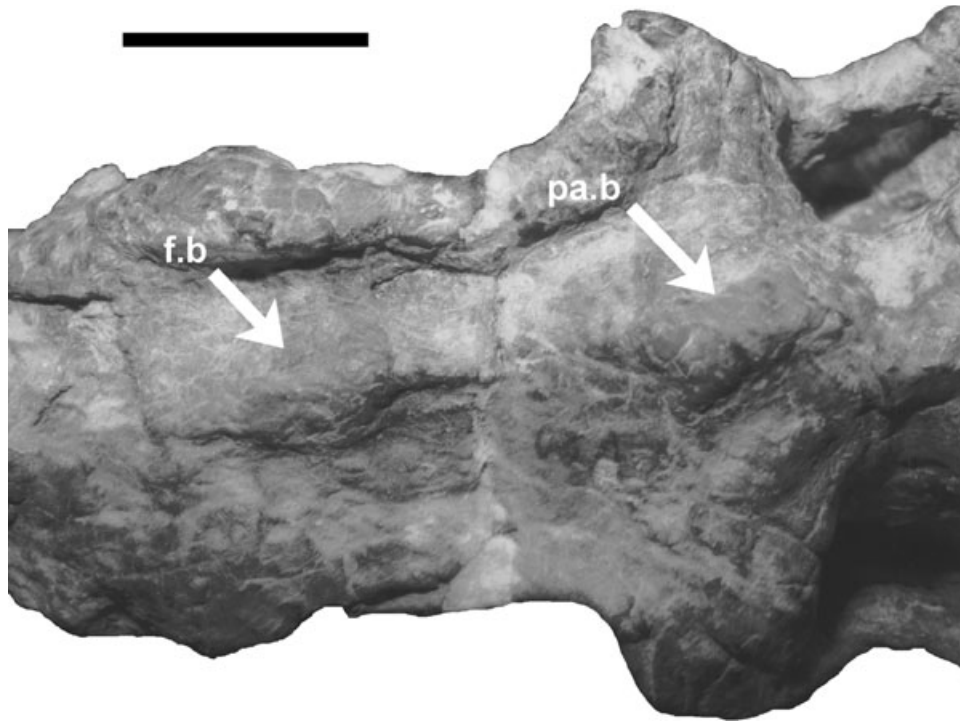
Figure 5. Skull roof of *Yunnanosaurus huangi* (NGMJ 004546) in dorsal view showing frontal and parietal bosses (arrowed). Scale bar equals 30 mm. The cranial end of the snout is to the right. See Appendix 2 for abbreviations.

comm., 2005), and *Efraasia*] possess these features. There is no evidence of a lateral maxillary ridge, thus differing from the condition present in *Lufengosaurus*. From the rostral end of the maxilla, the dorsoventral height of the element initially increases caudally, reaching its maximum at the level of the ascending process, but then decreases gradually so that the bone tapers to a narrow point at its caudal end. Although most of the medial surfaces of the maxillae are obscured, it is possible to determine that the height of the medial alveolar border was approximately equal to that of the lateral border, indicating that a 'lateral plate' (cf. Upchurch, 1995) was absent. There is some evidence of small rhomboidal interdental plates on the medial surface of the right maxilla. The dorsal surface of the maxilla, immediately rostral to the base of the ascending process, forms approximately half of the ventral margin of the external naris.

The ascending process arises from a point approximately one-third of the way from the rostral end of the bone (Fig. 3). It forms most of the caudal margin of the external naris and the rostral margin of the antorbital fossa. This process is stout and subelliptical in transverse cross section. Its caudal margin forms an angle of 60° with the tooth-bearing ramus of the maxilla. The apex of the right ascending process is either missing or encrusted by matrix:

there is an extensive contact with the nasal rostro-dorsally, but poor preservation of the specimen prevents determination of other articular relationships in this area (see below). The caudal margin of the ascending process gives rise to a stout ventrally directed projection, which extends into the antorbital fossa (Fig. 3). This feature is not seen in any other early sauropodomorph for which appropriate material is known (*Plateosaurus*, *Efraasia*, *Mussaurus*, *Coloradisaurus*, *Unaysaurus*, *Lufengosaurus*, *Massospondylus*, and *Jingshanosaurus*), and we consider this to be an autapomorphy of *Yunnanosaurus*. Neither the caudal margin of the ascending process nor the dorsal margin of the tooth-bearing ramus gives rise to a 'medial lamina': consequently, the antorbital fossa was not backed by a sheet of bone, and was open medially, as also occurs in *Jingshanosaurus* and *Mussaurus*. The 'lateral lamina' found in some other prosauropods (e.g. *Plateosaurus* and *Lufengosaurus*) is also absent, as in *Jingshanosaurus*, *Anchisaurus*, and *Thecodontosaurus*.

It is difficult to determine the exact number of maxillary tooth positions because of the poor preservation of the tooth rows. Only two teeth are preserved *in situ* on the right-hand side of the skull, whereas ten teeth are preserved on the left-hand side together with several emergent replacement tooth crowns. A conservative estimate suggests that there were 15 tooth
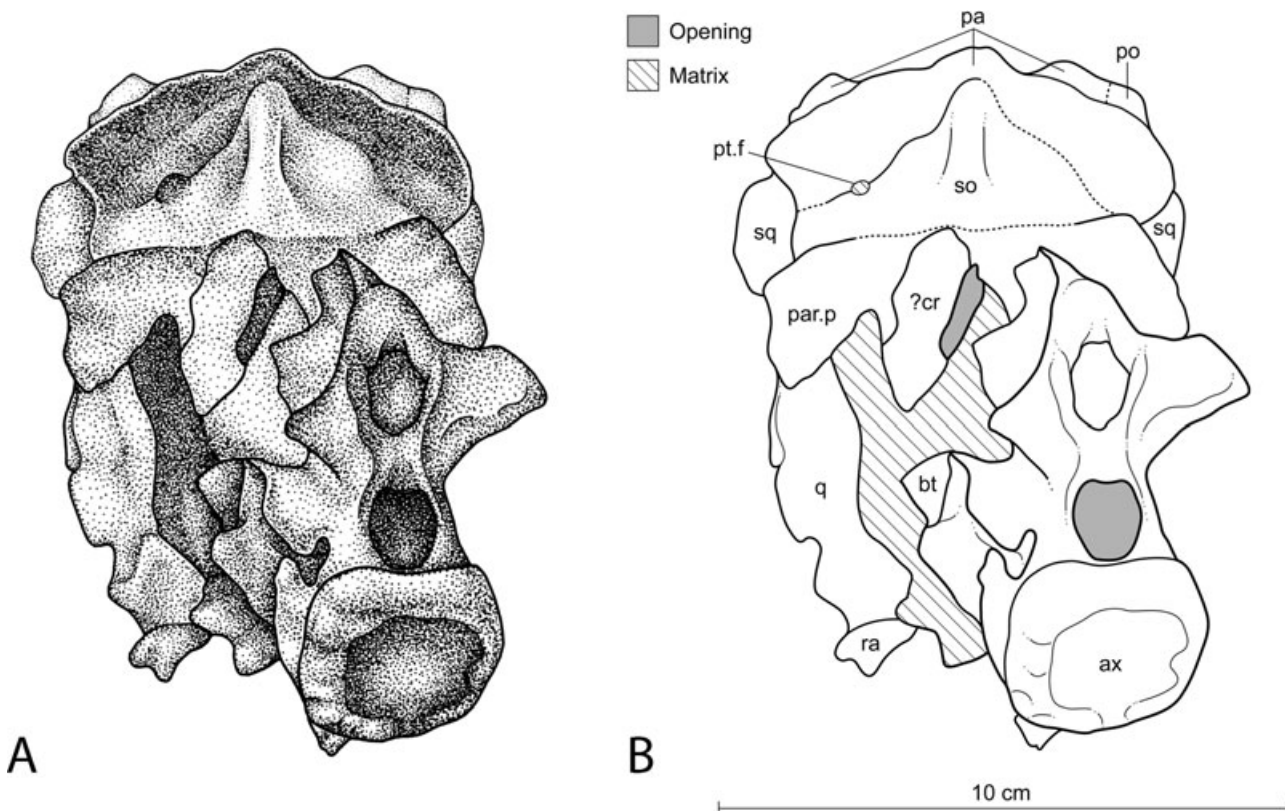
Figure 6. Skull and atlas-axis complex of *Yunnanosaurus huangi* (NGMJ 004546) in occipital view. A, drawing of skull as preserved. B, interpretative line drawing of the skull showing damaged areas, reconstruction, and areas obscured by matrix. See Appendix 2 for abbreviations.

positions, although Young (1942) suggested that up to 16 may have been present. The tooth row extends along the entire length of the maxilla, terminating at a point just in front of the rostral margin of the orbit.

Nasal

The nasals are poorly preserved and yield little anatomical data: large sections of the left nasal are broken dorsally and rostrally (Fig. 4). The remaining bone surface is heavily cracked as a result of the crushing of the skull. It is not possible to determine the position of the nasofrontal suture, but it probably extended transversely across the skull roof at a point level with the midpoint of the prefrontals, as in other prosauropods. Similarly, the midline suture between the nasals cannot be identified.

In dorsal view, the surface of the nasal is rostrocaudally and transversely convex. The main body of the bone gives rise to two processes. The larger ventrolateral process contacts the prefrontal (caudally), lachrymal (laterally), the ascending process of the maxilla (caudoventrally), and the nasal process of the premaxilla (rostrally), and is subtriangular in lateral view.

The second process is slender and extends rostrally to contact the dorsalmost parts of the premaxillary nasal processes. In lateral view, the nasal forms most of the dorsal margin of the external naris.

Young (1942: 71) mentioned a small bony protuberance situated on the midline of the nasals: however, it appears that this structure is formed from the raised broken margins of the nasals in this region, rather than representing a genuine feature. Consequently, it cannot be regarded as a diagnostic character of *Yunnanosaurus* (*contra* Steel, 1970).

Lachrymal

Young (1942: 66) noted correctly that the left lachrymal is missing: nevertheless, this element was labelled in Young's figure of the left-hand side of the skull (ibid. fig. 1). Young's figure gives the impression that the lachrymal had extensive contacts with the nasal and ascending process of the maxilla, excluding a contact between the latter and the prefrontal, and that the lachrymal formed the majority of the dorsal margin of the antorbital fossa. However, as the left lachrymal is definitely absent (P. M. Barrett, pers. obs., 2002), and as the right ascending process of the

maxilla is missing, the articular relationships of these elements cannot be determined.

The right lachrymal consists of a main shaft, which extends caudoventrally from the skull roof, and a rostrally orientated dorsal process, giving the bone an inverted 'L'-shape in lateral view (Fig. 2). Ventrally, the shaft is expanded – approximately equally both rostrally and caudally – to form a subtriangular process that meets the rostrodorsal margin of the jugal along a caudodorsally extending articular surface. It is possible that the ventral part of the lachrymal had a small contact with the maxilla (*contra* Young, 1942: 72). The main portion of the shaft is slender and is subtriangular in cross section along most of its length: the lateral margin of the shaft is an acute ridge. It is not possible to determine the position of the lachrymal foramen because of the presence of matrix and plaster; the medial surface of the lachrymal is similarly obscured. In many prosauropods (*Thecodontosaurus*, *Coloradisaurus*, *Massospondylus*, *Riojasaurus*, *Plateosaurus*, and *Efraasia*), the rostroventral part of the lachrymal shaft gives rise to a 'medial lamina' that contributes to the medial border of the antorbital fossa: this lamina appears to be absent in *Yunnanosaurus*, as in *Mussaurus*, *Anchisaurus*, and *Jingshanosaurus*. However, the lateral surface of the ventral process does bear a distinct, shallow subcircular sulcus (Fig. 2): no other prosauropod possesses this feature, and we provisionally regard it as an autapomorphy of *Yunnanosaurus*.

The dorsal process of the lachrymal has an extensive contact with the prefrontal caudodorsally, and articulates with the nasal dorsally and rostrally (i.e. it does not contact the prefrontal exclusively; *contra* Young, 1942: fig. 1). It tapers to a blunt tip as it extends rostrally. This part of the process is exposed on the skull roof in dorsal view (Fig. 4).

Prefrontal

The prefrontals are rostrocaudally elongate elements that are subtriangular in lateral view and strap-like in dorsal view (Fig. 4), as also occurs in *Lufengosaurus*, *Massospondylus*, and *Anchisaurus*: other prosauropods possess prefrontals that are either rostrocaudally short (*Coloradisaurus* and *Efraasia*) or subtriangular in dorsal outline (*Plateosaurus* and *Thecodontosaurus*). The rostral margin of the prefrontal is concave in dorsal view, producing a narrow medial process, which extends rostrally, and a broader lateral process, which extends ventrolaterally to clasp the caudodorsal surface of the lachrymal (Fig. 2). In dorsal view, the prefrontal is transversely widest at a point just posterior to its junction with the lachrymal, and tapers to narrow points both rostrally and caudally. In

its medial part, the dorsal surface of the prefrontal is flat to gently convex, whereas the ventrally inclined lateral process is strongly convex dorsoventrally. The prefrontal contacts the nasal rostrally and the frontal caudally, and comprises the rostrodorsal portion of the orbit.

Young (1942: fig. 2) indicated that the rostral process of the prefrontal contributed to the margin of the external naris. However, this is not the case: the rostralmost part of the prefrontal illustrated by Young is, in fact, part of the nasal.

Frontal

The frontals are subrectangular in dorsal view, and are separated from each other caudally by a faint midline suture: damage to the skull roof has obliterated the suture rostrally (Fig. 4). Similarly, the boundary between the frontals and nasals cannot be determined accurately (see above). Each frontal is transversely concave dorsally forming two rostrocaudally elongate parasagittal depressions. The medial margin of the bone forms a low ridge, which meets its partner on the midline of the skull, and the lateral margin is also thickened at its contact with the prefrontal: these ridges form the boundaries of the depressions mentioned above. However, these depressions have been accentuated by transverse crushing of the skull.

The frontals comprise most of the dorsal rim of the orbit as in most prosauropods (with the exception of *Lufengosaurus* and *Plateosaurus*). In lateral view, it can be seen that there is an extensive overlapping contact between the frontal and the prefrontal, with the caudal process of the latter overlapping the lateral margin of the former. A prominent protuberance of bone is present on the skull midline close to the midlength of the frontals (Figs 4, 5). This boss appears to be a genuine feature, rather than a product of deformation, and although irregular in outline, its smooth surface suggests that it was not a pathological feature. No other prosauropods for which appropriate material is known possess this feature, which can therefore be regarded as autapomorphic for *Yunnanosaurus* (see also Steel, 1970). The frontal is excluded from the margin of the supratemporal fenestra by the parietal and postorbital. The supratemporal fossa is absent (Fig. 4), similar to the condition in *Mussaurus*.

Parietal

The parietals are large, comprising approximately 25% of the total length of the skull roof. They appear to be fused medially, as no midline suture can be determined, and there is no evidence of a pineal foramen. The parietals consist of a robust central portion and

two laterally directed processes: a rostrolateral process, which contacts the postorbital and frontal, and a caudolateral process, which contacts the supraoccipital and squamosal (Figs 4, 6).

The frontoparietal suture is straight transversely and its central part is marked by a prominent boss of bone (Figs 4, 5). This boss is subovate in outline and has a smooth surface, suggesting that it is not composed of pathological bone. No other prosauropod has a comparable structure and this feature represents an autapomorphy of *Yunnanosaurus* (see also Steel, 1970). The rostrolateral processes extend perpendicular to the central part of the parietal, terminate in stout subtriangular apices, and have a gently convex dorsal surface, which leads smoothly into the supratemporal fenestra. These processes are rostrocaudally expanded, with maximum rostrocaudal lengths that are approximately twice those of the caudolateral processes in dorsal view (Fig. 4). This morphology differs from that in all other prosauropods and is autapomorphic for *Yunnanosaurus*. Parietals of *Unaysaurus*, *Thecodontosaurus*, and *Anchisaurus* lack a distinct rostrolateral process: in other prosauropods (*Massospondylus*, *Riojasaurus*, *Coloradisaurus*, *Plateosaurus*, and *Lufengosaurus*), the rostrolateral process is either more slender than the caudolateral process or is of subequal width to the latter.

In dorsal view, the central portions of the parietals are not strongly constricted. A conspicuous ridge extends along the midline of the skull, forming a low sagittal crest. The lateral surfaces of the parietals are concave anteroposteriorly, and weakly convex dorsoventrally. These surfaces extend ventrally to articulate with the braincase, although the sutures between the parietal and braincase elements cannot be identified as a result of preservational factors.

The caudal surface of each caudolateral process forms a ventrally directed sheet-like area that contacts the dorsal margin of the supraoccipital, so that the parietals are broadly exposed in caudal view (Fig. 6). Young (1942: 69, fig. 4) incorrectly identified these structures as tabulars. The ventral margin of this sheet-like process, together with the supraoccipital, defines a small post-temporal fenestra (Fig. 6; see below). In dorsal view, the caudolateral process curves gently as it extends caudally to its junction with the squamosal: these processes were incorrectly described as interparietals by Young (1942: 70, fig. 4). The caudolateral processes diverge from each other at an angle of approximately 160°, in dorsal view.

Postorbital

The postorbital is a triradiate bone consisting of rostral, caudal, and ventral processes. The rostral process is an elongate, rostrodorsally orientated, finger-like structure that forms the caudodorsal section of the orbital margin. Dorsally, the rounded tip of the rostral process slots into a shallow sulcus in the skull roof formed from approximately equal contributions of the frontal (rostrally) and rostrolateral process of the parietal (caudally). Contact with the parietal excludes the rostral process of the postorbital from the margin of the supratemporal fenestra.

The ventral process is long and slender, tapering as it extends ventrally and slightly rostrally, and has a subtriangular transverse cross section along most of its length. It is approximately equal in width both transversely and rostrocaudally. The tab-shaped caudal process is the shortest of the three. It extends almost horizontally and has an extensive overlapping contact with squamosal, forming the rostrolateral margin of the supratemporal fenestra and most of the dorsal margin of the infratemporal fenestra. The lateral surfaces of all three postorbital processes are flat to mildly convex.

An angle of approximately 120° separates each of the processes in lateral view. Elongation of the rostral process, relative to the caudal and ventral processes, has resulted in the caudal process being situated substantially lower than the dorsal apex of the rostral process, exposing the supratemporal opening in lateral view, as also occurs in *Massospondylus*.

Young (1942) identified separate postorbital and postfrontal bones, with the former comprising the postorbital bar and the latter contacting the skull roof. However, the structure identified as a postfrontal by Young (ibid, figs 1–3) is in fact the rostral process of a unitary postorbital, as in other dinosaurs (see Sereno & Novas, 1994).

Jugal

Both jugals were substantially complete at the time of Young's (1942) description. However, since that time the left jugal has been lost, although a smooth area of matrix indicates the extent of the latter. The following description is based therefore on the complete right jugal.

The jugal is a triradiate bone composed of a rostrally tapering maxillary process, a caudodorsally directed postorbital process, and a caudally orientated quadratojugal process. The main body of the jugal is relatively robust and has a lateral surface that is smoothly convex dorsoventrally. The contact between the jugal and maxilla cannot be determined accurately because of displacement of the elements relative to each other, but there is no evidence that the jugal contributed to the border of the antorbital fossa (*contra* Young, 1942: 72). Together with the postorbital process, the maxillary process comprises most of the ventral margin of the orbit.

The postorbital process is slender, slightly curved, tapers dorsally, and comprises the ventral half of the rostral border of the infratemporal fenestra. It meets the ventral process of the postorbital along a simple tongue-and-groove contact. Caudally, the quadratojugal and postorbital processes are separated by an angle of approximately 80°. The quadratojugal process tapers caudally to a slender point and is overlapped by the quadratojugal laterally. The quadratojugal process forms approximately two thirds of the length of the ventral margin of the infratemporal fenestra.

Quadratojugal

The quadratojugal is an approximately 'L'-shaped element, which consists of a horizontally orientated jugal process and a rostrodorsally orientated quadrate process. In lateral view, the angle between these two processes is approximately 60°. Rostrally, the jugal process tapers towards its contact with the jugal, whereas the caudal part of the jugal process forms the caudoventral corner of the skull, overlapping the quadrate laterally. The quadrate process is slender and tapers dorsally to a narrow pointed apex: this process has extensive contacts with the quadrate caudally and the squamosal rostrodorsally, excluding the quadrate from the caudal margin of the infratemporal fenestra. The quadratojugal of *Yunnanosaurus* lacks the expanded caudoventral process seen in *Lufengosaurus* and *Plateosaurus*.

Squamosal

Both squamosals are present and complete. The squamosal is a tetraradiate bone that comprises the caudodorsal corner of the skull. The rostral process is directed slightly rostroventrally, contributing to the ventral deflection of the upper temporal bar. It is largely obscured in lateral view, because of its extensive overlapping contact with the postorbital, but its medial surface forms much of the lateral margin of the supratemporal fenestra. In lateral view, the contact with the postorbital is 'V'-shaped. The rostral process is completely excluded from the margin of the infratemporal fenestra by the postorbital.

The quadratojugal process is the longest arising from the squamosal, and extends mainly ventrally and a little rostrally from the main body of the bone. It tapers ventrally towards its contact with the quadratojugal and appears to have a subelliptical transverse cross section. The quadratojugal process and the ventral border of the rostral process are separated by an angle of approximately 45°. A third process, the caudoventral process, arises from the caudal surface of the squamosal. In lateral view, an angle of around 90° separates the caudoventral and quadratojugal pro-

cesses: the recess between these processes forms the articular surface for the head of the quadrate. The caudoventral process is short, robust, and hooked in lateral view. Medially, it has an extensive contact with the paroccipital process. The caudolateral part of the squamosal, comprising parts of the caudoventral process and main body of the bone, is visible in occipital view. Finally, a short, stout parietal process extends rostromedially from the main body of the bone, contacting the caudolateral process of the parietal. It diverges from the rostral process of the squamosal at an angle of approximately 45° in dorsal view.

Quadrate

In lateral view, the quadrate is tall and bowed rostrally, with a subcrescentic outline. The quadrate head is subtriangular, terminates at a point level with the dorsal margin of the infratemporal fenestra, and is clasped between the quadratojugal and posteroventral processes of the squamosal. Ventrally, the quadrate divides into a lateral quadratojugal process and a medial pterygoid process, forming a large concave area on the rostral surface. The rostral margin of the quadratojugal process articulates with the quadratojugal ventrally and squamosal dorsally. The pterygoid process is visible through the infratemporal fenestra: it is large and subrectangular in outline, but its contact with the pterygoid is obscured by matrix. Caudally, the quadrate shaft is shallowly excavated so that it is smoothly concave both transversely and dorsoventrally along its length. As the lower jaws are preserved in articulation with the quadrates, it is not possible to determine the shape of the distal condyles in ventral view. Nevertheless, it can be seen that the distal condyles are expanded transversely and extended ventrally to a point approximately level with the maxillary tooth row. The medial articular condyle appears to extend slightly more ventrally than the lateral condyle. The articular surface for the lower jaws is rostrocaudally short. Presence/absence of a quadrate foramen could not be determined.

Palatal elements

A flat sheet of bone visible through the infratemporal fenestra probably represents the quadrate process of the pterygoid (Fig. 2). The medial parts of the paired palatal processes of the pterygoids can be seen through the orbit: the midline of each element is thickened into a distinct, longitudinally orientated ridge, but no other anatomical details can be discerned. Two small, flat sections of bone lying lateral to the pterygoids probably represent portions of the rostral process of the right palatine. A small, narrow, medially bowed element with a rostrocaudally expanded base is

present medial to the right postorbital bar, and is visible through the orbit. Its base lies in the region of the right pterygoid: it is possible therefore that this element is the right epipterygoid.

Young (1942) mentioned a small element, removed from the left orbit during preparation, which he identified as a transversum (= ectopterygoid). Unfortunately, this element could not be located and is presumed lost. Nevertheless, the element illustrated by Young (ibid. fig. 2) lacks the strongly hooked-shape that characterizes the ectopterygoid of other prosauropods: it seems more likely that this element was either the left epipterygoid or part of the left lachrymal. All other details of the palate are obscured by the surrounding skull bones, matrix, and crushing.

BRAINCASE

The braincase is obscured by the presence of the axis-atlas complex caudally, the lower jaws ventrally, and by matrix, plaster, and palatal bone fragments laterally and rostrally. The foramen magnum is partially occluded by a small cylindrical bone that may represent a cervical rib fragment, reducing the opening to an elongate, dorsoventrally orientated slit (Fig. 6).

Supraoccipital
In caudal view, the supraoccipital is a subtriangular element (Fig. 6). The ventral margin of the supraoccipital is the longest, and forms an approximately straight transverse contact with the exoccipital-opisthotic. The supraoccipital slopes caudoventrally from its contact with the skull roof at an angle of approximately 110° to the long axis of the skull. A median ridge extends ventrally from the central point of the dorsal margin of the supraoccipital to the dorsal margin of the foramen magnum. There is a small contact between the dorsolateral margins of the supraoccipital and the caudal border of the squamosal. A small notch in the lateral margin of the supraoccipital bounds a small foramen that probably housed the exit for the vena capitis medius. This opening is generally considered to be homologous to the post-temporal fenestra (Galton, 1985b). A similar notch is present on the supraoccipital of *Lufengosaurus*: consequently, a post-temporal fenestra should be scored as present in this taxon (*contra* Barrett *et al.*, 2005). However, it should be noted that this feature differs from that described as the post-temporal fenestra of *Lufengosaurus* by Young (1941: 7): the latter represents a break in the occipital area (Barrett *et al.*, 2005).

Exoccipital-opisthotic
Both paroccipital processes are present and project laterally and slightly caudally, paralleling the orientation of the caudolateral processes of the parietals

(Fig. 6). The contact between the exoccipital and opisthotic cannot be determined: these two elements appear to be fused. Similarly, the exact nature of their contact with the supraoccipital dorsal to the foramen magnum cannot be determined. The exoccipital portion of the paroccipital process forms at least the lateral margin of the foramen magnum. The paroccipital process is dorsoventrally narrowest adjacent to the foramen magnum, and increases in depth laterally before tapering toward its lateral termination. Consequently, in caudal view, the paroccipital processes are almost rhomboidal or spearhead shaped in outline, with a blunt rounded triangular tip. In lateral view, the process is rostrocaudally compressed, forming a flat plate that contacted the squamosal rostrally. The caudal surface of the paroccipital process is mildly convex dorsoventrally and mildly concave transversely. Foramina for the exits of cranial nerve XII are present on the ventral surface of the paroccipital process.

Other braincase elements
The left basal tuber is visible in caudal view (Fig. 6). Parts of the prootic, laterosphenoid, and basisphenoid are visible through the right orbit and infratemporal fenestra: there appears to be a large trigeminal foramen between them, but the sides of this opening have been damaged by preparation and it may not represent a genuine feature of the braincase. No other endocranial foramina are determinable. Unfortunately, the presence of other skull elements and damage prevents collection of useful anatomical data for these (and other) braincase elements.

MANDIBLE

Both mandibles are present and apparently complete (Figs 1–3). The mandible is slender, with a long retroarticular process that has an elongate triangular outline in dorsal view. An external mandibular fenestra is present: it has an elliptical outline in lateral view, with the long-axis of this ellipse orientated rostrocaudally, and its longest diameter is equal to approximately 12% of the mandible length. *Plateosaurus* and *Massospondylus* have external mandibular fenestrae that are almost identical in relative size to that of *Yunnanosaurus*; that of *Coloradisaurus* is marginally larger (~17% of mandible length), whereas *Riojasaurus* possesses a considerably smaller fenestra (~7% of mandible length). There is a well-developed coronoid eminence that is approximately twice the height of the tooth-bearing part of the dentary. As in *Massospondylus* and *Thecodontosaurus*, the jaw joint of *Yunnanosaurus* is on the same level as the dentary tooth row: this differs from the ventrally offset jaw

joint present in *Lufengosaurus*, *Plateosaurus*, *Coloradisaurus*, *Efraasia*, and *Unaysaurus*. Few details of the medial and dorsal surfaces of the mandibles can be determined, as the lower jaws closely adhere to the rest of the skull. A large internal mandibular fenestra is present, but the articular boundaries surrounding it are impossible to determine as the medial surfaces are obscured by the close apposition of the jaws and matrix. The splenial, coronoid, and articular are also completely obscured from view.

Dentary

The dentary comprises approximately half of the length of the mandible. It is a slender, elongate element that maintains an almost constant height along its length, although it does increase in depth slightly towards its caudal end. In lateral view, the rostral margin of the dentary is bluntly rounded and bears several large nutrient foramina. In medial view, the symphysis is small and the articular facet for the opposing dentary is subelliptical to slightly crescentic in outline. The long axis of the symphysis slopes caudoventrally at an angle of 45° to the horizontal. The available exposure of the medial surface suggests that no lateral plate was present.

The lateral surface of the dentary is gently convex dorsoventrally. There is some indication of several very small nutritive foramina just ventral to the tooth row. A low ridge extends rostroventrally from the dorsal part of the dentary, ventral to the tooth row. It is restricted to the area underlying the caudalmost third of the tooth row. The prominence of this feature may have been exaggerated by crushing. It is not possible to determine the number of tooth positions in the dentary: the left tooth row is completely obscured and a segment of the right tooth row is only partially visible. At least eight erupted teeth appear to be present in the rostral part of the right dentary, but the caudal extent of the tooth row cannot be determined. Young (1942) suggested that 10–13 teeth would have been present in each dentary.

Young (1942: fig. 1) indicated that the dentary was excluded from the border of the external mandibular fenestra by the surangular (dorsally) and angular (ventrally). However, it appears that the caudal margin of the dentary was forked, with a dorsal process that formed the rostral part of the coronoid eminence (and therefore the rostral boundary of the external mandibular fenestra) and a ventral process, which formed the ventral margin of the fenestra (see Young, 1942: fig. 2).

Surangular

The surangular is an elongate, strap-like element that forms much of the dorsal margin of the external man-

dibular fenestra. In lateral view, it is gently sigmoid in outline, first arching dorsally to form the apex of the coronoid eminence and then bows ventrally to the region of the jaw articulation. Finally, the caudalmost part of the surangular curves dorsally and tapers to a blunt point, forming the retroarticular process.

The surangular comprises approximately 50% of the height of the mandible at the level of the coronoid eminence: the dorsalmost parts of both surangulars are concealed by the jugals on both sides of the skull. Laterally, the bone surface is gently convex dorsoventrally. The surangular contacts the angular ventrally, caudal to the external mandibular fenestra.

Angular

The angular comprises the caudal part of the lower jaw in lateral view. Its lateral surface is gently concave rostrocaudally and flat to gently convex dorsoventrally. It is a strap-shaped element that reaches its maximum height in its middle portion and tapers both rostrally and caudally. In ventral view, the angular meets the prearticular along an almost straight rostrocaudally extending articulation.

Prearticular

In medioventral view, the prearticular is a block-shaped element that curves slightly caudodorsally. It tapers posteriorly to a blunt point and comprises much of the medial surface of the retroarticular process. The dorsal surface of the bone is shallowly concave both rostrocaudally and transversely: the shape of the articular cannot be determined. In ventral view, the main body of the prearticular expands medially in the region underlying the mandibular glenoid.

DENTITION

In labial view, the maxillary tooth crowns are mesiodistally expanded relative to the roots, although this expansion is not as pronounced as in other prosauropods and basal sauropods. This feature, in combination with marked apicobasal elongation of the crowns, gives the teeth a narrow, slender appearance (Fig. 7). The maxillary teeth are labiolingually compressed, taper to a blunt tip apically, and lack distal recurvature. The labial surfaces of the tooth crowns are convex both mesiodistally and apicobasally, so that the tooth apex is inclined slightly lingually. The tooth enamel on the labial surface is smooth and does not display the wrinkled texture characteristic of sauropods (cf. Wilson & Sereno, 1998). There is a slight indication of a shallow groove extending along the distal margin of the labial surface of the crown parallel to the distal crown margin. Apart from this feature, the

Figure 7. Left maxillary teeth of *Yunnanosaurus huangi* (NGMJ 004546). Scale bar equals 10 mm.

teeth are symmetrical about their long axes in labial view.

In general, the mesial and distal margins of the tooth crowns lack denticles, although a small minority of the preserved teeth have crenulated enamel at the tooth apex that gives the appearance of tiny bead-like denticles in this region. However, these features are not like the marginal denticles seen in other prosauropods. Lack of denticles is unique among basal sauropodomorphs and is considered to be an autapomorphy of *Yunnanosaurus* (see also Young, 1942, 1951; Galton, 1990; Galton & Upchurch, 2004). There is no indication of any tooth wear, although the lingual surfaces of the teeth cannot be examined to confirm this. Many tooth apices are missing, but this is clearly the result of breakage rather than occlusal or food-tooth wear. As far as can be determined, the mesial and distal crown margins display no evidence of high-angled wear facets: consequently, if any wear is present at all, it is likely to have been extremely limited in extent and confined to the lingual tip of the crown.

The maxillary teeth are largest in the rostral part of the maxilla and decrease in size caudally, both in terms of apicobasal length and mesiodistal width. None of the teeth are procumbent or recumbent: they all extend almost perpendicular to the maxilla, with the mesiodistal axes of the teeth orientated parallel to the ventral maxillary border. Consequently, there appears to be only limited overlap between adjacent tooth crowns. There is limited evidence of tooth replacement. In two of the left maxillary tooth positions, replacement crowns can be seen emerging distal to the functional tooth.

The single preserved premaxillary tooth is virtually identical to the maxillary teeth, although it appears to be slightly more cylindrical in cross section. Few details of the dentary teeth can be determined as they are largely obscured by the upper jaws: nevertheless,

where visible, they appear to be identical to the maxillary teeth.

ACCESSORY ELEMENTS

Several accessory skull elements are present, but were not mentioned or illustrated by Young (1942). Two elongate rod-like elements lie medial to the lower jaws. They extend rostrocaudally, appear to have a cylindrical or subelliptical transverse cross section, and are gently bowed along their length. These elements probably represent the ceratobranchials. They are preserved in approximate life position and are ~55 mm long.

A stapes is preserved *in situ* on the left-hand side of the occiput and is visible immediately caudal to the quadrate, projecting caudoventrally and slightly laterally. Most of the stapes is encased in matrix, but the exposed portion (consisting of the stapedial shaft only) is rod-like, with a subcylindrical transverse cross section.

PHYLOGENETIC ANALYSIS

Only three published studies have included *Yunnanosaurus* in a formal cladistic analysis (Sereno, 1999; Yates, 2003a; Galton & Upchurch, 2004). Galton (1990) and Pisani *et al*. (2002) have also commented on the phylogenetic position of *Yunnanosaurus*, but the former was not based on a numerical analysis and the latter was a supertree, and thus relied on manipulation of existing tree topologies rather than original character data. Consequently, the latter two studies are not considered further herein. Two unpublished phylogenies also include *Yunnanosaurus* (Upchurch *et al*. 2007; Yates, 2007), but we will refrain from commenting on these until they have appeared in print. Here, we investigate the potential effects of our new character data on the phylogenetic position of *Yun-*

nanosaurus using the data-matrices of Sereno (1999), Yates (2003a), and Galton & Upchurch (2004). For each of these analyses, we have modified the scoring of cranial characters of *Lufengosaurus* and *Yunnanosaurus* based on Barrett *et al*. (2005) and the current study, respectively. Otherwise, we have attempted to replicate the analytical procedures and assumptions of the original authors in order to allow meaningful discussion of the effects of new character scoring on tree topologies. The results of each of these re-analyses are described below.

Sereno (1999)

Sereno's (1999) analysis was based on nine ingroup taxa, with Sauropoda and Theropoda used as successive outgroups. The data matrix included 32 characters (18 cranial and 14 postcranial). Analysis of this matrix produced six most parsimonious trees (MPTs) with tree lengths (TLs) of 34 steps, a Consistency Index (CI) of 0.97 and a Retention Index (RI) of 0.98. Sereno (1999) applied a form of reduced consensus (Wilkinson, 1994) to these tree topologies, resulting in the *a posteriori* deletion of *Ammosaurus*, 'Gripposaurus' (= 'Gyposaurus' sinensis), and *Coloradisaurus*, which yielded a single tree in which *Yunnanosaurus* and *Massospondylus* were recovered as sister taxa, forming a monophyletic Massospondylidae.

Our observations on the skull of *Yunnanosaurus* required changes to the scoring of nine cranial characters (representing 50% of cranial characters or 28% of total characters in the data matrix; see Appendix 3). The modified data-matrix was analysed using the Exhaustive search option in PAUP 4.0b10 (Swofford, 2004). This analysis recovered 124 MPTs, each with the following attributes: TL = 38 steps; CI = 0.864; RI = 0.889; Rescaled Consistency Index (RCI) = 0.772. This result represents a substantial decrease in resolution compared with the original results obtained by Sereno (1999; see above) and from the re-analysis of Sereno's data presented by Barrett *et al*. (2005), which included modified scorings for the skull of *Lufengosaurus* but not for *Yunnanosaurus*.

A strict consensus tree of the 124 MPTs is poorly resolved (Fig. 8A). Within Prosauropoda, there is a monophyletic clade [comprising *Plateosaurus*, '*Sellosaurus*' (= *Efraasia*), *Coloradisaurus*, and *Lufengosaurus*], which in turn forms a polytomy with the remaining five prosauropods (*Ammosaurus*, '*Gripposaurus*', *Massospondylus*, *Riojasaurus*, and *Yunnanosaurus*). When the same *a posteriori* deletion used by Sereno (1999; see above) was applied to the 124 MPTs obtained from our re-analysis of the data, the number of remaining tree topologies was reduced to 12. However, these trees also show little internal resolution, with the remaining taxa falling into polytomies iden-
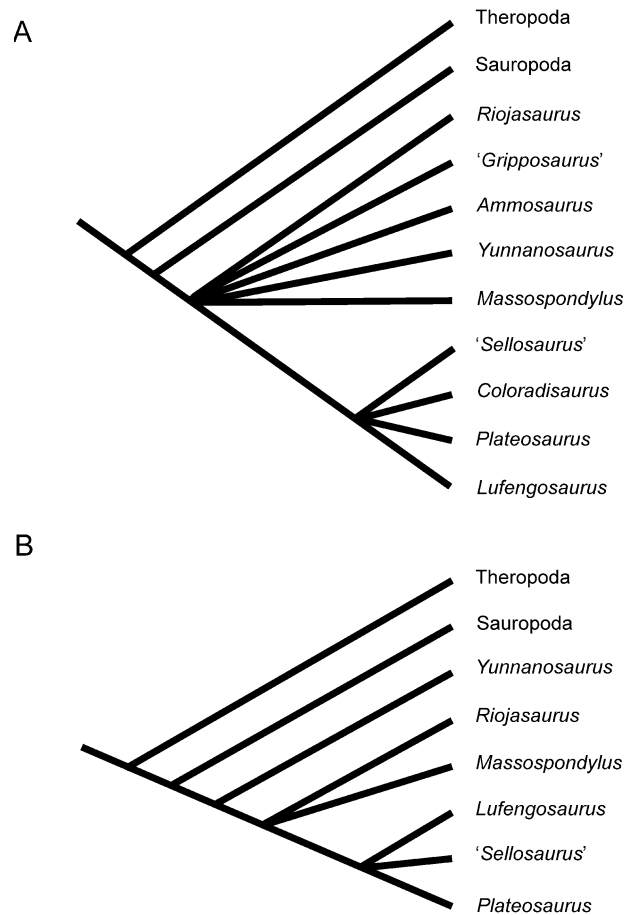

Figure 8. A, a strict consensus tree of the 124 most parsimonious trees found by the analysis of the modified version of Sereno's (1999) data matrix. B, a 50% majority-rule consensus tree based on the 12 reduced consensus topologies produced by re-analysis of the modified Sereno (1999) data matrix. '*Gripposaurus*' represents a referred individual of '*Gyposaurus*' *sinensis* (Young, 1948); material included as '*Sellosaurus*' is currently regarded as *Efraasia* (Yates, 2003b).

tical to those in the strict consensus tree. Inspection of these 12 topologies, and the construction of a 50% majority-rule consensus tree (Fig. 8B), reveals that none of these topologies places *Massospondylus* and *Yunnanosaurus* as sister taxa. Instead, *Massospondylus* is consistently placed closer to a clade containing *Plateosaurus*, *Lufengosaurus*, and *Efraasia* than it is to *Yunnanosaurus*. The latter is recovered as the most basal prosauropod in nine of the 12 reduced consensus topologies, and is the second most basal prosauropod in the remaining three trees.

Yates (2003a)

The analysis of Yates (2003a) included 21 ingroup taxa, with Ornithischia, *Marasuchus*, and Crurotarsi

as successively distant outgroups. The data matrix included 164 characters (51 cranial and 113 postcranial). Analysis of this matrix produced five MPTs (TL = 351 steps; CI = 0.516; RI = 0.668). Application of reduced consensus (Wilkinson, 1994) led to the *a posteriori* deletion of *Coloradisaurus* and yielded a tree in which *Lufengosaurus* was the sister taxon of *Yunnanosaurus* + *Massospondylus*.

New information on *Yunnanosaurus* has led to changes in the scoring of 15 cranial characters in the Yates (2003a) data matrix (representing 29% of cranial characters and 9% of total characters; see Appendix 3). This modified data-matrix was analysed using the branch-and-bound search in PAUP 4.0b10 (Swofford, 2004): a single MPT was recovered (TL = 356 steps; CI = 0.508; RI = 0.661; RCI = 0.336). Inclusion of the new cranial scorings for *Lufengosaurus* and *Yunnanosaurus* has therefore resulted in a decrease in MPT number by four, and an increase in tree length of five steps. The new tree topology (Fig. 9) is similar to the five MPTs found originally by Yates (2003a), and places *Coloradisaurus* as the sister taxon of *Massospondylus*, with *Yunnanosaurus* and *Lufengosaurus* as successively more distant outgroups to this pairing.

GALTON & UPCHURCH (2004)

Galton & Upchurch's (2004) dataset included 137 characters (43 cranial and 94 postcranial) for 23 ingroup taxa, with a theoretical outgroup that was assigned '0' for all character states. This analysis produced two MPTs (TL = 279 steps; CI = 0.541; RI = 0.635; RCI = 0.355), which differed only in the positioning of *Massospondylus* and *Yunnanosaurus*. One MPT recovered *Yunnanosaurus* as the sister taxon to a group consisting of: (*Massospondylus* (*Mussaurus* (*Coloradisaurus* ((*G. sinensis* + *Lufengosaurus*) ('*Euskelosaurus*' (*Plateosaurus* + '*Sellosaurus*' [= *Efraasia*])])))))). *Yunnanosaurus* and *Massospondylus* swapped positions in the second MPT.

The new information on *Yunnanosaurus* led to revised scorings for 22 cranial characters (representing 51% of cranial characters or 16% of the total characters; see Appendix 3). The modified Galton & Upchurch (2004) matrix was analysed using the Heuristic search in PAUP 4.0b10 (Swofford, 2004), producing a single MPT (Fig. 10: TL = 282 steps; CI = 0.535; RI = 0.629; RCI = 0.348). Curiously, this result is much more similar to that found originally by Galton & Upchurch (2004) than it is to that found by Barrett *et al.* (2005), which included revised scorings for the skull of *Lufengosaurus* only. The single MPT recovered by this study is identical to first of the two MPTs found by Galton & Upchurch (2004; see above), but is three steps longer. In short, it appears
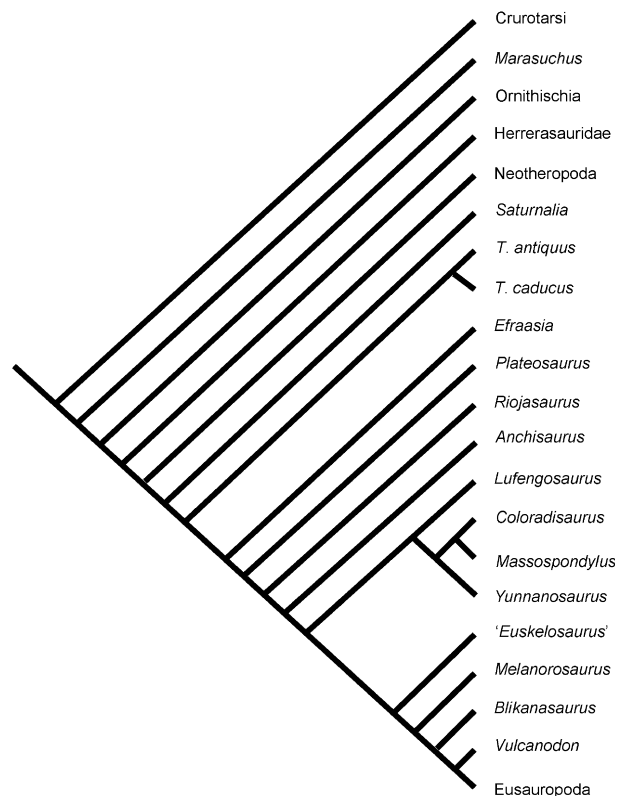

Figure 9. The single most parsimonious tree produced by analysis of the modified Yates (2003a) data matrix. For the sake of brevity, species of *Thecodontosaurus* are listed using the abbreviation of the generic name. The material included as '*Euskelosaurus*' is currently referred to *Plateosauravus cullingworthi* (Yates, 2003c).

that the addition of revised character scorings for the skull of *Yunnanosaurus* has largely reversed the changes produced by Barrett *et al.*'s (2005) new scoring for *Lufengosaurus*. This result is discussed in more detail below.

DISCUSSION

Comparisons between the holotype specimens of *L. huenei* and *Y. huangi* allowed Barrett *et al.* (2005) to demonstrate that these taxa were distinct on the basis of numerous differences in cranial structure (*contra* Rozhdestvensky, 1965). The identification of numerous cranial autapomorphies in *Y. huangi* (see above) provides additional support for the separation of these genera and the refutation of their proposed synonymy. Similarly, this suite of autapomorphies supports the separation of *Y. huangi* from *Massospondylus* (*contra* Cooper, 1981), which itself has a number of cranial features not present in *Yunnanosaurus* (see Sues *et al.*, 2004).
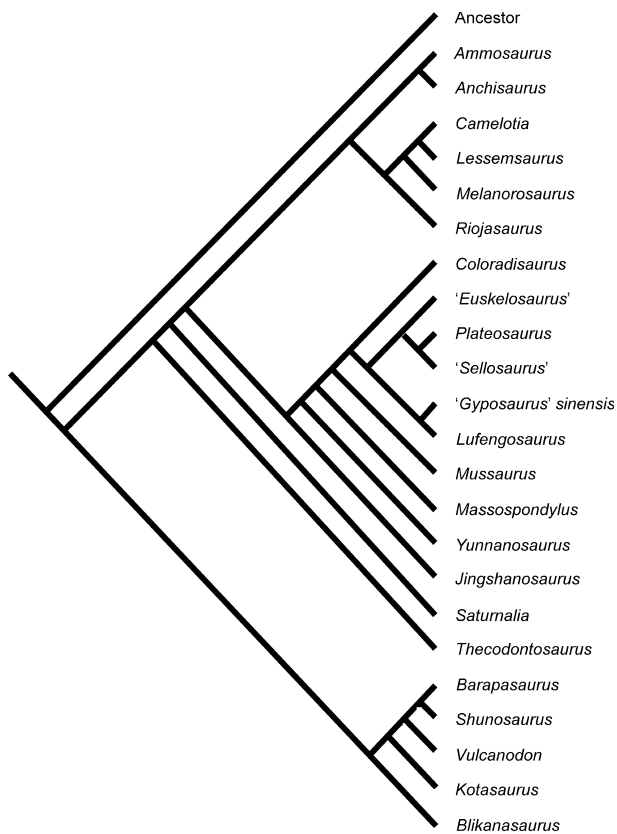
Figure 10. The single most parsimonious tree found by the analysis of the modified Galton & Upchurch (2004) data matrix. Material included as '*Sellosaurus*' is currently regarded as *Efraasia* (Yates, 2003b); specimens included as '*Euskelosaurus*' are currently referred to *Plateosauravus cullingworthi* (Yates, 2003c).

The phylogenetic relationships of *Yunnanosaurus* remain labile. In summary, the new cranial character scorings for *Yunnanosaurus* have had an impact on the topologies, resolution and tree lengths of all three previous analyses of basal sauropodomorph interrelationships (Sereno, 1999; Yates, 2003a; Galton & Upchurch, 2004). However, the differences between these analyses (e.g. in numbers of characters, character scoring, and ingroup composition) are too great to allow a meaningful or detailed consensus to be developed. Although each analysis has produced a different estimate of the relationships of *Yunnanosaurus*, and definitive statements are therefore difficult, three generalizations can be made.

1. It is interesting to note that the new cranial data for *Yunnanosaurus* has increased resolution in the two largest studies, whereas Barrett *et al.* (2005) found that the addition of new cranial data for *Lufengosaurus* alone had either no impact or led to decreased resolution. It is not clear why this occurred, although one possibility is that re-scoring for *Lufengosaurus* tended to change 'known' scores into '?', whereas this effect was not as strong when re-scoring *Yunnanosaurus* (see Appendix 3).

2. Both Sereno (1999) and Yates (2003a) found that *Yunnanosaurus* and *Massospondylus* are sister taxa, and recognized a monophyletic Massospondylidae. The new character scorings for *Yunnanosaurus* have somewhat weakened this conclusion, however, because this genus has been pushed further from *Massospondylus* in all three of our re-analyses, relative to the original topologies recovered by Sereno (1999), Yates (2003a), and Galton & Upchurch (2004). The modified Yates (2003a) data matrix still supports a monophyletic group (which we could call the Massospondylidae) that includes *Lufengosaurus*, *Yunnanosaurus*, *Massospondylus*, and *Coloradisaurus* (Fig. 9), although it is the latter two taxa that now form a sister-group relationship.

3. All three re-analyses support the view that *Yunnanosaurus* is probably more closely related to prosauropods such as *Massospondylus*, *Lufengosaurus*, and *Coloradisaurus*, than are *Ammosaurus* and *Riojasaurus* (although see Discussion of Sereno, 1999, above).

Further assessment of the phylogenetic relationships of *Yunnanosaurus* should await both the synthesis of character lists for basal Sauropodomorpha presented by different authors (e.g. Yates & Kitching, 2003; Yates, 2003a, 2004; Galton & Upchurch, 2004), and the incorporation of new data on the postcrania of *Lufengosaurus* and *Yunnanosaurus* that is currently under study by the authors. Despite some apparent similarities between *Yunnanosaurus* and true sauropods in terms of their dentitions (Salgado & Calvo, 1997; Wilson & Sereno, 1998; Barrett, 2000), there is no indication at present that the former is a member of the latter clade.

Finally, many of the autapomorphic features of *Y. huangi* are likely to be of palaeobiological interest. For example, the lack of nutritive foramina on the maxilla suggests that vascularization and innervation of the snout may have differed somewhat from that of other basal sauropodomorphs, which all possess this feature. Similarly, the external nares are unusually small for a sauropodomorph, although the functional significance of this is unknown at present. The function of the midline cranial bosses in *Yunnanosaurus* is also unknown: their small size suggests that they would have been ineffective for intra- or interspecific display unless they supported more conspicuous soft-tissue structures, but there is currently no evidence for the presence of the latter. However, as *Lufengosaurus* also possesses a series of cranial rugosities (Barrett *et al.*, 2005), which differ in size, shape, and position from those seen in *Yunnanosaurus*, it is tempting to speculate that these species-specific fea-

tures may have had some involvement in species recognition. As discussed elsewhere (Salgado & Calvo, 1997; Wilson & Sereno, 1998; Barrett, 1999, 2000; Galton & Upchurch, 2004), several worn, isolated tooth crowns assigned to *Yunnanosaurus* (Simmons, 1965; Galton, 1985a, 1986) are no longer considered to be referable to this genus: wear facets are unknown in genuine *Yunnanosaurus* teeth (see above; Barrett, 2000). Nevertheless, absence of marginal denticles from the *in situ* maxillary teeth of the holotype specimen of *Yunnanosaurus* is unusual relative to the situation in other basal sauropodomorphs, and may indicate some dietary specialization. Although intriguing, all of these suggestions should be regarded as tentative pending the discovery of better-preserved material and more detailed studies on prosauropod functional morphology.

ACKNOWLEDGEMENTS

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APPENDIX 1

Institutional abbreviations: AMNH, American Museum of Natural History, New York, USA; BMNH, The Natural History Museum, London, UK; BP, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MB, Humboldt Museum für Naturkunde, Berlin, Germany; NGMJ, Nanjing Geological Museum, Nanjing, China; SAM, Iziko South African Museum, Cape Town, South Africa; ULR, Museo de Ciencias Naturales, Universidad Nacional de La Rioja, La Rioja, Argentina; YPM, Peabody Museum of Natural History, Yale University, New Haven, USA.

APPENDIX 2

Abbreviations used in figures: ang, angular; ax, axis; bt, basal tuber; cr, cervical rib; d, dentary; d.r, dentary ridge; f, frontal; f.b, frontal boss; j, jugal; l, lachrymal; l.d, left dentary; l.f, lachrymal fossa; l.pmx, left premaxilla; mx, maxilla; mx.p, projection from maxillary ascending process; n, nasal; nc, neurocranium; pa, parietal; pa.b, parietal boss; pal, palatine; par.p, paroccipital process; pfr, prefrontal; pmx, premaxilla; po, postorbital; pt, pterygoid; pt.f, posttemporal fenestra; q, quadrate; qj, quadratojugal; r.ra, right retroarticular process; ra, retroarticular process; sa, surangular; so, supraoccipital; sq, squamosal; t, tooth.

APPENDIX 3

Revised character scores for cranial material of *Y. huangi* in the data matrices of Sereno (1999: 32 characters, 18 cranial), Yates (2003a: 164 characters, 51 cranial), and Galton & Upchurch (2004: 137 characters, 43 cranial). Postcranial character scores are unchanged. See text for full details of the analyses.

Character	5	10	15	20	25	30	35	40
Sereno (1999)	010?1	?111?	11121	11111	1011?	00???	?0	
Yates (2003a)	11110	101??	?????	01111	11110	?????	??1??	??00?
Galton & Upchurch (2004)	10001	101??	00?10	11000	?1111	0???0	01001	?0???

Character	45	50	55	60	65	70	75	80
Yates (2003a)	10?0?	11?1?	????1	1?1?0	?1??1	01100	0??01	0?010
Galton & Upchurch (2004)	11???	1110?	?0100	???0?	?0100	0???0	01100	000??

Character	85	90	95	100	105	110	115	120
Yates (2003a)	10100	1???1	?0111	11011	10101	??11?	00110	11011
Galton & Upchurch (2004)	?1011	?0001	?0001	00010	10110	00000	00000	00000

Character	125	130	135	140	145	150	155	160
Yates (2003a)	10110	11101	1?000	11001	01011	?1?01	0?11?	?????
Galton & Upchurch (2004)	0100?	0??11	1????	??				

Character	165
Yates (2003a)	????

In the Sereno (1999) matrix, the following cranial characters were re-scored: characters 1 and 22 were changed from '?' to '0'; character 21 was changed from '?' to '1'; characters 3 and 32 were changed from '1' to '0'; characters 30 and 31 were changed from '0' to '?'; and characters 4 and 6 were changed from '1' to '?'. Character 4 (form of maxillary foramina) is not applicable to *Yunnanosaurus* (as this feature is absent) and was therefore scored as '?'.

In the Yates (2003a) matrix, the following cranial characters were re-scored: characters 7, 16, and 38–39 were changed from '?' to '0'; characters 2, 18, and 41 were changed from '?' to '1'; character 24 was changed from '0' to '1'; character 5 was changed from '1' to '0'; characters 9, 11, and 50 were changed from '0' to '?'; and characters 12, 45, and 48 were changed from '1' to '?'. Characters 10 (form of maxillary foramina), 11 (morphology of medial lamina), 12 (length of medial lamina), 48 (orientation of tooth serrations), and 51 (distribution of tooth serrations) are not applicable to *Yunnanosaurus* (because of the absence of the features of interest) and were therefore scored as '?'.

In the Galton & Upchurch (2004) matrix, the following cranial characters were re-scored: characters 3, 7, 11, and 18–19 were changed from '?' to '0'; characters 6 and 14 were changed from '?' to '1'; characters 22 and 41 were changed from '0' to '1'; characters 4, 12, 15, 20, 31, and 37 were changed from '1' to '0'; characters 13, 36, and 40 were changed from '0' to '?'; and characters 9, 38, 39, and 43 were changed from '1' to '?'. Characters 9 (form of maxillary foramina), 13 (length of lateral lamina), and 38 (orientation of tooth serrations) were not applicable to *Yunnanosaurus* (because of the absence of the features of interest) and were therefore scored as '?'.

The data matrices were also modified to include the revised scorings for cranial material of *L. huenei* that are listed in Barrett *et al*. (2005). However, it should be noted that several of these scorings require modification in the light of new data. The amended scores used herein are listed below.

Sereno (1999): character 25 (presence/absence of frontal process intervening between prefrontal and nasal) changed from '?' to '0'.

Galton & Upchurch (2004): character 5 (maxillary contribution to external nares) changed from '?' to '1'; characters 10 (presence of maxillary/lachrymal contact) and 13 (length of lateral lamina) changed from '0' to '?'; character 19 (ratio between length of prefrontal and frontal) changed from '1' to '?'; and character 21 (presence/absence of frontal process intervening between prefrontal and nasal) changed from '?' to '0'.