

·特 稿·

Lanzhousaurus magnidens gen. et sp. nov. from Gansu Province, China: the largest-toothed herbivorous dinosaur in the world

中国甘肃发现世界上最大牙齿的植食性恐龙： 巨齿兰州龙(新属、新种)

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Abstract: A new ornithopod dinosaur, *Lanzhousaurus magnidens* gen. et sp. nov., from the Early Cretaceous of the Lanzhou Basin, Gansu Province, China, possesses the largest teeth of any herbivorous dinosaur yet discovered. The dental morphology of *Lanzhousaurus*, in which only 14, ~4 cm-wide tooth families are preserved in the tooth row of the 1 m long lower jaw, augments the known morphological diversity of dinosaurs. Cladistic analysis recovers a close relationship between *L. magnidens* and *Lurdusaurus arenatus* from the Early Cretaceous of Africa. Together, these species represent a previously unrecognized, massively-constructed quadrupedal lineage in the evolution of ornithopod dinosaurs. This discovery also implies a close connection between Eurasia and Africa during the Early Cretaceous.

Key words: dinosaur; ornithopod dinosaur; teeth; Early Cretaceous; Lanzhou Basin, Gansu, China

摘要: 巨齿兰州龙(新属、新种)是发现于中国甘肃省兰州盆地早白垩世地层中的一新鸟脚类恐龙,其牙齿是世界上已知植食性恐龙中最大的。兰州龙下颌长1 m,每侧有14个齿槽,而单个牙齿宽约4 cm,这是已知恐龙中的首次报道。分支系统学分析发现巨齿兰州龙与非洲早白垩世的*Lurdusaurus arenatus*关系密切。它们代表了鸟脚类恐龙进化中四足行走的笨重的一新支。兰州龙的发现也表明欧亚大陆与非洲在早白垩世具有较密切的联系。

关键词: 恐龙; 鸟脚类恐龙; 牙齿; 早白垩世; 中国甘肃兰州盆地

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Iguanodontian ornithopods are the most diverse and dominant Cretaceous Laurasian herbivorous dinosaurs^[1-5]. Early Cretaceous iguanodontians are generally facultative bipeds such as *Iguanodon atherfieldensis* with a body length of 6–7 meters and skull length of half a meter^[4,6]. The teeth of iguanodontians are generally small, as exemplified by the dental battery of hadrosaurian (duck-billed) dinosaurs, in which as many as 60, ~1 cm-wide, closely packed tooth families have been documented in a single tooth row^[5].

Lanzhousaurus magnidens gen. et sp. nov. is an iguanodontian dinosaur discovered from the Early Cretaceous^[7] of Gansu Province, northwestern China in 2003, and is different from all other iguanodontians in possessing large individual teeth and a small tooth count per tooth row, with a mere 14, but ~4 cm-wide, tooth families preserved in a single dentary tooth row.

Systematic Paleontology

Dinosauria Owen, 1842

Ornithischia Seeley, 1887

Ornithopoda Marsh, 1881

Iguanodontia Sereno, 1986

Styracosterna Sereno, 1986

Lanzhousaurus magnidens gen. et sp. nov.

Etymology: Lanzhou (Chinese), name of the capital city of Gansu Province, P. R. China; magnus (Latin), big; dens (Latin), tooth.

Holotype: Partial skeleton of a single individual including mandible (missing predentary, right coronoid and right articular), isolated maxillary teeth, isolated right dentary teeth and complete, in situ left dentary teeth, a series of fourteen vertebrae (six cervicals and eight dorsals), both sternal plates, ribs, and both pubes, deposited in Fossil Research and Development Center of the Third Geology and Mineral Resources Exploration Academy of Gansu Province: GSLTZP01-001 (Fig. 1).

Locality and horizon: Zhongpu, Lintao, Gansu Province, P. R. China; Hekou Group, Early Cretaceous^[7].

Diagnosis: *Lanzhousaurus magnidens* is different from all other iguanodontians in possessing large individual teeth and a small tooth count per tooth row, with a mere 14, but ~4 cm-wide, tooth families preserved in a single dentary tooth row.

Description

The dentary of *Lanzhousaurus* (Fig. 1) possesses many features also found in *Camptosaurus*^[8] and *Iguanodon*^[6,9], but

absent in more derived forms^[5]. As in *Camptosaurus*^[4,8] and *Iguanodon bernissartensis*^[4,9], no space is allotted in *Lanzhousaurus* for a pronounced diastema at the rostral end of the tooth row. The ramus of the dentary has parallel dorsal and ventral sides, and does not expand and turn downward at its rostral end like it does in *Camptosaurus*^[4,8] and *Iguanodon atherfieldensis*^[4,6]. The alveolar trough curves caudolaterally toward the elevated and caudodorsally inclined coronoid process as in *Camptosaurus*^[4,8], *Iguanodon bernissartensis*^[4,9] and *Ouranosaurus*^[4,10]. In other derived iguanodontians^[4,5], the opposite conditions are true: the rostral end of the dentary ramus expands and curves downward, and the coronoid process is both perpendicular to and separated from the dentary ramus by a horizontal shelf. In medial view, a relatively straight groove that is sequentially perforated by alveolar foramina underscores the alveolar parapet. Ventral to this groove, the dentary is incised horizontally by Meckel's mandibular canal.

The surangular is the largest element of the post-dentary part of the lower jaw. A dorsal process has a rugose and rostromedially-directed articular surface for the coronoid. Below this process is an elliptical, relatively large accessory surangular foramen^[11], a feature also reported in *Camptosaurus*^[4,8], *Ouranosaurus*^[4,10], and *Altirhinus*^[4,12]. The surangular tapers sharply toward the jaw articulation. Lateral to the quadrate cotylus, there is a laterally projection lip. A round, relatively small surangular foramen lies ventral to this projection. The caudal end of the surangular hooks upward, and constitutes about two-thirds of the jaw articular surface; the remaining third is formed by the medial situated articular bone.

The angular is broadly exposed laterally, as in *Camptosaurus*^[4,8], *Ouranosaurus*^[4,10], and *Altirhinus*^[4,12]. Its rostral portion is covered by the gradually tapering caudal end of the dentary, and extends rostrally to the position below the fifth most caudal tooth position, underlying Meckel's canal in medial view. The main body of the angular wraps around the surangular, the articular and the prearticular ventrally.

The articular forms the caudomedial corner of the lower jaw, and is supported by the surangular laterally, the angular ventrally, and the prearticular rostrally. The prearticular is a sheet of bone that, starting from the articular, expands rostrally to meet the dentary. It forms the medial wall of the adductor fossa. The coronoid covers both the dentary and the surangular medially, and terminates ventrally on the rostradorsal corner of the prearticular as a tiny rod. Only a portion of an isolated splenial is preserved; it is long and

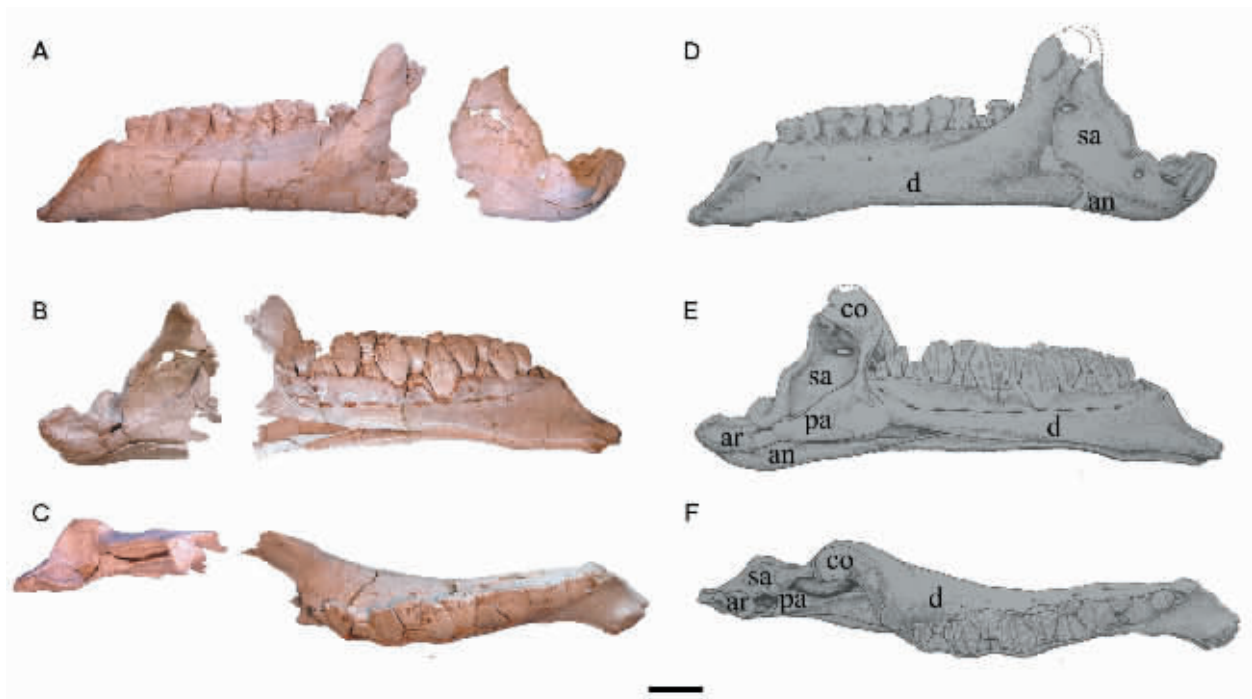


Fig.1 Left mandible of *Lanzhousaurus magnidens* gen. et sp. nov. in lateral (A, D), medial (B, E), and dorsal (C, F) views.

Scale bar equals 10 cm. Abbreviations: an-angular; ar-articular; co-coronoid; d-dentary; pa-prearticular; sa-surangular

rod-like, covering Meckel’s canal medially.

The dentition of *Lanzhousaurus* is unique among iguanodontian dinosaurs. The 50 cm long alveolar trough of the left dentary preserves in situ one functional tooth row of 14 teeth, as well as one replacement tooth row (Fig. 1B). One isolated tooth from the right dentary measures 75 mm wide and 140 mm long (Fig. 2), and is the largest of any herbivorous dinosaur yet discovered. The crown of each dentary tooth is broader, and more diamond-shaped, than that of a maxillary tooth, unlike the similar-sized maxillary and dentary teeth of *Camptosaurus*^[4,8] and more primitive iguanodontians^[4,13]. More than ten weak ridges, none more prominent than any other adorn the enameled lingual surface. The ridges are separated by grooves that sometimes bifurcate basally. Remnants of enamel are also evident on the labial side, as in *Iguanodon*^[4,6,9] and *Ouranosaurus*^[4,10]. Marginal denticles are present as mammillations on both the mesial and distal edges.

Unlike the dentary tooth crown, each

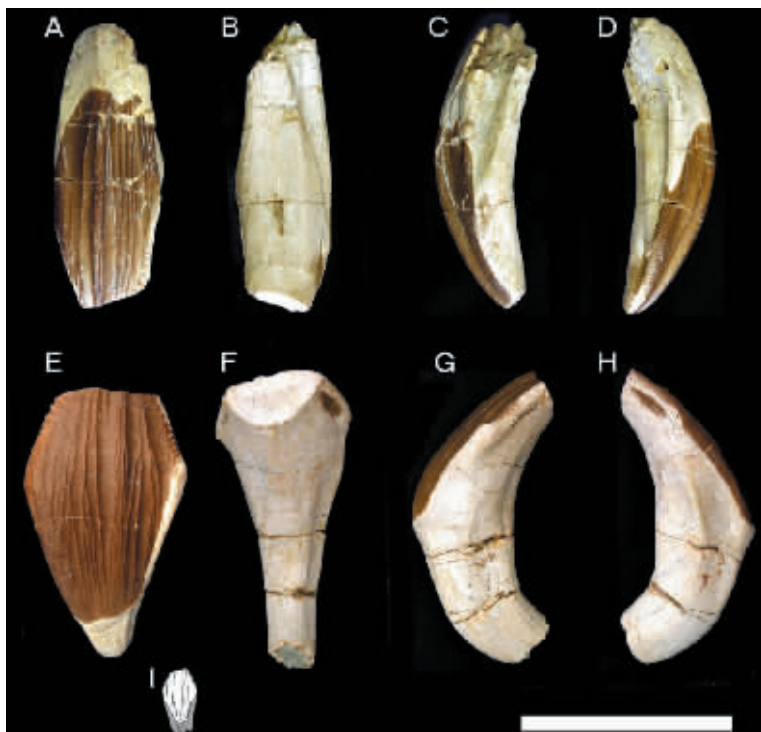


Fig.2 *Lanzhousaurus magnidens* gen. et sp. nov.

Right maxillary tooth in labial (A), lingual (B), mesial (C), and distal (D) views. Right dentary tooth in lingual (E), labial (F), distal (G), and mesial (H) views. Lingual view of a dentary tooth of *Altirhinus kurzanovi* is shown for comparison (I). Scale bar equals 10 cm

maxillary tooth crown has one prominent primary ridge situated slightly distal to the midline, flanked by several weak, secondary ridges on both sides on the labial face. On both the mesial and distal edges, a bundle of weak ridges radiate from the base of the crown that terminate as mammillations of the marginal denticles. Deep grooves incise the mesial and distal sides, respectively, whereas only a shallow depression embays the lingual side. Remnants of enamel are also present on the lingual side of the maxillary crown.

A series of 14 vertebrae is preserved, representing the last 6 cervicals and first 8 dorsals (Fig. 3A). They are very much resemble those of *Iguanodon*^[4,6,9]. The cervical centra have deeply convex cranial and concave caudal surfaces, with prominent ventral keels. The neural arches directed laterally, with the prezygapophyses rising from their proximal ends. The postzygapophyses are supported by long, caudolateral processes from the very low neural spine. The dorsal vertebrae have amphiplatyan centra, the parapophyses shift to the neural arches, the diapophyses are long and caudolaterally directed processes, and the neural spines are about twice the height of the centra. Robust isolated ribs are also preserved, with slightly expanded distal ends (Fig. 3D–J).

The sternal plate of *Lanzhousaurus* is hatchet-like (Fig. 3B), a key feature of the Styracosterna^[4,14]. By contrast, in the less derived *Camptosaurus*^[4,8] and *Dryosaurus*^[4,15], the sternal is reniform. Among members of the Styracosterna, *Lanzhousaurus*'s sternal bone exhibits some primitive features, such as the relatively long blade (more than half of the total length, in contrast to less than half of the total length in derived forms) and the relatively flat distal portion (that is rod-like in more derived forms).

The pubis of *Lanzhousaurus* is typical for styracosternans, with a deep prepubic process and relatively short pubic shaft (Fig. 3C). In contrast, the pubes of the less derived *Camptosaurus*^[4,8] and *Dryosaurus*^[4,15] have narrow prepubic processes and long pubic shafts, each about twice the length of the prepubic process. Among members of the Styracosterna, the pubis of *Lanzhousaurus* is more similar to that of basal forms, such as *Iguanodon*^[4,6,9] than to derived forms, such as *Probaetrossaurus*^[4,16], in which the prepubic process is relatively long and has a constricted proximal portion.

Discussion

Based on a cladistic analysis, *Lanzhousaurus* is firmly recovered as a member of the Styracosterna (Fig. 4) by

virtue of a suite of derived features, such as the relatively narrow, lozenge-shaped maxillary teeth with mammilliform marginal denticles, hatchet-shaped sternal plates, and pubis with expanded cranial blade and short caudal ramus. By contrast, in the less derived *Camptosaurus*^[4,8], the maxillary teeth are about the same size as the dentary teeth, the maxillary crowns are shield-shaped with simple, tongue-shaped marginal denticles, the sternal bones are kidney-shaped, the cranial pubic blades do not expand distally, and the caudal pubic rami are as long as the ischium^[4,8].

Among members of the Styracosterna, the closest taxon to *Lanzhousaurus* is the Nigerian iguanodontian *Lurdusaurus*^[4,17], although the precise nature of the relationship between these two taxa cannot be confirmed due to dearth of directly comparable parts except for partial vertebrae. Both *Lanzhousaurus* and *Lurdusaurus* are less derived than the Hadrosauriformes. Hadrosauriforms evolved derived features such as more than 20 teeth per tooth row and one or two prominent ridges on the dentary crown, while *Lanzhousaurus* retains a plesiomorphic 14 teeth per tooth row and the dentary crowns with multiple, equally prominent ridges. Hadrosauriforms also evolved closely appressed metacarpals II–IV, and their femora possess large, triangular fourth trochanters and at least partially enclosed cranial intercondylar grooves^[8], while *Lurdusaurus* has spreading metacarpals II–IV and a femur with a pendent fourth trochanter and cranially open intercondylar groove^[4,17].

The discovery of close relationship between *Lanzhousaurus* and *Lurdusaurus*, and their basal position in the phylogeny of the Styracosterna, reveal the existence of another, previously undocumented clade of iguanodontian dinosaurs. Members of this clade are distinguished by their massively-constructed body forms. *Lurdusaurus* is estimated at nearly 9 m long with a weight of 5500 kg. *Lanzhousaurus* is also massively-constructed, as indicated by the robustness of its lower jaw and ribs, and is estimated at about 10 m long and no lighter than *Lurdusaurus*, based on comparison of their vertebrae. Among non-hadrosaurid hadrosauriforms, only *Iguanodon bernissartensis* reaches a similar size, but with a weight of about half that of *Lurdusaurus*^[4]. The average adult body weights of 7–12 m long hadrosaurids are 3000 kg^[5]. Massively-constructed bodies indicate quadrupedality for both *Lanzhousaurus* and *Lurdusaurus*, in contrast to facultative bipedality generally considered for hadrosauriforms^[4,5]. One notable observation is that the proportional lengths of the skulls do not change evidently in styracosternans, which are about one-tenth of the

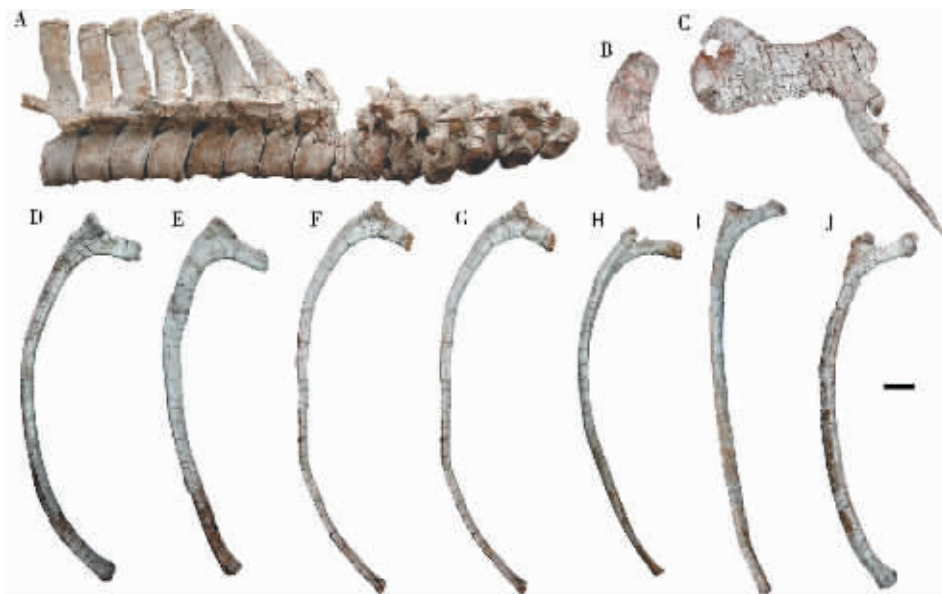


Fig.3 *Lanzhousaurus magnidens* gen. et sp. nov.

A series of six cervical and eight dorsal vertebrae in right lateral view (A), right sternal plate in dorsal view(B), left pubis in lateral view (C),and several isolated, left dorsal ribs in caudal view (D) views. Scale bar equals 10 cm

body length, no matter what their weight.

Lanzhousaurus possesses a new dental morphology in which the size of each tooth hypertrophies remarkably and the number of teeth per tooth row decreases. By contrast, in the evolution of hadrosauriforms, the size of individual teeth diminishes, the number of teeth per tooth row increases, and one or more rows of replacement teeth develop, culminating in the renowned dental batteries in the most derived Hadrosauridae^[4,5]. Although *Lanzhousaurus*, as in all other hadrosauriforms, evolved the system of pleurokinesis^[18,19] to grind food efficiently, the lack of prominent ridges on its dentary teeth and the existence of enamel on both the lingual and labial sides indicate a relatively weak interlocking between its upper and lower jaws compared to that of hadrosaurid dental battery. Therefore, *Lanzhousaurus* might have been limited to relatively softer foodstuffs than hadrosauriforms.

The discovery of *Lanzhousaurus* spreads the geographical distribution of basal styracosternans into Asia^[20], and indicates a close connection between Eurasia and Africa in the Early Cretaceous, a contention also supported by several other dinosaur taxa^[21,22].

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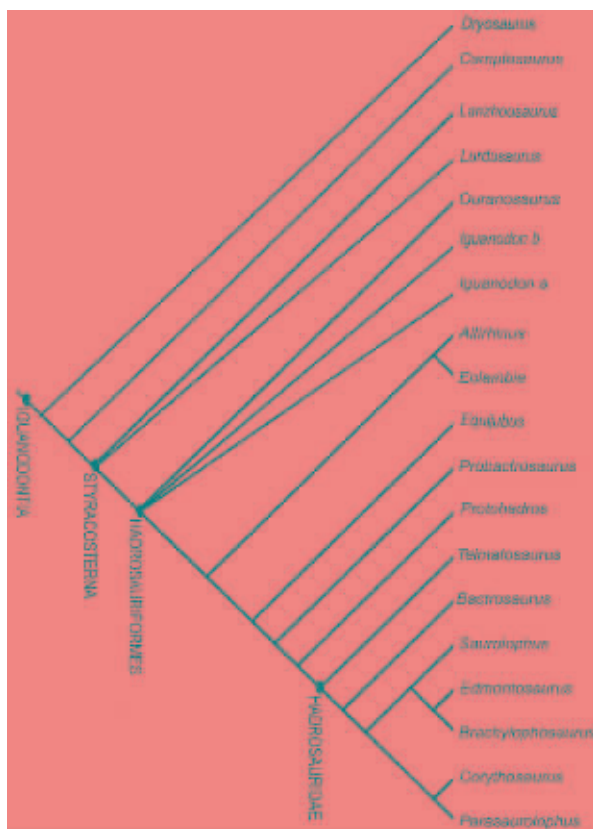


Fig.4 Phylogenetic relationship of *Lanzhousaurus magnidens* gen. et sp. nov. to other iguanodontian dinosaurs. The topology is based on the strict consensus of six equally parsimonious and shortest trees from a PAUP branch-and-bound search for 79 characters of 19 comparative taxa, with all multi-state characters unordered. (CI: 0.68; RI: 0.86)

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Supplementary Information

1. Measurements (in millimeters) of *Lanzhousaurus magnidens*

C1–C6 correspond to preserved cervical vertebrae from the most cranial to the most caudal ones, respectively. D1–D8 correspond to the preserved dorsal vertebrae from the most cranial to the most caudal ones, respectively. Ribs D–J correspond to D–J in Fig. 3, respectively.

Dentary				
Length along ventral border				670
Height along coronoid process				305
Width along mid-length				170
Post-dentary				
Length along ventral border				265
Height along dorsal process of angular				280
Vertebra	Centrum, length	Centrum, width(cranial/caudal)	Centrum, height(cranial/caudal)	Height, above centrum
C1	140	150/150	90/105	100
C2	135	150/170	90/120	120
C3	125	145/160	90/140	150
C4	125	140/170	110/155	180
C5	110	130/155	130/140	240
C6	? 155	135/125	130/160	290
D1	110	120/130	140/150	?
D2	110	120/120	145/150	360
D3	115	125/130	155/150	400
D4	115	130/130	155/150	420
D5	120	130/135	150/150	430
D6	120	130/150	140/150	400
D7	120	150/150	145/150	400
D8	115	155/165	160/155	435
Rib	Length	Width, proximal end	Width, mid length	Width, distal end
D	1130	220	65	75
E	1090	260	70	70
F	1180	245	40	60
G	1250	205	50	50
H	1100	220	50	45
I	1180	240	55	65
J	1140	225	50	80

续前表

Sternal bone	
Length	450
Width, maximum	150
Width, minimum	80
Pubis	
Prepubic process, length	620
Prepubic process, width, proximal end	310
Pubic shaft, length	800

2. Character list

The 79 characters used in this analysis are based on 67 characters from Norman (2002) (N1–67), combining 11 characters from You et al (2003) (Y2, 10, 12, 13, 16, 31, 32, 36, 37, 38 and 39) and 1 character from Kobayashi and Azuma (2003) (K15).

Two new character states added for N2 (based on Y8) and N28, respectively.

- 1 N1. Dorsal aspect of the premaxilla narrower than width across orbital region of skull roof (0), lateral expansion of premaxillae equals or exceeds width across orbital region of skull roof (1)
- 2 N2/Y8. Premaxilla oral part: ventral inflection: absent (0); incipient (1); below dentary tooth row (2)
- 3 N3. Lateral margin of the premaxilla reflected dorsally. Absent (0), present (1)
- 4 N4. Premaxilla overlaps prefrontal (0), extends caudally, beyond caudal margin of prefrontal (1)
- 5 N5. Fenestrae present in the caudal extensions of the premaxillae. Absent (0), present (1)
- 6 N6. Boundary of the external naris defined by the premaxilla and nasal (0), premaxilla only (1)
- 7 N7. Caudal narial depression. Absent (0), present (1), secondarily covered by premaxilla (2)
- 8 N8. Nasal cavity position. Rostromedial to orbits (0), diverticulae above orbits (1)
- 9 N9. Helmet-shaped hollow crest. Absent (0), present (1)
- 10 N10. Position of external antorbital fenestra. Between lacrimal and maxilla (0), on rostral dorsal margin of maxilla (1)
- 11 N11. Dorsal process of the maxilla. Narrow, finger-shaped process (0), expanded, laterally flattened plate-like structure (1)
- 12 N12. Lacrimal–nasal contact: present (0), absent (1)
- 13 N13. Palpebral bone: present (0), absent or fused to orbital margin (1)
- 14 N14. Rostral portion of the jugal: tapering (0), expanded dorsoventrally (1), expanded and bluntly truncated (2)
- 15 N15. Jugal–maxilla suture. Scarf joint (0), ‘finger-in-recess’ joint (1), butt-jointed (2)
- 16 N16. Ventral edge of the jugal. Smooth, shallow curve (0), strongly angular (1)
- 17 N17. Jugal–ectopterygoid articulation. Present (0), absent (1)
- 18 N18. Frontal shape. Flat rectangular (0), short, broad, covered by large scarf joint for nasals (1), large scarf joint includes premaxillae (2)
- 19 N19. Frontal in orbital margin: present (0), excluded (1)
- 20 N20. Quadrate (paraquadratic) foramen. Present (0), absent (1)
- 21 N21. Quadrate articular condyle. Transversely broad (0), narrow and hemispherical (1)
- 22 N22. Gap or ‘diastema’ between prementary and 1st dentary tooth. Short (0), pronounced (1)
- 23 N23. Dentary ramus. Straight (0), rostral end strongly deflected ventrally (1)
- 24 N24. Dentary ramus. Parallel sided (0), deepens rostrally (1)
- 25 N25. Coronoid process shape. Elevated, but oblique (0), long, finger-shaped, perpendicular (1), markedly rostrocaudally expanded apex (2)
- 26 N26. Coronoid process position. Laterally offset and dentition curves into its base (0), laterally offset and a horizontal shelf separates dentition from coronoid process (1)

- 27 N27. Surangular foramen. Present (0), absent (1)
- 28 N28. Angular position. Largely exposed laterally (0), visible on lateral surface of the lower jaw (1), not visible laterally (2)
- 29 N29. Dentary crown shape in lingual aspect. Broad, shield-like lingual surface with more than one vertical ridge (0), narrow, diamond-shaped, single median ridge (1)
- 30 N30. Dentary enamel. Thin veneer labially, thick lingually (0), exclusively lingually (1)
- 31 N31. Marginal denticles. Simple, tongue-shaped (0), curved, mammillated ledge (1), absent or reduced to small papillae (2)
- 32 N32. Tooth root emplacement. Not cemented (0), partially cemented (1), rugose, angular-sided roots (2)
- 33 N33. Alveolar trough grooves. Shaped by dentary crowns (0), narrow parallel-sided grooves (1)
- 34 N34. Relative width of maxillary and dentary crowns. Maxillary crowns approximately equal in width with dentary crowns (0), narrower (1)
- 35 N35. Dentary tooth size; broad and shield-like (0), small, narrow and lanceolate (1)
- 36 N36. Maxillary crown shape. Shield-shaped (0), elongate lozenge (1), sub-diamond-shaped (2)
- 37 N37. Ridge pattern on maxillary crowns. Very prominent primary ridge (0), reduced primary ridge (1)
- 38 N38. Angulation of crown face relative to root on dentary teeth. Smooth (0), abrupt (1)
- 39 N39. Occlusal surface of dentary tooth row. Single tooth depth (0), multiple tooth depth (1)
- 40 N40. Replacement crowns in dentary. One (0), two (1), three or more (2)
- 41 N41. Mid-thoracic spinous processes. Short and rectangular height and length very similar (0), height more than twice length (1), height more than 4 times length (2)
- 42 N42. Sacral vertebral count. Seven or fewer (0), eight or more (1)
- 43 N43. Scapular blade. Straight (0), curved (1), curved and flared (2)
- 44 N44. Scapular 'acromion'. Prominent on anterior margin of scapula (0), reflected laterally (1)
- 45 N45. Sternal shape. Reniform (approximately kidney shaped) (0), hatchet-shaped (1)
- 46 N46. Humerus shape. Gently sigmoid with low, rounded deltopectoral crest (dpc) (0), short, angular with prominent dpc (1)
- 47 N47. Radius proportions. Less than 80% of the length of the humerus (0), greater than 80% of humeral length (1)
- 48 N48. Carpal structure. Fully ossified (0), reduced (1)
- 49 N49. Metacarpal 1 shape. Normal elongate bone (0), short, block-like set against carpals (1), absent (2)
- 50 N50. Metacarpals II-IV arrangement. Dumbbell-shaped and spreading (0), closely appressed (1), elongate (2)
- 51 N51. Manus digit 1. Present (0), absent (1)
- 52 N52. Manus ungual digit 1. Claw-like (0), conical (1), absent (2)
- 53 N53. Manus unguals II & III. Claw-like (0), flattened, twisted and hoof-like (1)
- 54 N54. Cranial process of ilium. Long, laterally compressed (0), strongly downturned (1)
- 55 N55. Dorsal edge of ilium above ischial peduncle. Horizontal, no significant notch above ischial peduncle (0), strongly notched (1)
- 56 N56. Dorsal flange on ilium. Thickened dorsal edge above ischial peduncle (0), prominent, everted, with a pendant flange (1)
- 57 N57. Caudal blade of ilium. Triangular, tapering caudally (0), rectangular (1)
- 58 N58. Cranial pubic blade. Blade-like, unexpanded distally (0), blade with constricted proximal portion followed by a distal expansion (1), short constriction and deeply expanded (2)
- 59 N59. Caudal pubic ramus. Terminates adjacent to distal end of ischium (0), shorter than ischium, no pubic symphysis (1)
- 60 N60. Ischial shaft. Curved (0), straight (1)
- 61 N61. Ischial tip. Craniocaudal expansion (0), narrow (1)
- 62 N62. Femoral shaft. Distal half of shaft curved caudally (0), straight (1)
- 63 N63. Femur, 4th trochanter. Pendant (0), large, triangular (1), curved, laterally compressed eminence (2)
- 64 N64. Femur, cranial intercondylar groove. Open, U-shaped trough (0), partially enclosed by expansion of cranial condyles (1), fully enclosed canal (2)
- 65 N65. Femur, distal condyle shape. Moderately expanded craniocaudally (0), strongly expanded (1)
- 66 N66. Metatarsal 1. Well developed and articulates with proximal phalanx (0), slender, splint-like (1), absent (2)
- 67 N67. Pedal ungual phalanges. Dorsoventrally flattened, but elongate and pointed (0), elongate, but bluntly truncated tip with prominent claw grooves retained (1), broad, short with rounded shield (hoof)-like shape and reduced or absent claw groove (2)
- 68 Y2. Preorbital length/basal skull length. short, about half(0). half to two-thirds(1). long, more than two-thirds(2)
- 69 Y10. Premaxilla oral part, ventral margin denticulation; absent (0); present (1)
- 70 Y12. Maxilla, length ratio between rostral/caudal portions. About the same length(0). Relatively longer rostral portion, but < twice the length of the caudal portion(1). Extremely long rostral portion, about twice the length of the caudal portion(2)
- 71 Y13. Maxilla, dorsal process, relative position to lacrimal ventral level. Above(0). Below(1)
- 72 Y16. Lacrimal, shape. Block-shaped(0). Long, with a rostroventral process(1)

- 73 Y31. Tooth count per tooth row. fewer than 20(0). 20–29(1). more than 29(2)
- 74 Y32. Inter–crown spaces. Present(0). Absent(1)
- 75 Y36. Maxillary crown, position of primary ridge. offset the midline(0); median(1)
- 76 Y37. Maxillary crown, accessory ridges. Present (0); absent (1)
- 77 Y38. Dentary crown, ridges. Multiple ridges without a dominant one (0); two subequal ridges; one prominent primary ridge (1)
- 78 Y39. Dentary crown, position of primary ridge. Offset the midline(0); median(1)
- 79 K15. Accessory foramen in the surangular. (0) Present; (1) absent

3. Data matrix

	10	20	30	40
<i>Altirhinus</i>	0200000001100010000001111100011101010001			
<i>Bactrosaurus</i>	020000000?0?0111100?00002112011211010011			
<i>Brachylophosaurus</i>	1200000001101121110111002112112211121012			
<i>Camptosaurus</i>	0000000000000000?0010000000000000000000			
<i>Corythosaurus</i>	0201112111111221121111112112112211121112			
<i>Dryosaurus</i>	000000000010000?0000000000000000000000			
<i>Edmontosaurus</i>	1210000001101121100111002112112211121012			
<i>Eolambia</i>	0?0?00000????1110?0??101110?01110101?0?1			
<i>Equijubus</i>	020000000?1?0?0?0?000001?010?1100010001			
<i>Iguanodon a</i>	0100000000010011000001001001001001010000			
<i>Iguanodon b</i>	0100000000010011000000010001001001010000			
<i>Lanzhousaurus</i>	????????????????????0000000001001010000			
<i>Lurdusaurus</i>	??????00????????00?????0??????????????			
<i>Ouranosaurus</i>	0110000000000111000001010000001001010000			
<i>Parasaurolophus</i>	0201012101111221121111112112112211121112			
<i>Probactrosaurus</i>	010000?00?????10000?000011010112110?0011			
<i>Protohadros</i>	?2000000011?1?10?010111110101111101?011			
<i>Saurolophus</i>	1201001001111121110111002112112211121?12			
<i>Telmatosaurus</i>	0200000001?1?1?0?001000021111112110100?1			
	50	60	70	
<i>Altirhinus</i>	??001000?10111000111?01???12120011001–0			
<i>Bactrosaurus</i>	1021100??1???000021?01221?2111111111201			
<i>Brachylophosaurus</i>	112111112212111112111122122200112111211			
<i>Camptosaurus</i>	100000001001000000000000001100001000–0			
<i>Corythosaurus</i>	212111112212111112100122122200112111211			
<i>Dryosaurus</i>	000000000000000000000000000010000000000–?			
<i>Edmontosaurus</i>	112111112212111112111122122200112111211			
<i>Eolambia</i>	100??1?01?0111000?00??10??????????????0			
<i>Equijubus</i>	????????????????????????????1111111000–1			
<i>Iguanodon a</i>	1000100011011000011000110112120011001–1			
<i>Iguanodon b</i>	1000100011011100011000110112120011001–1			
<i>Lanzhousaurus</i>	1???1????????????11?????????????01000–0			
<i>Lurdusaurus</i>	??00100010011000011000000??????????????			
<i>Ouranosaurus</i>	20?0100011011000021000110?121200?1001–0			
<i>Parasaurolophus</i>	212111112212111112100122122200112111211			
<i>Probactrosaurus</i>	1000101012011000021000111?11?1?110021?			
<i>Protohadros</i>	????????????????????????????1021?2111201			
<i>Saurolophus</i>	112111112212111112110122122200112111211			
<i>Telmatosaurus</i>	??10?0????????????????0121??111112111201			