Geol. Mag. **144** (*2*), *2007, pp. 247–262.* © *2007 Cambridge University Press*

doi:10.1017/S0016756806003062 First published online 9 February 2007 *Printed in the United Kingdom*

A re-evaluation of *Chinshakiangosaurus chunghoensis* Ye *vide* Dong 1992 (Dinosauria, Sauropodomorpha): implications for cranial evolution in basal sauropod dinosaurs

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(*Received* 9 June 2005; *accepted* 8 June 2006)

Abstract – Re-description of the left dentary of *Chinshakiangosaurus chunghoensis* reveals that it possesses an unusual combination of 'prosauropod' and 'sauropod' character states. Cladistic analysis places *Chinshakiangosaurus* as one of the most basal sauropods known currently. Mapping of dentary and dental characters onto the most parsimonious topologies yields insights into the sequence of acquisition of a number of feeding-related characters. For example, it seems that basal sauropodomorphs (traditional prosauropod taxa) possessed a fleshy cheek that attached to the mandible along a marked ridge, and that the same structure was present in the most basal sauropods. The early sauropod skull developed a lateral plate that reinforced the bases of the tooth crowns labially, and had wrinkled tooth enamel and a concavity on the mesial portion of the lingual part of each crown, while retaining a fleshy cheek and a relatively weak symphysis. More advanced sauropods (eusauropods) lost the cheek, perhaps in order to increase the gape of the jaws in response to a change in feeding style that involved collection of larger quantities of poor quality foliage.

Keywords: dentary, Dinosauria, phylogeny, Sauropoda, Sauropodomorpha.

1. Introduction

The origin of sauropods has been mysterious and controversial almost since the recognition of this group by Marsh in 1878. Pre-cladistic studies typically regarded prosauropods as ancestral to sauropods, with the former giving rise to the latter during the Late Triassic Period through an increase in body size and the concomitant change from bipedality to quadrupedality (Matthew, 1915; Abel, 1919; Romer, 1956, p. 618; Charig, Attridge & Crompton, 1965; Bonaparte, 1986). The first phylogenetic analysis of sauropodomorph relationships supported prosauropod paraphyly (Gauthier, 1986), but most early cladistic studies contradicted the traditional hypothesis and concluded that prosauropods and sauropods are monophyletic sister-taxa (Sereno, 1989, 1999; Galton, 1990; Gauffre, 1993). This interpretation rapidly became the new orthodoxy, with several cladistic analyses of relationships within Sauropoda employing Prosauropoda as the nearest outgroup (Calvo & Salgado, 1995; Salgado, Coria & Calvo, 1997; Upchurch, 1998; Wilson & Sereno, 1998; Wilson, 2002; Upchurch, Barrett & Dodson, 2004). This standpoint created a gap in our understanding of the origins of sauropods, especially because no members of this clade could be recognized from the Late Triassic Period. In the past five years, however, new discoveries, re-examination of existing specimens and further application of cladistic analysis, have revealed a more detailed and complex picture of basal sauropodomorph relationships and the origin of sauropods. For example, *Isanosaurus* from Thailand (Buffetaut *et al.* 2000), and *Blikanasaurus* (Galton & van Heerden, 1985) and *Antetonitrus* (Yates & Kitching, 2003) from South Africa represent very basal sauropods from the Late Triassic Period. Furthermore, a number of recent cladistic analyses (Yates, 2003, 2004, 2005; Pol & Powell, 2005; Yates & Kitching, 2003) have cast doubt on the monophyly of the Prosauropoda and indicate that some taxa (such as *Anchisaurus* and *Melanorosaurus*) might be regarded as basal sauropods. Other recent analyses (e.g. Galton & Upchurch, 2004), however, continue to support the view that most basal sauropodomorphs from the Late Triassic and Early Jurassic Periods belong to a monophyletic Prosauropoda. Consequently, the phylogenetic relationships of basal sauropodomorphs are currently in a state of flux. It is important, therefore, that we continue to re-evaluate existing taxa, especially those that display combinations of character states that

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have previously united Prosauropoda and Sauropoda. One such taxon forms the focus of this paper: *Chinshakiangosaurus* from Lower Jurassic deposits in China.

In 1970, one of us (ZX) and colleagues collected sauropodomorph material from the lower part of the Fengjiahe Formation of Zhonghe, Yungyin County, Dianzhong Basin, central Yunnan, People's Republic of China (Ye, 1975; Dong, 1992). This unit consists of grey-red and purplish-red mudstones, siltstones and sandstones, which are believed to have been deposited under fluviolacustrine conditions, and is suggested to be a lateral equivalent of the Dull Purplish Beds of the Lower Lufeng Formation (Dong, 1992). Ye (1975) suggested an Early Jurassic age for the Fengjiahe Formation, a conclusion supported by biostratigraphical correlations using ostracods, bivalves and other aquatic invertebrates (Chen *et al.* 1982). The dinosaur material consisted of one or more partial skeletons, including a 12–13 m long individual that was later designated as the holotype (IVPP V14474: see Dong, 1992). Ye (1975) proposed the name *Chinshakiangosaurus chunghoensis* for IVPP V14474; a second species name, *C. zhonghoensis*, was later erected by Zhao (1985) for the same specimen (probably as a result of differences in transliteration from Chinese to English). Neither author provided a diagnosis, description or illustration of the material, with the result that these taxa were *nomina nuda*. Subsequently, Dong (1992) provided a brief description of the partial mandible, cervical centrum and femur that form part of the holotype specimen, and figured the mandible under the name *Chinshakiangosaurus chunghoensis* Ye; this action satisfies ICZN criteria for the erection of new names, with the consequence that the correct authorship is *Chinshakiangosaurus chunghoensis* Ye *vide* Dong, 1992. In addition to those elements already mentioned, IVPP V14474 includes dorsal vertebrae, several cranial caudal vertebrae, a pair of scapulae, an incomplete pelvic girdle, and the hind limbs. Unfortunately, the majority of this material is currently in storage and cannot be accessed at present.

Dong (1992) noted some similarities between the teeth of *Chinshakiangosaurus* and those of sauropods, but suggested that more detailed comparisons indicated that this taxon is a member of the Melanorosauridae (Prosauropoda). No subsequent studies have considered *Chinshakiangosaurus*, except for the recent review by Upchurch, Barrett & Dodson (2004). The latter placed *Chinshakiangosaurus* within the Sauropoda (though without discussion) and regarded it as a *nomen dubium* (but see 'Diagnosis' below).

Chinshakiangosaurus is important for two reasons: (1) it displays an unusual combination of character states and (2) it potentially provides an extremely rare opportunity to examine cranial features in a very basal sauropod. In this study, therefore, we provide the first detailed description, comparison and illustration of the mandible of *Chinshakiangosaurus*, and use cladistic analysis to determine its probable phylogenetic relationships. We then consider the sequence of character state acquisition in the lower jaws and teeth of basal sauropodomorphs in order to gain new insights into the cranial evolution and feeding strategies of the earliest sauropods.

2. Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA.
FMNH, Field Museum of Natural History, Chicago, USA.
HMN, Humboldt Museum für Naturkunde, Berlin, Germany.
IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China.
NGM, Nanjing Geological Museum, Nanjing, People's Republic of China.
YXA, Yuxi Regional Administrative Academy, Yunnan, People's Republic of China.

3. Systematic palaeontology

DINOSAURIA Owen, 1842

SAUROPODOMORPHA von Huene, 1932

SAUROPODA Marsh, 1878

Chinshakiangosaurus chunghoensis Ye *vide* Dong, 1992

Holotype. A partial skeleton (IVPP V14474) comprising a nearly complete left dentary, at least one cervical, dorsal vertebrae, several cranial caudals, both scapulae, incomplete pelvic girdle, and the hind limbs.

Diagnosis. The dentary displays a unique combination of character states, being the only known taxon in which there is a ridge on the central and caudal part of the lateral surface, and a lateral plate (which increases in height towards the rostral end of the jaws) supporting the tooth crowns labially. In addition, the cladistic analyses performed in this study indicate that the height:length ratio of the dentary (> 0.2), and the loss of the constriction between the tooth crowns and their roots, potentially represent autapomorphic reversals (see Appendix 1).

Locality and horizon. Lower part of the Fengjiahe Formation (Lower Jurassic) of Zhonghe, Yungyin county, Dianzhong Basin, Yunnan Province, People's Republic of China.

Comments. The designation of this taxon as a *nomen dubium* by Upchurch, Barrett & Dodson (2004) was premature, given the unique combination of character states and possible autapomorphic character reversals observed in the holotype dentary. We propose, therefore, that *Chinshakiangosaurus* should be regarded as a

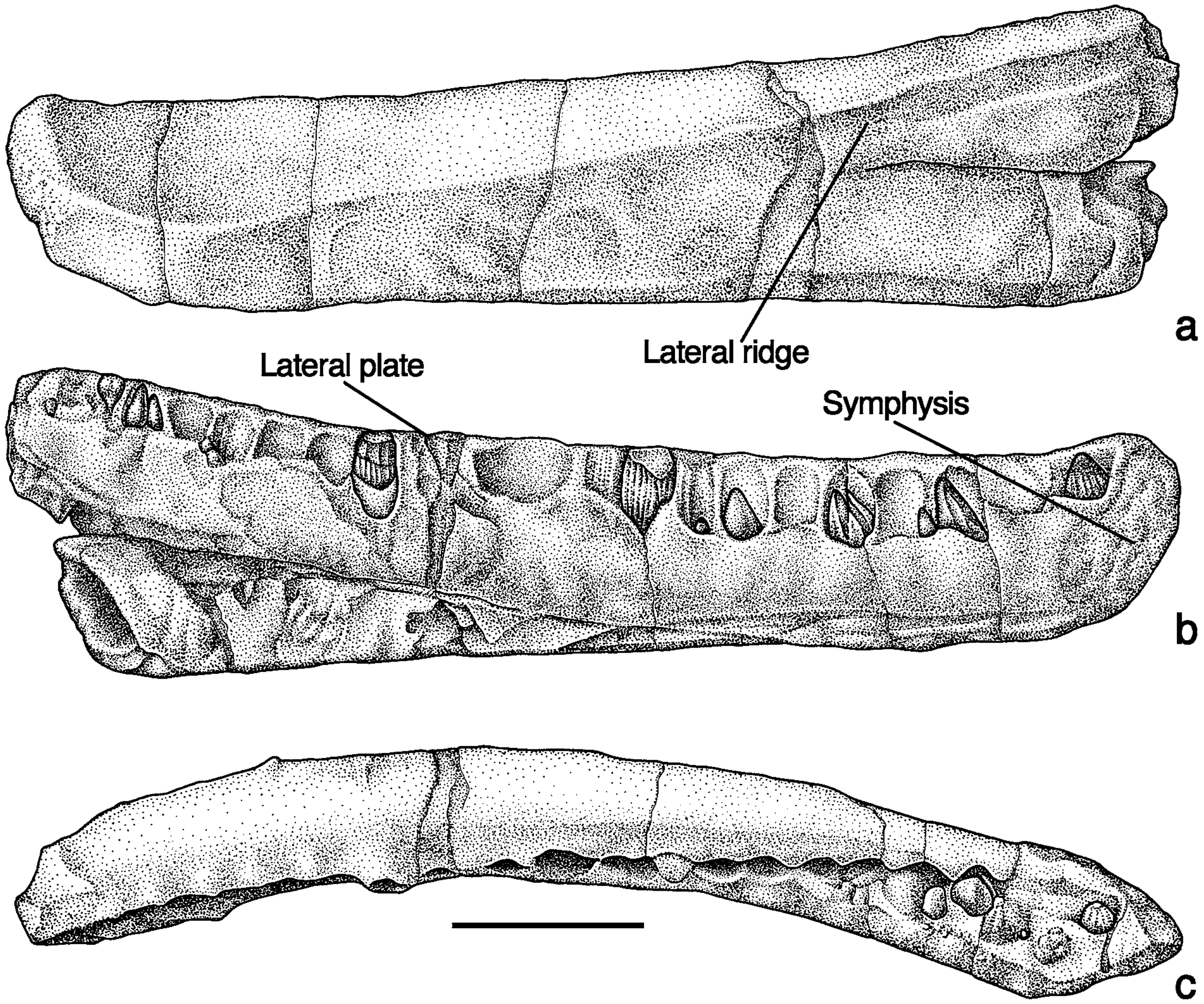

Figure 1. Left dentary of *Chinshakiangosaurus chunghoensis* (IVPP V14474) in (a) lateral; (b) medial; (c) dorsal views. Scale bar = 50 mm.

provisionally valid taxon pending more detailed study. Moreover, the status of *Chinshakiangosaurus* should be based on an assessment of all of the material, but to date only limited information on the mandible, one cervical and the femur has been available.

4. Description

4.a. Dentary (Fig. 1)

IVPP V14474 includes an almost complete left dentary that lacks only its caudalmost part. The specimen has been slightly deformed by crushing; its dorsolateral margin has been pushed ventromedially along most of its length, but otherwise it is relatively well preserved. The dentary is long and slender and is dorsoventrally tallest at its caudal margin. It tapers very gradually in dorsoventral height towards the symphysis (Fig. 1). In lateral view, the ventral margin is almost straight and the dorsal margin is very gently concave. The rostral margin is bluntly rounded and does not possess a distinct 'chin'. Thus *Chinshakiangosaurus* lacks the derived dorsoventrally enlarged symphyseal region that characterizes eusauropods (Upchurch, 1998; Upchurch & Barrett, 2000; Upchurch, Barrett & Dodson, 2004).

The lateral surface of the dentary (Fig. 1a) is gently convex dorsoventrally in its rostral part. Caudally, a marked ridge arises at the caudodorsal corner of the dentary and extends rostroventrally before fading out at about two-thirds of the length of the bone from the caudal end. This ridge has been slightly exaggerated by crushing, but would remain as a genuine feature if distortion were accounted for. Such a ridge is a derived character state that is present in most prosauropods (Galton & Upchurch, 2004), where it is believed to represent a buccal emargination associated with a fleshy cheek (Galton, 1986). This structure, however, has never been found in any sauropod except *Anchisaurus* (Galton, 1986; Yates, 2004; see 'Discussion'). The area immediately ventral to this ridge is gently convex dorsoventrally, except at its caudal end where a shallow depression covers the ventrolateral part of the dentary. The area dorsal to the ridge

Table 1. Dimensions of the *Chinshakiangosaurus* specimen

Description	Meas.
Total length of dentary as preserved (along the dorsal margin)	275
Total length of dentary as preserved (along ventral margin)	240
Dorsoventral height of the symphysis	46
Rostrocaudal width of the symphysis	30
Dorsoventral height of the broken caudal end of the dentary	72
Depth of lateral plate at its rostral end	20
Depth of lateral plate at its caudal end	11
Maximum mesiodistal width of the 14th tooth crown	12

Measurements of the partial left dentary and the best-preserved tooth (in position 14) of *Chinshakiangosaurus chunghoensis* (IVPP V14474). Abbreviation: Meas. – measurement. All measurements in millimetres.

(that is, within the buccal emargination) is almost flat dorsoventrally and rostrocaudally. There are at least two shallow depressions, just ventral to the dental parapet, that may represent nutritive foramina, but these are indistinct and their identification cannot be confirmed. There is no evidence for the attachment of a rhamphotheca at the rostral end of the dentary.

The caudal end of the dentary displays some evidence that it was divided into caudodorsal and caudoventral processes. A notch between these two processes probably marks the rostralmost boundary of the external mandibular fenestra, and this feature lies within the central portion of the caudolateral depression mentioned above.

In medial view (Fig. 1b), there is a dorsoventrally narrow Meckelian canal that is open caudally, tapers in dorsoventral height and gradually fades out into the ventral surface of the bone rostrally. The medial surface is dorsoventrally flat caudally, becoming more strongly convex rostrally. The symphysis is large and rostrocaudally expanded, but is widest dorsoventrally (Table 1). The symphysis is sub-elliptical in outline, with the long axis of this ellipse extending caudoventrally at an angle of approximately 30° to the vertical. There is a distinct lateral plate that, if fully erupted teeth were present, would have covered the basal third of their labial surfaces. As in eusauropods (Upchurch, 1995, 1998; Yates & Kitching, 2003; Upchurch, Barrett & Dodson, 2004), this lateral plate is lowest at its caudal end and increases in height rostrally (Table 1). There is some evidence for small interdental plates dividing adjacent alveoli medially, but these are poorly preserved. Nineteen tooth positions are preserved, probably representing the entire tooth row; this tooth count is greater than that in all known sauropods, but fewer than in *Plateosaurus* and closely related prosauropods (Yates & Kitching, 2003). The alveoli are smallest at the caudal end of the tooth row and increase in diameter and depth towards the symphysis. Increasing tooth size towards the rostral end of the jaws is a derived state present in most sauropods and many juvenile prosauropods (Upchurch, 1998; Yates & Kitching, 2003). There is no gap between the first alveolus and the rostral end of the dentary, unlike the situation in most prosauropods (Sereno, 1989; Yates & Kitching, 2003; Galton & Upchurch, 2004).

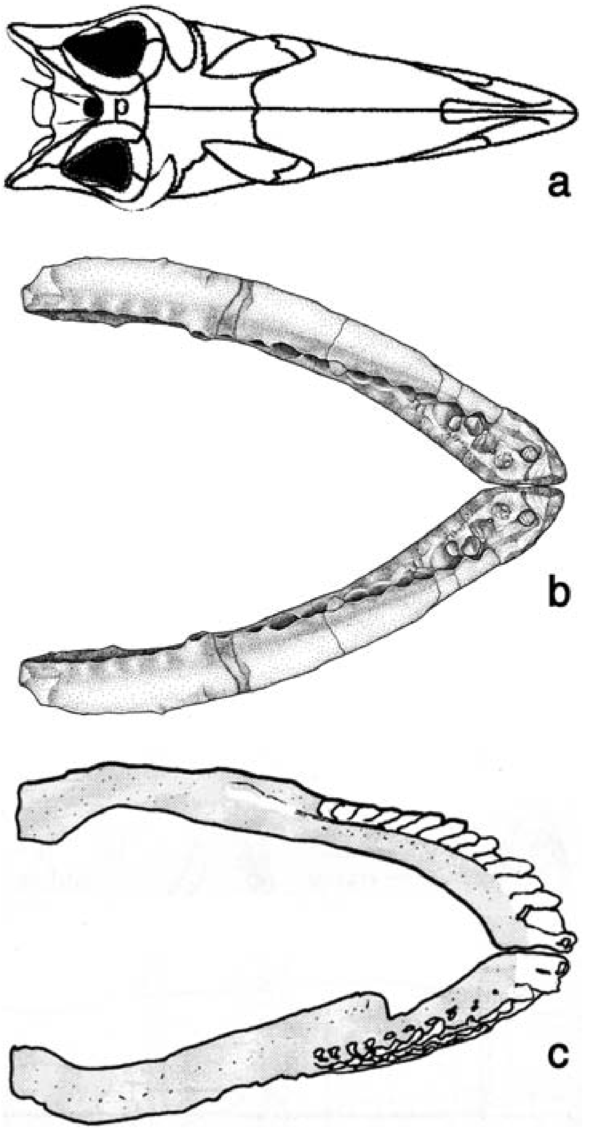

Figure 2. Comparative dorsal profiles of the snout/mandible of representative sauropodomorphs: (a) skull of *Plateosaurus* (AMNH 6810; after Galton, 1985*b*); (b) reconstruction of the conjoined dentaries of *Chinshakiangosaurus* (IVPP V14474) created by reflecting the left dentary through the sagittal plane; (c) *Brachiosaurus* (HMN S66; after Upchurch, 1998).

In dorsal view (Figs 1c, 2), the dentary is bowed laterally so that, with the symphysis held vertically, it can be seen that the paired lower jaws would have formed a relatively broad ‘U’-shape, suggesting that the skull of *Chinshakiangosaurus* did not possess the acute triangular snout present in prosauropods, basal theropods and basal ornithischians (Upchurch, 1998; Yates & Kitching, 2003). The ventral margin of the dentary is gently rounded transversely throughout its length. This surface is slightly wider transversely at its rostral end and narrows caudally.

4.b. Dentition (Fig. 3)

The dentary preserves seven unerupted teeth (alveoli 1, 2, 3, 5, 7, 8, 19), one root with the crown sheared away, and two partially erupted crowns that have been damaged apically (alveoli 9 and 14). Of these, none are completely visible, though several offer some informative characters. The limited information available suggests that tooth size increased towards the rostral end of the jaws, supporting the observation based on alveolus size above. The teeth are mesiodistally broad, but do not appear to have been greatly expanded relative to the root. Thus the teeth are more lanceolate, like those of most prosauropods, rather than strongly spatulate as in sauropods (Galton, 1986; Upchurch, 1998; Yates & Kitching, 2003). The crown margins appear to have been coarsely denticulate, with these denticles extending along at least the apical third of the tooth crown, though their more basal extent cannot be assessed. The tooth enamel is wrinkled and reticulate as in eusauropods (Wilson & Sereno, 1998). Cross-sections through the partially erupted teeth indicate that the crowns are labiolingually compressed. The labial surface of the crown is convex mesiodistally, apart from the presence of a longitudinal groove on the distal part. The lingual surface is convex mesiodistally in its distal part but the mesial portion has a broad longitudinal groove; the latter is potentially homologous with the more prominent lingual concavity present on the teeth of eusauropods (Upchurch, 1995, 1998; Upchurch, Barrett & Dodson, 2004). The tooth root is sub-circular in cross-section. The teeth are too poorly preserved to determine whether they contacted each other and/or formed an imbricate arrangement.

5. Phylogenetic analyses

In order to investigate its phylogenetic relationships, character data for *Chinshakiangosaurus* has been coded into two of the largest and most recent cladistic data-matrices for basal sauropodomorphs (Yates & Kitching, 2003; Galton & Upchurch, 2004). Our incomplete knowledge of *Chinshakiangosaurus* means that only a small number of characters can be coded: 8.4 % for Yates & Kitching (2003) and 9.4 % for Galton & Upchurch (2004) (see Appendix 2 for details). The unaltered data-matrices (that is, excluding *Chinshakiangosaurus*) were analysed using PAUP 4.0b10 (Swofford, 2002), in order to ensure that the original analyses could be replicated. In both cases, the results obtained were identical to those reported by the authors in their studies; this indicates that any changes in topology observed in the modified analyses must be the result of including *Chinshakiangosaurus*.

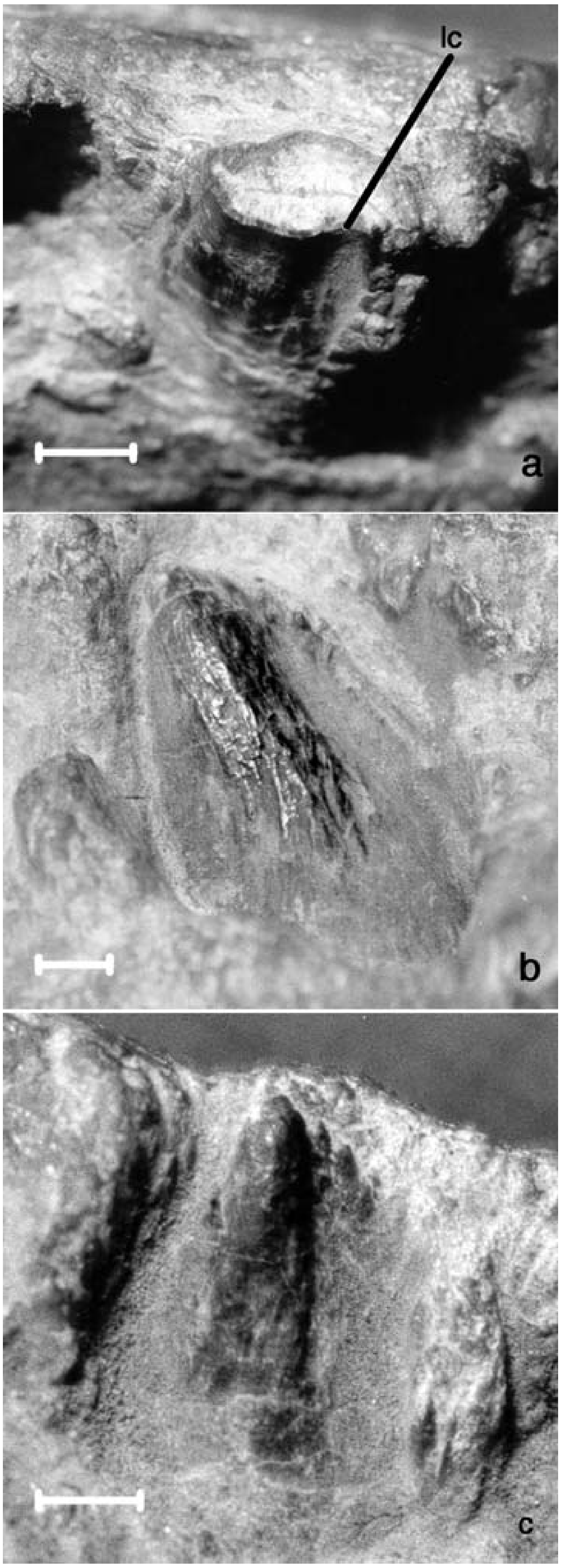

Figure 3. Representative teeth of *Chinshakiangosaurus chunghoensis* (IVPP V14474): (a) tooth no. 14, showing the broken apex and part of the lingual surface ('lc' marks the position of the lingual concavity on the mesial part of this surface); (b) tooth no. 3 in lingual view, showing the wrinkled enamel and some serrations; (c) tooth no. 19 in lingual view, showing the marginal serrations and lingual ridge. Scale bars = 5 mm.

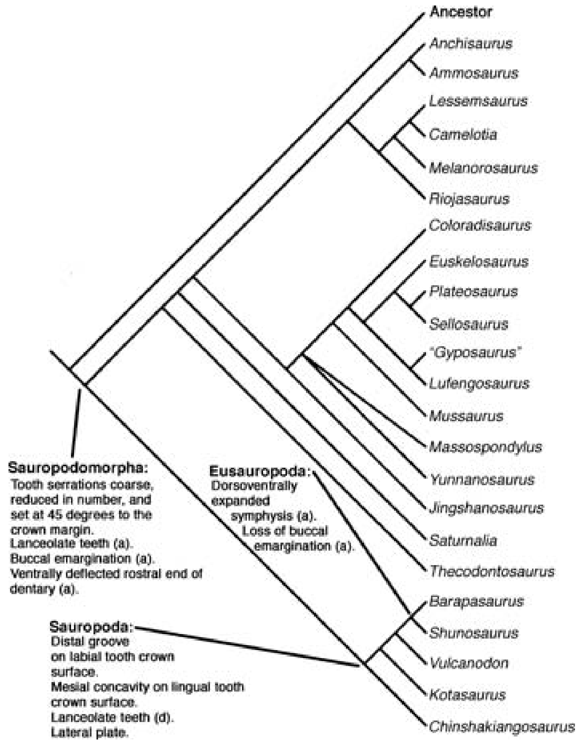

Figure 4. A cladogram of basal sauropodomorph relationships. This topology was obtained by subjecting the modified version of the Galton & Upchurch (2004) data-matrix to the Heuristic search in PAUP 4.0b10 (Swofford, 2002). Tree statistics are summarized in the text. Note that *Blikanasaurus* has been deleted *a posteriori* in order to clarify the relationships among basal sauropods (see text for details). Some of the key character state transformations, relevant to the evolution of the sauropod skull, are listed. Synapomorphies marked by '(a)' or '(d)' occupy their positions under accelerated and delayed transformation respectively. Full details of apomorphy distributions are presented in Appendix 1.

5.a. Results

5.a.1. Galton & Upchurch (2004)

Inclusion of *Chinshakiangosaurus* means that the modified Galton & Upchurch data-matrix is composed of 137 osteological characters for 24 ingroup sauropodomorphs and one outgroup (the hypothetical 'Ancestor'). This new matrix was analysed using the Heuristic search in PAUP 4.0b10 (Swofford, 2002), with the same starting assumptions and conditions as those utilized by Galton & Upchurch (2004). This yielded six most parsimonious trees (MPTs) of length 281 steps ($CI = 0.555$, $RI = 0.635$, $RCI = 0.352$). Thus, the inclusion of *Chinshakiangosaurus* has resulted in an increase in the number of MPTs (by four), and an increase in tree length (by two steps) relative to the original analysis. The new MPT topologies are essentially identical to those found by Galton & Upchurch (2004): *Chinshakiangosaurus* is placed at the base of the Sauropoda along with *Blikanasaurus* (Fig. 4). It is the uncertainty of the relationships between *Chinshakiangosaurus*, *Blikanasaurus* and the remaining sauropods (a monophyletic clade containing *Kotasaurus*, *Vulcanodon*, *Shunosaurus* and *Barapasaurus*) that is responsible for the increased number of MPTs. If *Blikanasaurus* is deleted, *a posteriori*, from the six MPTs (a form of reduced consensus: see Wilkinson, 1994), then we obtain two tree topologies that match those found by Galton & Upchurch (2004), with *Chinshakiangosaurus* placed as the most basal sauropod (Fig. 4).

The robustness of this analysis has been explored using a PTP test, bootstrapping and Templeton's tests, as implemented in PAUP 4.0b10 (Swofford, 2002). The PTP test used 10 000 replicates and the Heuristic search option. The modified data-matrix passed this test with a p-value of < 0.0001. This indicates that the data-matrix as a whole contains a strong non-random signal, but does not necessarily confirm that the position of *Chinshakiangosaurus* is strongly supported. The bootstrap analysis also used 10 000 replicates and the Heuristic search option. The bootstrap value for the position of *Chinshakiangosaurus* is, not surprisingly, $< 50\%$. This low support is partly caused by the fact that *Chinshakiangosaurus* itself can only be coded for a small number of characters. However, poor support is also caused by the instability of *Blikanasaurus*. The latter is extremely incomplete, being known only from the distal part of a left hind limb (Galton & van Heerden, 1985, 1998). If *Blikanasaurus* is deleted from the analysis prior to the application of bootstrapping, support for the position of *Chinshakiangosaurus* increases to 76 %. As a final test of the relationships of *Chinshakiangosaurus*, a topological constraint was created in which the latter taxon is forced to cluster within the monophyletic Prosauropoda (*sensu* Galton & Upchurch, 2004). With this constraint enforced, the data-matrix was analysed using a Heuristic search (Swofford, 2002) and the shortest trees were collected. This analysis yielded 30 MPTs of tree length 285 steps. A Templeton's test was then used to compare these 'constrained MPTs' with the 'unconstrained MPTs'. The results (p-values $= 0.450$–0.465) indicate that placement of *Chinshakiangosaurus* within the Prosauropoda is not a statistically significantly worse explanation of the data, than is its position within the basal Sauropoda.

5.a.2. Yates & Kitching (2003)

Inclusion of *Chinshakiangosaurus* means that the modified Yates & Kitching data-matrix is composed of 212 osteological characters for 20 ingroup sauropodomorphs and two outgroups (*Herrerasaurus* and Neotheropoda). This new matrix was analysed using the Branch-and-bound search in PAUP 4.0b10 (Swofford, 2002), with the same starting assumptions and conditions as those utilized by Yates & Kitching (2003). This yielded seven MPTs of length 457 steps ($CI = 0.534$, $RI = 0.726$, $RCI = 0.388$). Thus, the

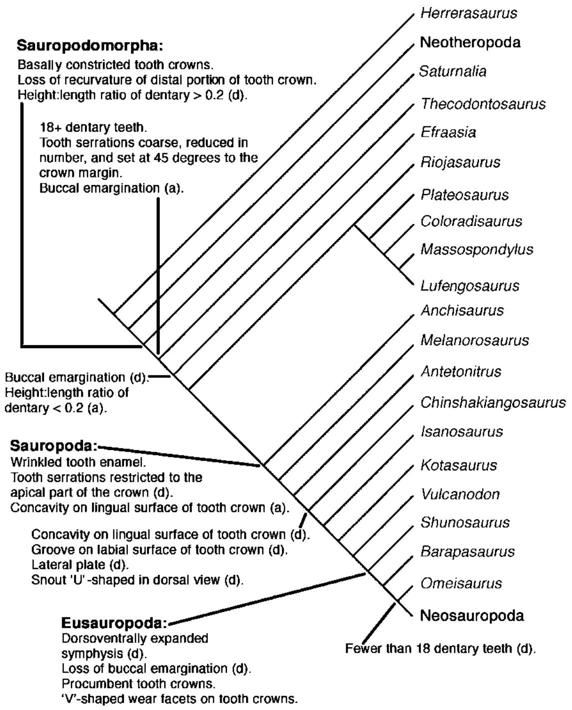

Figure 5. A cladogram of basal sauropodomorph relationships. This topology was obtained by subjecting the modified version of the Yates & Kitching (2003) data-matrix to the Branch-and-bound search in PAUP 4.0b10 (Swofford, 2002). Tree statistics are summarized in the text. Note that *Blikanasaurus* has been deleted *a posteriori* in order to clarify the relationships among basal sauropods (see text for details). Some of the key character state transformations, relevant to the evolution of the sauropod skull, are listed. Synapomorphies marked by '(a)' or '(d)' occupy their positions under accelerated and delayed transformation respectively. Full details of apomorphy distributions are presented in Appendix 1.

inclusion of *Chinshakiangosaurus* has resulted in an increase in MPT number (by two) and tree length (by eight steps). The new MPT topologies are essentially identical to those found by Yates & Kitching (2003). The application of reduced consensus (Wilkinson, 1994) indicates that a single tree topology (Fig. 5) can be obtained via the *a posteriori* deletion of *Blikanasaurus*. In this reduced consensus tree, *Chinshakiangosaurus* is placed within basal Sauropoda, above *Anchisaurus*, *Melanorosaurus* and *Antetonitrus*, and below *Isanosaurus*, *Kotasaurus*, *Vulcanodon*, *Shunosaurus*, *Barapasaurus*, *Omeisaurus* and Neosauropoda.

The robustness of this analysis has been explored using a PTP test, bootstrapping and a Templeton's test, as outlined above. The modified data-matrix passed the PTP test with a p-value of < 0.0001. This indicates that the data-matrix as a whole contains a strong non-random signal, but again does not necessarily provide strong support for the position of *Chinshakiangosaurus*. The bootstrap value for the position of *Chinshakiangosaurus* is 53 % (though the majority-rule consensus tree does not resolve the relationships between *Chinshakiangosaurus*, *Blikanasaurus*, *Antetonitrus* and a clade containing higher sauropods). Again, this probably reflects the large amount of missing data for *Chinshakiangosaurus* and many of the taxa that cluster close to it within the basal Sauropoda. For example, if *Blikanasaurus* is deleted from the analysis prior to the application of bootstrapping, support for the position of *Chinshakiangosaurus* increases to 71 % and the relationships with *Antetonitrus* and higher sauropods are fully resolved. As described above, a constraint tree was used to force *Chinshakiangosaurus* to cluster within the Prosauropoda (*sensu* Yates & Kitching, 2003, that is, within a relatively small clade containing *Riojasaurus*, *Plateosaurus*, *Massospondylus*, *Coloradisaurus* and *Lufengosaurus*). This analysis found ten MPTs of length 480 steps. A Templeton's test was then used to compare the 'constrained MPTs' with the 'unconstrained MPTs'. The results (p-values = 0.0005–0.0006) indicate that placement of *Chinshakiangosaurus* within the Prosauropoda is a statistically significantly worse explanation of the data than is its position within the basal Sauropoda.

6. Discussion

Here, we are concerned with two main issues: (1) given the limited information available, can we justify placement of *Chinshakiangosaurus* within the basal Sauropoda?, and (2) what are the implications of *Chinshakiangosaurus* for our understanding of early sauropod cranial evolution?

6.a. Is *Chinshakiangosaurus* a basal sauropod?

The very incomplete character data currently available for *Chinshakiangosaurus* obviously places a severe limit on our ability to test its phylogenetic relationships. Nevertheless, the data-matrices of both Yates & Kitching (2003) and Galton & Upchurch (2004) place *Chinshakiangosaurus* as a basal sauropod. Bootstrap values are inevitably low, but the Templeton's tests for the Yates & Kitching data indicate that the proposed position for *Chinshakiangosaurus* is a statistically better interpretation of the data than alternatives that would place this taxon within the Prosauropoda.

Chinshakiangosaurus shares the following synapomorphies with other sauropods, according to *both* Yates & Kitching (2003) and Galton & Upchurch (2004), except where stated otherwise. (NB: the distribution of some of these features is affected by missing data and may depend on whether accelerated or delayed transformation optimization is employed; see Appendix 1 for further details):

1. Presence of a lateral plate of bone that supports the basal portions of tooth crowns labially. This feature was first noted as a synapomorphy of Eusauropoda by Upchurch (1995). It was not

included as a character by Galton & Upchurch (2004) because it could only be coded for one of their ingroup taxa (*Shunosaurus*). However, if the lateral plate had been added to the modified version of the Galton & Upchurch (2004) matrix employed in this study, it would also have unequivocally united *Chinshakiangosaurus* with other sauropods, in agreement with the Yates & Kitching (2003) analysis.
2. Snout 'U'-shaped in dorsal profile. This feature was first recognized as a synapomorphy of Eusauropoda by Upchurch (1998).
3. Lingual surface of each tooth crown concave. This feature was cited as a synapomorphy of Eusauropoda by Upchurch (1995). *Chinshakiangosaurus* displays the derived state incipiently (a shallow concavity on the mesial portion of the lingual surface of the crown), whereas in more derived sauropods the entire lingual surface is often deeply excavated.
4. Groove on the labial surface of the tooth crown, near the distal margin. Upchurch (1995) noted the presence of two labial grooves, near the mesial and distal margins of the crown, respectively, as a synapomorphy of Eusauropoda. *Chinshakiangosaurus* demonstrates that this feature should be split into two separate characters, because it appears that the distal groove evolved earlier than the mesial one.
5. Wrinkled tooth enamel. This feature was first cited as a synapomorphy of Eusauropoda by Wilson & Sereno (1998). The distribution of this character state is slightly problematic (see Appendix 1) because it is also found in *Anchisaurus*, which could be a true prosauropod (*sensu* Galton & Upchurch, 2004) or the most basal of all known sauropods (Yates & Kitching, 2003). Nevertheless, it is worth noting that *Chinshakiangosaurus* possesses wrinkled tooth enamel, and that this is a derived feature that is only known in unequivocal sauropods and *Anchisaurus*.
6. Cranial face of the femur straight in lateral view. This derived character state only unites *Chinshakiangosaurus* with other sauropods according to Galton & Upchurch (2004).

Thus, in summary, it would be prudent to regard the proposed phylogenetic relationships of *Chinshakiangosaurus* with some caution. Nevertheless, the best available evidence indicates that this taxon is probably a very basal sauropod. The preservation of a mandible and teeth in this taxon therefore provides an important glimpse into early sauropod cranial evolution.

6.b. Mapping cranial character evolution

The major shifts in feeding strategy, from carnivorous basal saurischian, through omnivorous or herbivorous 'prosauropod-grade' animals, to truly herbivorous sauropods, should have been accompanied by some profound modifications to the skull and dentition. To date, however, there has been such a large morphological gap between the various basal members of the major dinosaurian clades and the eusauropods, that it has proved very difficult to determine or even constrain the sequence of character state changes during the initial phases of sauropod evolution. The proposal by Yates & Kitching (2003) and Yates (2004) that *Anchisaurus* is the most basal of all known sauropods would help to fill this gap, but the relationships of this taxon remain controversial. If, as Galton & Upchurch (2004) have proposed, *Anchisaurus* is in fact a prosauropod closely related to the melanorosaurids, then our knowledge of the most basal sauropod skulls must rely very heavily on *Chinshakiangosaurus*. Thus, *Chinshakiangosaurus*, despite the large amount of unavailable data, represents an important taxon because it is either the most basal of all sauropods where skull material is known (Galton & Upchurch, 2004), or it provides an intermediate between *Anchisaurus* and Eusauropoda (Yates & Kitching, 2003). In order to explore early sauropod cranial evolution, the characters that can be scored for *Chinshakiangosaurus* have been mapped onto the MPTs found by the analyses of the modified Yates & Kitching (2003) and Galton & Upchurch (2004) datasets (Figs 4, 5). Despite the ambiguities caused by missing data, both delayed and accelerated transformation optimization in PAUP (see Appendix 1) indicate that there is considerable agreement regarding the sequence of character state acquisition. For convenience, we have divided the following discussion into three phases of sauropodomorph evolution: 'basal Sauropodomorpha' (*Saturnalia*, *Thecodontosaurus* and true prosauropods), 'basal Sauropoda' (*Anchisaurus* and *Chinshakiangosaurus*) and 'Eusauropoda' (*Shunosaurus*, *Omeisaurus* and neosauropods).

1. Basal Sauropodomorpha. Some of the earliest cranial synapomorphies acquired in the most plesiomorphic sauropodomorphs include: tooth serrations are fewer in number and larger, and are set at 45° to the crown margin; tooth crowns are lanceolate (they loose their apical recurvature and develop a basal constriction); ridge on the lateral surface of the dentary and associated buccal emargination are present; rostral end of the dentary curves downwards; number of dentary teeth is increased to 18 or more (see also Galton, 1985*a*, 1986).
2. Basal Sauropoda. The earliest sauropods retained the buccal emargination and lateral ridge, coarsely serrated lanceolate teeth, 18 or more dentary teeth, and a relatively unexpanded symphysis. However, these features were combined with several innovations, such as wrinkled tooth enamel. At some

point during the evolution between very basal sauropods like *Anchisaurus* and more derived forms such as Chinshakiangosaurus, a series of additional derived character states were acquired. These features include: a lateral plate that supports the bases of the tooth crowns labially; a groove on the labial surface of each tooth crown near the distal margin; incipient excavation of the lingual surface of the tooth crown near its mesial margin; and a snout that is broad and 'U'-shaped in dorsal view rather than narrow and pointed.

3. Eusauropoda. The skulls of eusauropods, such as *Shunosaurus* and *Omeisaurus*, indicate that several additional modifications had occurred relative to more basal forms. The main innovations include: presence of a strong dorsoventral expansion of the dentary symphysis; loss of the buccal emargination and lateral ridge on the dentary; a reduction in the size of the external mandibular fenestra (closed altogether in *Omeisaurus* and neosauropods); presence of a groove on the labial surface of the tooth crown near the mesial margin; increased prominence of the excavation on the lingual surface of the tooth crown; tooth crowns become procumbent; and in sauropods above the level of *Shunosaurus*, the number of dentary teeth is reduced to less than 18. Furthermore, it should be noted that the evolution of these features also coincides with the appearance of occlusion in sauropods, as shown by the presence of high-angled, 'V'-shaped wear facets on the margins of the tooth crowns (Wilson & Sereno, 1998; Upchurch & Barrett, 2000).

Relatively few studies have examined the functional significance of individual cranial characters in sauropodomorphs. As a result, the biomechanical and palaeoecological roles of many features, such as wrinkled tooth enamel, are not understood at present. Nevertheless, functional studies and comparative anatomy provide insights into some of these cranial and dental characters, as summarized below:

1. The loss of the recurvature of the tooth crowns as they become lanceolate, and the acquisition of a smaller number of coarser serrations, seem to be associated with increased amounts of vegetation in the diet (Galton, 1985*a*, 1986; Crompton & Attridge, 1986; Barrett, 2000). Laterally compressed, recurved, sharply pointed and finely serrated teeth are well suited for a carnivorous diet, and are found in many basal archosaurs, early dinosaurs (such as *Herrerasaurus*) and most theropods (e.g. Abler, 1992). The teeth of both ornithischian and sauropodomorph dinosaurs become more symmetrical in labial view, develop a basal constriction in most forms and typically possess a small number of coarse serrations (Galton, 1985*a*, 1986; Crompton & Attridge, 1986). Barrett (2000) noted that the possession of recurved premaxillary and lanceolate maxillary/dentary teeth in extant iguanid lizards is correlated with diets that included a mixture of animal and plant material. Prosauropods (such as *Massospondylus* and *Jingshanosaurus*) often display this 'omnivorous' pattern. In contrast, eusauropods have lost the recurvature of the mesial teeth and have a more typically herbivorous condition, in which the tooth crowns are more markedly expanded mesiodistally and are often heavily worn (Barrett, 2000; Upchurch & Barrett, 2000).
2. The buccal emargination is found in basal sauropodomorphs and Ornithischia. This structure is associated with a ridge on the dentary and large nutritive foramina on the lateral surface of this element and the maxilla. Together, these features are believed to indicate the presence of a fleshy cheek that would help retain plant material in the mouth during oral processing (Galton, 1973, 1986). Some recent studies have cast doubt on this interpretation on the basis of the 'extant phylogenetic bracket' (EPB) (Witmer, 1995; Papp & Witmer, 1998; Czerkas, 1999). As these authors point out, neither extant crocodiles nor birds have a fleshy cheek or the facial musculature that creates the contractile muscular cheek in mammals. However, there are several empirical and theoretical arguments countering the claim that Ornithischia and prosauropods did not have a fleshy cheek. For example, if mammals were extinct, their EPB (Lissamphibia and Sauropsida) would indicate that they lacked cheeks; this is because this structure appeared during the evolution of mammals from their basal synapsid ancestors (Kemp, 1982) and was not present in the common ancestor of the three taxa within the EPB. Thus, the EPB does not take evolutionary novelty into account and can, therefore, constrain inferences of function (based purely on phylogenetic grounds) even in the face of functional/biomechanical evidence to the contrary. The pleurokinetic jaw mechanism and tooth batteries of advanced ornithopods (Norman, 1984; Weishampel, 1984) indicate that these animals processed their food orally before swallowing; cheeks would be necessary to prevent triturated food from falling out of the mouth during chewing (see also Galton, 1973). Moreover, the dermal bone laid down in the cheek region of certain ankylosaurs demonstrates that dermal tissue was present in the buccal emargination in at least some ornithischians and that the presence of a fleshy cheek was likely in life (Barrett, 2001). Thus, we conclude that the buccal emargination and lateral ridge in

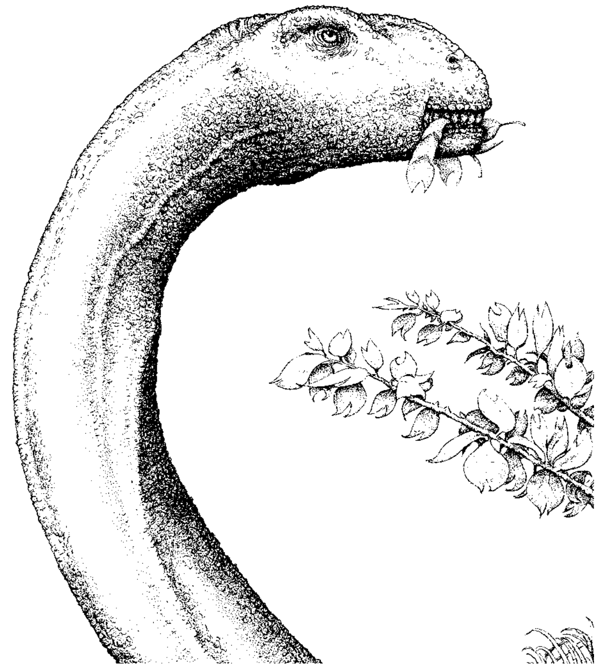

Figure 6. Restoration of *Chinshakiangosaurus chunghoensis* with a fleshy cheek. Courtesy of Robert Laws.

basal sauropodomorphs represent evidence for the presence of fleshy cheeks in these taxa (Fig. 6).

3. The sub-triangular dorsal profile of the snout in basal sauropodomorphs represents a plesiomorphic state that also occurs in the earliest ornithischians and theropods (Sereno, 1991; Sereno *et al.* 1993; Upchurch, 1998, p. 48). Because this morphology is found in carnivorous, omnivorous and herbivorous reptiles, it cannot be easily linked to a particular feeding style. Nevertheless, there are well-documented links between snout width and dietary preference in living herbivorous mammals (e.g. Jarman, 1974; Janis & Ehrhardt, 1988). The narrow snout of primitive dinosaurs must have had implications for food gathering; such a structure is well suited for grasping small prey items and selecting particular portions of a plant (analogous to the selective browsing of various small bovids and cervids among extant herbivores: Jarman, 1974). Conversely, the broadening of the snout displayed by *Chinshakiangosaurus* and eusauropods (Fig. 2) could be interpreted as indicating a shift in feeding strategy away from 'precision' towards the bulk gathering of greater quantities of food material required by taxa with a larger body size (as in the larger bovids and cervids: Jarman, 1974). The acquisition of a broader and more rounded snout also occurs independently in ankylosaurs and advanced ornithopods (e.g. Ostrom, 1961; Barrett, 2001).
4. The lateral plate supports the bases of the tooth crowns labially. This structure lies in direct contact with the crowns themselves and increases in prominence towards the rostral ends of the upper and lower jaws. The latter feature appears to be associated with the size of the tooth crowns, because the largest teeth in eusauropods are usually found at the front of the snout. The biomechanical function of the lateral plate has not yet been investigated rigorously. However, this structure seems to reinforce the crowns against forces that would tend to pull them forwards and outwards. Such forces may have been generated if sauropods fed using a 'cropping' jaw action that tugged and tore foliage from plants.
5. Dorsoventral expansion of the dentary symphysis could conceivably strengthen the mandibles against forces generated during jaw closure. In particular, this expansion of the symphysis increases the surface area available for joining the left and right mandibular rami on the midline, potentially helping to resist forces that would tend to drive them apart. Furthermore, the rostral ends of the jaws may have experienced the greatest biting forces (as judged by the increased size of the teeth and lateral plate) and might therefore have needed reinforcement.

If the above functional interpretations are correct, we can now examine some of the key phases in early sauropodomorph evolutionary history. The most basal sauropodomorphs (such as *Saturnalia* and *Thecodontosaurus*) were small (1–2 m) bipedal taxa (Langer *et al.* 1999; Benton *et al.* 2000; Yates, 2002). Although these forms may have possessed more elongate necks than those of ornithischians and theropods (Upchurch & Barrett, 2000), it seems unlikely that they were exploiting the high-browsing herbivorous niche occupied by later sauropods. Rather, the possession of a sub-triangular narrow-snouted skull, fleshy cheek, recurved rostral teeth and more lanceolate coarsely serrated centrally and caudally located crowns suggest that these early sauropodomorphs were selective omnivores or herbivores. However, the small body size of these taxa would have prevented the bulk processing of large quantities of poor quality plant material exploited by later sauropods (Farlow, 1987).

Anchisaurus may provide an important glimpse into the feeding strategies of the most basal sauropods. It indicates that the very earliest sauropods inherited the small bipedal body-plan, narrow snout, fleshy cheek and coarsely serrated lanceolate teeth that were first acquired in basal sauropodomorphs (Yates, 2004). Sauropods above the level of *Anchisaurus*, however, seem to have invaded a new niche that involved the consumption of increasing quantities of poor quality plant material. This would have required a shift away from selective feeding towards bulk processing, using the long passage time and bacterial breakdown or gut fermentation that can be achieved in large-bodied herbivores (Farlow, 1987). This is demonstrated by the increase in body size to around 10–12 m, the development of a broad 'U'-shaped snout, and the reinforcement of the teeth against forwardly and outwardly directed forces by the lateral plate, which are features present in *Chinshakiangosaurus* and eusauropods. *Chinshakiangosaurus*, however, displays an intermediate stage in the transition from selective omnivore/herbivore to bulk processor, because it retains the fleshy cheek (Fig. 6) and the relatively weak symphysis.

Further modifications to the skull are seen in basal eusauropods such as *Shunosaurus* and *Omeisaurus*. In particular, these forms expand the symphysis dorsoventrally and lose the buccal emargination. This raises the question of why herbivorous sauropods, having inherited a fleshy cheek, should need to lose it later in their evolutionary history. One possibility is that loss of the fleshy cheek facilitated a wider gape. This could have allowed the more centrally and caudally placed teeth to play an additional role in food gathering. Another possibility is that a wider gape permitted bulk ingestion of greater quantities of vegetation per mouthful and/or ingestion of larger individual food items. These possibilities are not mutually exclusive and may have combined to promote the loss of the fleshy cheek in basal eusauropods; such interpretations are all compatible with the idea of a shift to large body size and gut fermentation of bulk fodder (Farlow, 1987).

Development of a precise occlusion also occurs in eusauropods, potentially indicating an increase in oral processing over the basal sauropodomorph condition (Upchurch & Barrett, 2000), but the presence/absence of occlusion cannot be established in *Chinshakiangosaurus* on the basis of current data. It seems anomalous that the fleshy cheek should be lost just as the amount of oral processing increases. It is possible that the increased tooth wear in eusauropods reflects a more precise occlusion of the teeth so that every bite-stroke resulted in tooth–tooth contact. Furthermore, the transition from selective feeding to bulk processing may have increased the number of bite-strokes per unit time utilized during feeding. These ideas can only be tested once we have more detailed information on the dentitions and jaw mechanics of basal sauropods.

6.c. Cranial material from other early sauropods

As well as *Chinshakiangosaurus*, there are other fragmentary taxa from the Lower and Middle Jurassic deposits of China and elsewhere that possess cranial elements. These specimens also display intriguing mosaics of 'prosauropod' and 'sauropod' features, though in many cases they are either too fragmentary or too poorly described to be incorporated into a phylogenetic analysis at present. Here, therefore, we briefly review these specimens and consider their potential significance in the light of the phylogenetic relationships and character state distributions discussed above.

An isolated maxilla (FMNH CUP 2042), from the Lower Jurassic Lower Lufeng Formation of Yunnan (Barrett, 1999), includes a lateral plate and teeth with reticulate enamel ornament, lingual concavities and ridges, all of which are suggestive of a position within Sauropoda. The concavity on the lingual surface of each tooth crown is strongly developed, and the labial surface bears both a mesial and a distal groove. Together, these features suggest that this specimen belonged to a sauropod that is more closely related to eusauropods than is *Chinshakiangosaurus*. This maxilla contains at least 16 alveoli, which is consistent with the evidence from *Chinshakiangosaurus* and *Shunosaurus* that early sauropods retained the derived elevated tooth numbers that are also found in many prosauropods (see Appendix 1).

Isolated teeth (e.g. FMNH CUP 2051, 2056), also from the Lower Lufeng Formation, have been referred to the prosauropod *Yunnanosaurus* (Galton, 1985*a*, 1986). The crowns possess large, high-angled mesial and distal wear facets, which led several authors to propose that they were referable to Sauropoda (Salgado & Calvo, 1997; Wilson & Sereno, 1998; Barrett, 2000). However, these teeth lack wrinkled tooth enamel and possess a sub-cylindrical cross-section. One possibility is that these teeth belong to a prosauropod (*sensu* Galton & Upchurch, 2004), or a sauropod that is even more basal than *Anchisaurus* and *Chinshakiangosaurus*, but this would imply the appearance of precise tooth–tooth contact independently of that seen in eusauropods. Alternatively, these teeth could belong to a more derived sauropod, such as a basal eusauropod, but this requires reversals in terms of the loss of wrinkled tooth enamel and the lingual concavity. In either case, these teeth suggest the presence of a hitherto unrecognized sauropodomorph taxon in the Lower Lufeng (Galton & Upchurch, 2004). The unusual combination of character states present in this taxon is not congruent with the evolutionary scenario for sauropod feeding outlined above (in which wrinkled enamel precedes occlusion); however, definitive evidence of occlusion (or lack thereof) in pivotal taxa such as *Chinshakiangosaurus* obscures the acquisition sequence of these features.

Material of *Gongxianosaurus*, from the Lower Jurassic Ziliujing Formation of Yunnan, includes premaxillae, mandibles and isolated teeth (He *et al.* 1998). At least some of the teeth appear to show evidence of occlusal wear (apical wear facets?: He *et al.* 1998, pl. 1, fig. 2b), lingual concavities and wrinkled enamel ornament, supporting referral to Eusauropoda. Unfortunately, the brief description does not mention the presence/absence of other important feeding-related features, such as the buccal emargination.

Yimenosaurus (YXV 8701), a sauropodomorph of uncertain affinities from the Fengjiahe Formation of Yunnan, possesses an unusual combination of features, including teeth with denticles, lingual concavities and labial grooves, a large external mandibular fenestra and a ventrally displaced jaw joint (Bai, Yang & Wang, 1990). These features suggest that *Yimenosaurus* is a basal sauropod that lies outside of the Eusauropoda, but is more closely related to that clade than is *Chinshakiangosaurus*. The current description of *Yimenosaurus*, however, does not provide information on the presence/absence of tooth wear or buccal emargination.

The phylogenetic position of the Lower Lufeng 'prosauropod' *Yunnanosaurus* remains questionable; most recent analyses (e.g. Benton *et al.* 2000; Yates & Kitching, 2003; Galton & Upchurch, 2004) have either ignored this taxon or utilized character data derived from the original descriptions. It is conceivable that *Yunnanosaurus* will eventually cluster within basal Sauropoda, in a position that is even more basal than *Chinshakiangosaurus*. However, the cranial material of the type specimen of the type species, *Y. huangi*, is rather fragmentary and its ability to provide information on the early stages of cranial evolution is inevitably restricted (NGM 004546: PMB and PU, pers. obs. 2002).

Allain *et al.* (2004) described a new Early Jurassic (Toarcian) sauropod from Morocco, named *Tazoudasaurus naimi*. This specimen includes a dentary with teeth. The dentary does not expand dorsoventrally towards its rostral end, and the teeth are spatulate and serrated. These character states suggest that *Tazoudasaurus* probably represents a basal sauropod, lying outside of the Eusauropoda, but perhaps more derived than *Chinshakiangosaurus* because of the former's spatulate rather than lanceolate tooth crowns. A more complete understanding of the significance of the Moroccan material must await its inclusion in cladistic analysis.

Finally, Buffetaut (2005) described *Archaeodontosaurus descouensi*, from the Middle Jurassic (Bathonian) of northwest Madagascar, based on a partial right dentary containing several unerupted and broken teeth. The symphysis is robust, the lateral ridge is absent, the lateral plate is probably present (though the medial margins of the alveoli are damaged) and the teeth possess wrinkled enamel. Although broad, the dorsal profile of the lower jaw would seem to have been very similar to that in *Chinshakiangosaurus* (Fig. 2), suggesting that *Archaeodontosaurus* was perhaps more basal than most eusauropods. Furthermore, the teeth have large serrations set at 45° to the crown, and the lingual surfaces of the crowns are convex rather than concave. Thus, although the majority of observable character states suggest that *Archaeodontosaurus* represents some form of basal eusauropod that is more derived than *Chinshakiangosaurus* and *Tazoudasaurus*, the convex lingual tooth crown surfaces conflict with this overall assessment. Buffetaut (2005) noted this inconsistency and argued that the presence of prosauropod-like teeth in an otherwise rather eusauropod-like dentary indicates a more complex mosaic history for character state acquisition in basal sauropod jaws and teeth. This view is supported by the character state distributions summarized in Appendix 1, and the addition of the taxa listed above to future cladistic analyses is likely to complicate this picture further. However, some of this mosaic complexity is removed or reduced once it is accepted that sauropods evolved from taxa with rather prosauropod-like skulls and teeth; the presence of convex lingual crown surfaces and serrations then become symplesiomorphies shared by basal sauropodomorphs and the most basal sauropods. Furthermore, we predict that the sequence of character state acquisition for mandibular features will remain relatively simple, whereas tooth crown evolution is likely to involve several instances of convergence and reversal because of the possible greater plasticity of teeth in response to changes in diet and feeding strategy. Current evidence already suggests that the presence/absence of dental serrations, the shape, size and orientation of serrations, and the cross-sectional shape of tooth crowns, are quite variable within sauropodomorphs (and indeed within Dinosauria as a whole). Such predictions concerning the relative plasticity of mandibular and dental characters require further testing via more detailed cladistic analyses.

In short, many of the enigmatic sauropod-like specimens from Lower and Middle Jurassic deposits potentially belong to taxa that are more closely related to Eusauropoda than is *Chinshakiangosaurus*. Nevertheless, incorporation of all of this material into phylogenetic analyses will probably yield new insights into the early evolution of sauropod crania and feeding mechanisms. In some cases (e.g. *Yunnanosaurus*) this work is being undertaken at present by PMB and PU, whereas in others (e.g. *Gongxianosaurus* and *Yimenosaurus*), phylogenetic analysis must await more detailed descriptions.

7. Conclusion

Chinshakiangosaurus represents one of the earliest and most basal sauropods in which cranial material is preserved. This taxon demonstrates that basal sauropods possessed a fleshy cheek associated with a buccal emargination and a lateral ridge on the dentary. This discovery is important for at least two reasons. First, the lateral ridge on the dentary has been used as one of the synapomorphies uniting a monophyletic Prosauropoda (Sereno, 1989, 1999; Galton, 1990; Gauffre, 1993; Galton & Upchurch, 2004). The recent reinterpretation of *Anchisaurus* as a basal sauropod (Yates & Kitching, 2003; Yates, 2004) and the new data on *Chinshakiangosaurus* indicate that the lateral ridge is probably a sauropodomorph synapomorphy, and therefore further undermines the monophyly of the Prosauropoda (*sensu* Galton & Upchurch, 2004). Second, the suggestion that a fleshy cheek was present in the most basal sauropods, but was lost in eusauropods, raises interesting functional and palaeoecological questions. The phylogenetic distribution of this character state, when combined with other feeding-related characters (such as jaw structure, body size and so on), suggests that the earliest sauropods underwent a major evolutionary transition during the shift from small-bodied selective omnivores/herbivores to large-bodied forms that used long passage time to process large quantities of poor quality plant material.

This study illustrates that our understanding of the functional and palaeoecological significance of many of the structures in the sauropodomorph skull is still in its infancy. Here we have formulated a number of explanatory hypotheses, and tested them as far as current knowledge of phylogenetic relationships and comparative anatomy allow. However, it is important that future studies should test these ideas further by applying advanced biomechanical methods (such as Finite Element Analysis: Rayfield *et al.* 2001; Rayfield, 2003) and incorporate information from taxa that are currently inadequately known (e.g. *Yimenosaurus*: Bai, Yang & Wang, 1990). In the meantime, it is hoped that this study illustrates the valuable insights that can be obtained through the combination of phylogenetic analysis and the re-evaluation of fragmentary specimens that are all too often overlooked.

Acknowledgements. Our work in China was supported by grants from The Royal Society (PU and PMB), a NERC fellowship (ref. GT59906ES) (PU) and The Natural History Museum (PMB). XX wishes to thank the National Natural Science Foundation of China for support (ref. 40125006). PU and PMB thank colleagues at IVPP for their hospitality. Zhou Zhonghe kindly supplied a copy of Ye (1975), which was translated by Dilshat Hewzulla (NHM). Translations of He *et al.* (1998) and Bai, Yang & Wang (1990) were made by W. Downs and obtained courtesy of The Polyglot Paleontologist website (http://ravenel.si.edu/paleo/paleoglot/index.cfm). We are grateful to Debbie Maizels (Biological and Medical Illustration, Zoobotanica, Old Coulsdon, Surrey) for supplying the illustrations for Figure 1, and Robert Laws for producing Figure 6.

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Appendix 1. Character state distributions

This appendix summarizes the phylogenetic distribution of the cranial characters that can be coded for *Chinshakiangosaurus*. In order to explore these distributions fully, the character states have been mapped onto the topologies found in this study based on the Yates & Kitching (2003) and Galton & Upchurch (2004) data-matrices, using both delayed and accelerated transformation optimization in PAUP (Swofford, 2002). NB: The application of accelerated transformation (ACCTRAN) can produce anomalous character state distributions when character state data are absent. In particular, ACCTRAN reconstructs the character state transformation at the lowest node possible, and can therefore imply the presence of a state even though one or more taxa do not preserve the relevant anatomical elements.

Galton & Upchurch (2004)

DELTRAN:

Sauropodomorpha

1. Tooth serrations are set at 45° to the margin of the crown.

Sauropoda (*Chinshakiangosaurus* plus other sauropods)

1. Concavity on the lingual surface of each tooth crown.
2. Prominent grooves on the labial surface of each tooth crown, one near the mesial and one near the distal margin. Note that *Chinshakiangosaurus* only has a groove near the distal margin, suggesting that this feature evolved before the mesial groove.
3. Tooth crowns are lanceolate (convergently acquired in prosauropods above the level of *Thecodontosaurus*).

Autapomorphy of *Chinshakiangosaurus*

1. Under delayed transformation, the ridge on the lateral surface of the dentary occurs in *Chinshakiangosaurus* and convergently in Prosauropoda.

ACCTRAN:

Sauropodomorpha

1. Dentary curves ventrally as it approaches the symphysis (reversed in *Chinshakiangosaurus*).
2. Lateral ridge on dentary (reversed in eusauropods).
3. Tooth serrations are at 45° to the crown margins.
4. Tooth crowns are lanceolate (reversed in *Thecodontosaurus*).

Sauropoda (including *Chinshakiangosaurus*)

1. Concavity on lingual surface of each tooth crown.
2. Prominent grooves present on the labial surface of each tooth crown, one near the mesial margin and one near the distal margin (Note that *Chinshakiangosaurus* only has the groove near the distal margin).

Eusauropoda

1. The rostral end of the dentary expands dorsoventrally.
2. The lateral ridge on the dentary is lost.

Yates & Kitching (2003)

DELTRAN:

Sauropodomorpha

1. Teeth with basally constricted crowns (reversed in *Chinshakiangosaurus*).
2. Distal recurvature of tooth crowns absent.

Thecodontosaurus + *Efraasia* + Prosauropoda + Sauropoda (that is, all sauropodomorphs except *Saturnalia*)

1. First dentary tooth is inset from the symphysis (reversed in sauropods, including *Chinshakiangosaurus*). This is a different interpretation from that in Galton & Upchurch (2004), where the inset first dentary tooth is a prosauropod synapomorphy.
2. Number of dentary teeth increased to 18 or more (reversed in sauropods above the level of *Chinshakiangosaurus*).
3. Tooth serrations are large and coarse and set at 45° to the margin of the crown.

Efraasia + Prosauropoda + Sauropoda (that is, all sauropodomorphs except *Thecodontosaurus* and *Saturnalia*)

1. Caudal end of dentary tooth row is inset medially to form a buccal emargination that is underlain by a lateral ridge (reversed in sauropods above the level of *Chinshakiangosaurus*).

Sauropoda (including *Anchisaurus* and *Melanorosaurus*)

1. First dentary tooth lies next to the symphysis with no gap between them (this is a reversal to the plesiomorphic state).
2. Wrinkled tooth enamel. This is a different interpretation from that of Galton & Upchurch (2004) in which wrinkled tooth enamel appears twice independently, once in *Anchisaurus* within the Prosauropoda, and once in sauropods including *Chinshakiangosaurus*.

3. Tooth serrations restricted to the distal part of the tooth crown (convergently acquired in *Massospondylus*).

Chinshakiangosaurus + *Isanosaurus* + *Kotasaurus* + *Vulcanodon* + Eusauropoda

1. Lateral plate on premaxillae, maxillae and dentary supporting the labial bases of tooth crowns.
2. Upper jaw is ‘U’-shaped in dorsal view. This is coded as present in *Chinshakiangosaurus* even though only the lower jaw is known, because the lower jaw and upper jaw have to be approximately the same shape in order to occlude correctly during jaw closure.
3. Concavity on lingual surface of tooth crowns.
4. Labial grooves present on tooth crowns (only the distal one is present at this node; the mesial one may have been added later, at the node where *Kotasaurus* joins the tree).

Eusauropoda (*Shunosaurus*, *Barapasaurus*, *Omeisaurus*, and neosauropods)

1. Loss of the buccal emargination and lateral ridge at the caudal end of the dentary tooth row (this is a reversal to the plesiomorphic state).
2. Dorsoventral expansion of the dentary symphysis.
3. Dentary tooth crowns become procumbent.

Omeisaurus + Neosauropoda

1. Number of dentary teeth reduced to less than 18 (reversal to the plesiomorphic state). This could occur in *Barapasaurus* but *Shunosaurus* and *Chinshakiangosaurus* demonstrate that basal sauropods retained a larger number of dentary teeth.

ACCTRAN:

Sauropodomorpha

1. Height:length ratio of dentary increased to > 0.2 (convergently acquired in *Chinshakiangosaurus*, and reversed in *Efraasia* + Prosauropoda + Sauropoda).
2. Teeth with basal constriction (reversed in *Chinshakiangosaurus*).
3. Loss of recurvature of the distal portion of tooth crowns.

Thecodontosaurus plus other sauropodomorphs (that is, all sauropodomorphs except *Saturnalia*)

1. Caudal part of the dentary tooth row is inset medially creating a buccal emargination that is underlain by a lateral ridge (reversed in sauropods above *Chinshakiangosaurus*).
2. Inset first dentary tooth (reversed in sauropods at the level of *Chinshakiangosaurus*).
3. Number of dentary teeth increased to 18 or more (reversed in sauropods above the level of *Shunosaurus*).
4. Tooth serrations are coarse and set at 45° to the crown margin.

Efraasia + Prosauropoda + Sauropoda

1. Height:length ratio of the dentary is < 0.2 (a reversal).

Sauropoda (including *Anchisaurus*)

1. First dentary tooth is not inset from the symphysis (this is a reversal to the plesiomorphic state).
2. Wrinkled tooth enamel.
3. Concavity on the lingual surface of each tooth crown (this is not actually seen in *Anchisaurus*, but missing data means that under Acctran it could be present).

Melanorosaurus + *Antetonitrus* + *Chinshakiangosaurus* + *Isanosaurus*+*Kotasaurus* + *Vulcanodon* + Eusauropoda

1. Upper jaw is ‘U’-shaped in dorsal view.
2. Longitudinal labial grooves on tooth crowns.

Autapomorphies of *Chinshakiangosaurus*

1. Height:length ratio of the dentary increases to > 0.2 (also present in the most basal sauropodomorphs, *Saturnalia* and *Thecodontosaurus*).
2. Teeth lose their basal constriction (reversal to the plesiomorphic state).

Isanosaurus + *Kotasaurus* + *Vulcanodon* + Eusauropoda

1. Dorsoventral expansion of the dentary symphysis.
2. Dentary tooth crowns become procumbent.

Barapasaurus + *Omeisaurus* + Neosauropoda

1. Number of dentary teeth reduced to less than 18 (a reversal to the plesiomorphic state).

Appendix 2. Character codings

This appendix summarizes the character codings for *Chinshakiangosaurus* used in the re-analyses of the data-matrices of Yates & Kitching (2003) and Galton & Upchurch (2004). Numbers preceded by ‘C’ refer to characters used by these studies. Note that both Excel and Nexus versions of the full data-matrices used in this study can be obtained from PU on request.

Codings for *Chinshakiangosaurus* for Yates & Kitching (2003):
C2 = 1; C54 = 1; C55 = 1; C56 = 0; C57 = 0; C58 = 1; C59 = 0; C63 = 0; C65 = 1; C66 = 0; C68 = 1; C69 = 1; C70 = 1; C71 = 1; C72 = 1; C73 = 1; C86 = 0; C174 = 2.
All other characters were coded as ‘?’.

Codings for *Chinshakiangosaurus* for Galton & Upchurch (2004):
C30 = 0; C31 = 0; C32 = 1; C38 = 1; C39 = 0; C40 = 1; C41 = 1; C42 = 1; C43 = 0; C49 = 0; C109 = 0; C112 = 1; C113 = 1.
All other characters were coded as ‘?’.