The Linnean Society of London ZOOLOGICAL Journal of the Linnean Society

*Zoological Journal of the Linnean Society*, 2013, **168**, 98–206. With 30 figures

# Osteology of the Late Jurassic Portuguese sauropod dinosaur *Lusotitan atalaiensis* (Macronaria) and the evolutionary history of basal titanosauriforms

PHILIP D. MANNION[1,2]*, PAUL UPCHURCH[3], ROSIE N. BARNES[3] and OCTÁVIO MATEUS[4,5]

[1]*Department of Earth Science and Engineering, Imperial College London, South Kensington Campus, London, SW7 2AZ, UK*
[2]*Museum für Naturkunde, Invalidenstrasse 43, 10115 Berlin, Germany*
[3]*Department of Earth Sciences, UCL, University College London, Gower Street, London WC1E 6BT, UK*
[4]*Department of Earth Sciences (CICEGE-FCT), Universidade Nova da Lisboa, 2829-516 Monte de Caparica, Portugal*
[5]*Museu da Lourinhã, Rua João Luís de Moura, 2530-157 Lourinhã, Portugal*

*Received 20 July 2012; revised 24 January 2013; accepted for publication 12 February 2013*

Titanosauriforms represent a diverse and globally distributed clade of neosauropod dinosaurs, but their interrelationships remain poorly understood. Here we redescribe *Lusotitan atalaiensis* from the Late Jurassic Lourinhã Formation of Portugal, a taxon previously referred to *Brachiosaurus*. The lectotype includes cervical, dorsal, and caudal vertebrae, and elements from the forelimb, hindlimb, and pelvic girdle. *Lusotitan* is a valid taxon and can be diagnosed by six autapomorphies, including the presence of elongate postzygapophyses that project well beyond the posterior margin of the neural arch in anterior-to-middle caudal vertebrae. A new phylogenetic analysis, focused on elucidating the evolutionary relationships of basal titanosauriforms, is presented, comprising 63 taxa scored for 279 characters. Many of these characters are heavily revised or novel to our study, and a number of ingroup taxa have never previously been incorporated into a phylogenetic analysis. We treated quantitative characters as discrete and continuous data in two parallel analyses, and explored the effect of implied weighting. Although we recovered monophyletic brachiosaurid and somphospondylan sister clades within Titanosauriformes, their compositions were affected by alternative treatments of quantitative data and, especially, by the weighting of such data. This suggests that the treatment of quantitative data is important and the wrong decisions might lead to incorrect tree topologies. In particular, the diversity of Titanosauria was greatly increased by the use of implied weights. Our results support the generic separation of the contemporaneous taxa *Brachiosaurus*, *Giraffatitan*, and *Lusotitan*, with the latter recovered as either a brachiosaurid or the sister taxon to Titanosauriformes. Although *Janenschia* was recovered as a basal macronarian, outside Titanosauria, the sympatric *Australodocus* provides body fossil evidence for the pre-Cretaceous origin of titanosaurs. We recovered evidence for a sauropod with close affinities to the Chinese taxon *Mamenchisaurus* in the Late Jurassic Tendaguru beds of Africa, and present new information demonstrating the wider distribution of caudal pneumaticity within Titanosauria. The earliest known titanosauriform body fossils are from the late Oxfordian (Late Jurassic), although trackway evidence indicates a Middle Jurassic origin. Diversity increased throughout the Late Jurassic, and titanosauriforms did not undergo a severe extinction across the Jurassic/Cretaceous boundary, in contrast to diplodocids and non-neosauropods. Titanosauriform diversity increased in the Barremian and Aptian–Albian as a result of radiations of derived somphospondylans and lithostrotians, respectively, but there was a severe drop (up to 40%) in species numbers at, or near, the Albian/Cenomanian boundary, representing a faunal turnover whereby basal titanosauriforms were replaced by derived titanosaurs, although this transition occurred in a spatiotemporally staggered fashion.

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doi: 10.1111/zoj.12029

*Corresponding author. E-mail: philipdmannion@gmail.com
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ADDITIONAL KEYWORDS: biogeography – continuous data – Cretaceous – Gondwana – implied weighting – Laurasia – Lourinhã – Mamenchisauridae – Mesozoic – phylogeny – pneumaticity – Titanosauria.

## INTRODUCTION

The Late Jurassic terrestrial fauna of Portugal comprises a diverse dinosaur assemblage (Lapparent & Zbyszewski, 1957; Antunes & Mateus, 2003; Mateus, 2006). Sauropods are represented by at least four taxa: a diplodocid (*Dinheirosaurus lourinhanensis*; Bonaparte & Mateus, 1999; Mannion *et al*., 2012), a probable basal eusauropod (*Lourinhasaurus alenquerensis*; Lapparent & Zbyszewski, 1957; Dantas *et al*., 1998; Upchurch, Barrett & Dodson, 2004a), a turiasaur (Mateus, 2009; Ortega *et al*., 2010; Mocho, Ortega & Royo-Torres, 2012; Mateus, Mannion & Upchurch, in review), and *Lusotitan atalaiensis*. The latter was originally considered a new species of *Brachiosaurus* (Lapparent & Zbyszewski, 1957) before being assigned to its own genus within Titanosauriformes (Antunes & Mateus, 2003; Upchurch *et al*., 2004a), although it has never been fully described.

*Brachiosaurus altithorax* is known from the Late Jurassic Morrison Formation of North America (Riggs, 1903) and a second species, *Brachiosaurus brancai*, was described from the contemporaneous Tendaguru Formation of Tanzania (Janensch, 1914). A recent revision demonstrated numerous anatomical differences between these two titanosauriform species and argued for their generic separation, proposing the new binomial *Giraffatitan brancai* for the African taxon (Taylor, 2009). Chure *et al*. (2010; see also Whitlock, 2011a) questioned this separation based on the sister-taxon relationship of the two species recovered in Taylor's (2009) phylogenetic analysis (see also Royo-Torres, 2009). Following Taylor (2009), Ksepka & Norell (2010), Carballido *et al*. (2012), and D'Emic (2012, 2013) included *Brachiosaurus* and *Giraffatitan* as separate operational taxonomic units (OTUs). Ksepka & Norell (2010) recovered them in a polytomy with three North American Cretaceous taxa, Carballido *et al*. (2012) placed them in a polytomy with Somphospondyli, whereas *Giraffatitan* was recovered in a basal position to *Brachiosaurus* in the analysis of D'Emic (2012, 2013). However, none of these analyses included *Lusotitan*; thus, we currently do not know how the Portuguese form is related to these two taxa, or to other basal titanosauriforms.

Titanosauriformes represents the most diverse clade of sauropod dinosaurs, with over 90 distinct species (Salgado, Coria & Calvo, 1997; Wilson & Upchurch, 2003, 2009; Upchurch *et al*., 2004a, 2011a; Curry Rogers, 2005; Wilson, 2005a; Mannion & Calvo, 2011; Mannion *et al*., 2011b; Mannion & Otero, 2012), a global distribution (McIntosh, 1990; Upchurch *et al*., 2004a; Cerda *et al*., 2012a), and a temporal range extending from the Middle Jurassic through to the end-Cretaceous (Day *et al*., 2002, 2004; Upchurch & Martin, 2003; Upchurch *et al*., 2004a). However, the inter-relationships of titanosauriforms are poorly understood, with little resolution or consensus (e.g. Salgado *et al*., 1997; Sanz *et al*., 1999; Smith *et al*., 2001; Wilson, 2002; Upchurch *et al*., 2004a; Curry Rogers, 2005; Calvo *et al*., 2007; Canudo, Royo-Torres & Cuenca-Bescós, 2008; González Riga, Previtera & Pirrone, 2009; Hocknull *et al*., 2009; Ksepka & Norell, 2010; Carballido *et al*., 2011a, b; Gallina & Apesteguía, 2011; Mannion, 2011; Mannion & Upchurch, 2011; Santucci & Arruda-Campos, 2011; Zaher *et al*., 2011; Royo-Torres, Alcalá & Cobos, 2012). Furthermore, most titanosauriform analyses have focused on titanosaurs, with only a small sample of putative basal titanosauriforms included. The exception to this is a recent analysis by D'Emic (2012) that concentrated on basal forms: 25 ingroup taxa were included, representing approximately 50% of putative basal members of Titanosauriformes (see below).

In this paper, we provide a detailed redescription and new diagnosis of the Portuguese sauropod *Lusotitan atalaiensis*. This work represents part of a series of papers in which we will revise the Late Jurassic Portuguese sauropod fauna (see also Mannion *et al*., 2012). We also present a new phylogenetic analysis, consisting of revised and novel characters, focused on elucidating the evolutionary relationships of basal titanosauriforms.

### Institutional abbreviations

CAMSM, Sedgwick Museum, University of Cambridge, UK; CM, Carnegie Museum of Natural History, Pittsburgh, PA, USA; CPT, Museo de la Fundación Conjunto Paleontológico de Teruel-Dinópolis, Aragón, Spain; DMNH, Denver Museum of Natural History, Denver, CO, USA; FMNH, Field Museum of Natural History, Chicago, IL, USA; HMN, Humboldt Museum für Naturkunde, Berlin, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos

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Aires, Argentina; MAPA, Museo Aragones de Paleontología, Aragón, Spain; MCF, Museo 'Carmen Funes', Neuquén, Argentina; MG, Museu Geológico do Instituto Geológico e Mineiro, Lisbon, Portugal (formerly MG and SGP); MNHN, Muséum National d'Histoire Naturelle, Paris, France; MPG, Museo Paleontológico de Galve, Aragón, Spain; NHMUK, Natural History Museum, London, UK; SAM, South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; SMU, Department of Geological Sciences, Southern Methodist University, Dallas, TX, USA; USNM, Smithsonian National Museum of Natural History, Washington DC, USA; UWGM, University of Wyoming Geological Museum, Laramie, WY, USA; YPM, Yale Peabody Museum, New Haven, CT, USA; ZDM, Zigong Dinosaur Museum, Sichuan, China.

### Anatomical and other abbreviations

aEI, average elongation index value: the anteroposterior length of centrum (excluding articular ball) divided by the mean average value of the mediolateral width and dorsoventral height of the posterior articular surface of the centrum (Upchurch, 1995, 1998; Chure *et al*., 2010); CCM, character completeness metric: the percentage of characters that a taxon can be coded for in a phylogenetic analysis (Mannion & Upchurch, 2010b); Cd, caudal vertebra; CPRL, centroprezygapophyseal lamina; Dv, dorsal vertebra; SI, slenderness index: apicobasal length of tooth crown divided by its maximum mesiodistal width (Upchurch, 1998); SPOL, spinopostzygapophyseal lamina; SPRL, spinoprezygapophyseal lamina.

## SYSTEMATIC PALAEONTOLOGY

Sauropoda Marsh, 1878

Neosauropoda Bonaparte, 1986

Macronaria Wilson & Sereno, 1998

? Brachiosauridae Riggs, 1904

*Lusotitan* Antunes & Mateus, 2003

Type species: *Lusotitan atalaiensis*

1957 *Brachiosaurus atalaiensis* Lapparent & Zbyszewski, 1957

1970 *Brachiosaurus atalaiensis* Steel, 1970

1990 *Brachiosaurus atalaiensis* (McIntosh, 1990)

2004 '*Brachiosaurus*' *atalaiensis* Upchurch *et al*., 2004a

*Lectotype:* MG 4798, 4801–4810, 4938, 4944, 4950, 4952, 4958, 4964–4966, 4981, 4982, 4985, 8807, 8793–8795 – two anterior cervical vertebrae, one anterior dorsal centrum and arch, one middle-posterior dorsal centrum, one posterior dorsal neural spine, 21 caudal vertebrae, thoracic rib fragments, one sacral rib, 12 chevrons, distal end of scapula, fragment of sternal plate, proximal halves of right and left humeri, right radius and distal end of left radius, proximal end of right ulna, posterior two-thirds of left ilium, left pubis, left ischium, left tibia, proximal end of left fibula and left astragalus.

*Lusotitan* was based on remains from several localities, but no type specimen was assigned by Lapparent & Zbyszewski (1957); as such, Antunes & Mateus (2003) elected the most complete individual as the lectotype. These elements are closely associated, with some articulation (Lapparent & Zbyszewski, 1957: fig. 3), and preservation is consistent. There is neither duplication of elements nor any notable contrast in size, supporting the view that this probably represents a single individual.

A number of elements could not be located in the MG collections and so any information provided is based purely on figures in Lapparent & Zbyszewski (1957). These missing elements comprise: the two cervical vertebrae, the anterior dorsal vertebra, two caudal vertebrae, ten chevrons, the scapula, ulna, and fibula.

*Locality and horizon:* Peralta, near Atalaia, Lourinhã, Portugal; Sobral Member, Lourinhã Formation; late Kimmeridgian–early Tithonian, Late Jurassic (Lapparent & Zbyszewski, 1957; Antunes & Mateus, 2003; Mateus, 2006; Schneider, Fürsich & Werner, 2009; Kullberg *et al*., 2012).

*Revised diagnosis: Lusotitan atalaiensis* can be diagnosed on the basis of six autapomorphies: (1) lateral margins of anterior-most caudal transverse processes are convex in anterior view; (2) anterior-to-middle caudal centra (excluding the anterior-most few caudal vertebrae) possess prominent pits (usually transversely elongate) on their posterior (and often anterior) articular surfaces; (3) anterior-to-middle caudal postzygapophyses (excluding the anterior-most few caudal vertebrae) form transversely compressed, elongate processes that project well beyond the posterior margin of the neural arch; (4) shoulder-like region lateral to the base of the neural spine, in between the prezygapophyses and postzygapophyses, in anterior-to-middle caudal vertebrae; (5) tibia strongly bowed laterally; (6) no vertical groove extending up the shaft between the lateral and medial malleoli of the tibia.

*Additional comments:* Lapparent & Zbyszewski (1957) did not provide a diagnosis for *Lusotitan* ('*Brachiosaurus*') *atalaiensis*, merely noting overall similarities with *Brachiosaurus* and *Giraffatitan*. Only Antunes & Mateus (2003: 83) have attempted to provide a diagnosis for *Lusotitan*: 'mid-dorsals with

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very large pleurocoels; anterior caudals have well developed transverse processes; mid-caudal neural spine inclined almost vertically; posterior caudal centra has convex anterior face; mid- and posterior caudal centra are wider than high; slender pelvis; notch at the posterodorsal margin of ilium; postacetabular process of ilium bulky and without notch between this process and the ischial peduncle; obturator foramen of pubis closed; distal end of pubis anteroposteriorly expanded; tibia bowed laterally; proximal end of fibula is not rounded, but has an angular outline'. Nearly all of these features have a wider distribution amongst Sauropoda or reflect incomplete preservation, and cannot be used to diagnose *Lusotitan*. Upchurch *et al*. (2004a: 308) also commented that no autapomorphies of either *Brachiosaurus* or *Giraffatitan* have been noted in the Portuguese material and that *Lusotitan* differs from *Giraffatitan* in possessing a less steeply inclined ischial shaft.

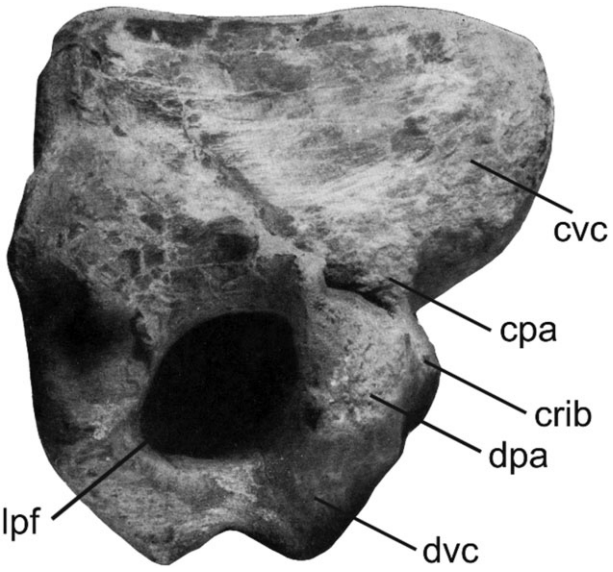


**Figure 1.** *Lusotitan atalaiensis*. Photograph of adhered cervical and dorsal vertebrae, reproduced from Lapparent & Zbyszewski (1957). The cervical vertebra is in ventral view and the dorsal vertebra is in right lateral view. Abbreviations: cpa, cervical parapophysis; crib, cervical rib; cvc, cervical vertebra centrum; dpa, dorsal parapophysis; dvc, dorsal vertebra centrum; lpf, lateral pneumatic foramen. No scale bar available.

## Description and comparisons

### *Axial skeleton*

*Cervical vertebrae:* Two anterior cervical vertebrae were listed as present, with Lapparent & Zbyszewski (1957: pl. 25, fig. 85) figuring the better preserved of the two; however, we were unable to locate either element. The element is somewhat confusing as figured and our interpretation of it here should be treated with caution (Fig. 1). We interpret this element to comprise two adhered vertebrae: a cervical centrum in ventral view and an anterior dorsal centrum with neural arch in right lateral view in the upper and lower halves of the figure, respectively (Fig. 1). The dorsal vertebra will be described in the following section. Our basis for concluding that the upper element is a cervical vertebra relates to the position of what we assume to be the parapophysis (possibly including a portion of fused rib), which is situated on the lateroventral margin, close to the anterior end of the centrum (Fig. 1). Little anatomical information can be gleaned from the opisthocoelous cervical centrum: the ventral surface appears to be gently concave transversely, comparable to the titanosauriforms *Australodocus* (Remes, 2007), *Giraffatitan* (Upchurch *et al*., 2004a), and *Sauroposeidon* (M. J. Wedel, pers. comm., 2010), as well as *Tendaguria* (Bonaparte, Heinrich & Wild, 2000) and diplodocids (Upchurch, 1995, 1998). It lacks a ventral keel, which is also absent in most macronarians, with the exception of the titanosauriforms *Erketu*, *Gondwanatitan*, and *Mongolosaurus* [Mannion (2011) and references therein].

*Dorsal vertebrae:* The anterior dorsal vertebra mentioned above preserves a relatively complete centrum and a portion of the neural arch (Fig. 1). Its anterior position in the dorsal sequence is inferred from the location of the probable parapophysis, situated just above midheight on the lateral surface of the centrum. The centrum is opisthocoelous and the ventral margin is strongly arched dorsally in lateral view. A deep lateral pneumatic foramen occupies approximately the middle half of the centrum; this foramen has the reversed 'D'-shape (i.e. an acute posterior margin) common to the anterior dorsal vertebrae of macronarians (Upchurch, 1998). No further anatomical information can be observed from the figure in Lapparent & Zbyszewski (1957: pl. 25, fig. 85).

The centrum and base of the neural arch of a poorly preserved middle–posterior dorsal vertebra (Fig. 2) are also present (MG 4985-1; Lapparent & Zbyszewski, 1957: pl. 22, figs 71–72; see Table 1 for measurements). Ventrally, the centrum is transversely convex with no ridges or fossae, which differs from the midline ridge present on the dorsal centra of several other sauropods, including *Brachiosaurus* and *Giraffatitan* (Upchurch *et al*., 2004a). At its anterior end, the dorsoventrally compressed centrum is relatively flat, with some degree of irregular convexity immediately below and in front of the neural canal floor; the posterior articular face is moderately concave. All macronarians possess opisthocoelous

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**Figure 2.** *Lusotitan atalaiensis*. Photograph of middle-posterior dorsal vertebra (MG 4985-1) in left lateral view. Scale bar = 100 mm.

centra throughout the dorsal series (Salgado *et al*., 1997; Wilson & Sereno, 1998), and so its absence would be an unusual feature in *Lusotitan*. However, it is difficult to ascertain whether this articular morphology is genuine or the result of crushing and breakage, although it seems unlikely that it could have formed a well-developed condyle. A lateral pneumatic foramen is present on either side of the centrum, although its exact outline cannot be determined. It ramifies extensively, both dorsally and ventrally, with no midline septum preserved, indicating that the latter must have been extremely thin (Fig. 2). This is the condition in most neosauropods (Upchurch, 1998), although it is also present in some basal eusauropods (Royo-Torres, Cobos & Alcalá, 2006; Mannion, 2010). The internal tissue structure cannot be observed.

Lapparent & Zbyszewski (1957: 40) mentioned the existence of a dorsal neural spine, but neither described nor figured this element. It consists of the upper part of a poorly preserved, large neural spine (Fig. 3) from the dorsal (or possibly anterior sacral) region. The spine summit has been strongly deformed, such that it is bent downwards on the right side and upwards on the left side. The summit of the spine is robust, with a transversely convex dorsal surface. There appears to be evidence for triangular aliform processes, although these are the robust posteroventral portions of the spine summit rather than distinct wing-like plates. Towards the top of the lateral surface of the spine, the underside of the summit (i.e. where it overhangs the lateral surface) is deeply excavated. The core of the neural spine, as preserved, is a transversely compressed, anteroposteriorly widened plate. Despite its incomplete nature, in lateral view the spine is relatively tall and the impression is that it projected upwards and slightly backwards. Although there are laminae preserved, these have mostly been broken away, leaving only their bases. At the anterolateral margins, the bases of two stout laminae can be seen: these may represent spinoprezygapophyseal laminae (SPRLs), in which case they seem to have ascended almost to the summit of the spine. The anterior surface of the neural spine forms a roughened, prespinal rugosity. At about midheight on the posterior surface, vertical ridges may indicate the bases of spinopostzygapophyseal laminae (SPOLs), with a postspinal lamina 'infilling' the midline between them. Neither the prespinal nor postspinal lamina forms a distinct ridge. Adhered to the right lateral surface of the spine is a portion of rib.

*Ribs:* Lapparent & Zbyszewski (1957) noted that several rib fragments were preserved, although none were figured and they could not be located for examination. The only information provided for these elements comes from Lapparent & Zbyszewski (1957: 41; translated from the French by M. T. Carrano): 'Several portions of sauropod ribs were recovered at Atalaia. Some are flat and 7.5 cm wide; others are round and have a diameter of 4 to 5 cm. Their total length is not known.' Little can be gleaned from this, although the flat and wide ribs sound reminiscent of the plank-like anterior thoracic ribs present in titanosauriforms (Wilson, 2002). The subcircular elements may represent cervical ribs, fragments of the first thoracic rib, or posterior thoracic ribs (Upchurch *et al*., 2004a).

A left sacral rib (Fig. 4) was previously misidentified as a metacarpal (Lapparent & Zbyszewski, 1957: 42; see Antunes & Mateus, 2003). The convex proximal end rapidly narrows into the main shaft, which has a dorsoventrally compressed and elliptical parasagittal cross-section. The posterodorsal part of the proximal end gives rise to an anteroposteriorly thin plate that extends along the length of the rib, approaching the anterior margin of the iliac articulation. On the dorsal surface of the rib, close to the proximal end, there is an excavated area that is divided into a smaller posterior and larger anterior region by a transverse ridge. Where this ridge merges with the dorsally facing surface of part of the proximal end, there is a small, prong-like lateral projec-

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**Table 1.** Measurements of the middle-posterior dorsal centrum and caudal vertebrae of *Lusotitan atalaiensis*

| | CL | ACH | ACW | PCH | PCW | DFA | DFP | NAH | PRL | NSL | NSW | CRL |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Dv | 193 | 238 | 337 | 258 | 330 | – | – | – | – | – | – | – |
| CdA | 168 | 258 | 264 | 247 | 270 | 17 | 32 | 142 | 47 | 121 | 47 | – |
| CdB | 149 | 239 | 258 | 225 | 236 | – | – | – | – | – | – | – |
| CdC | 155 | 151 | – | 174 | – | 8 | 37 | 64 | – | – | – | 423 |
| CdD | 154 | 164 | 197 | 164 | 184 | 17 | 37 | 58 | 58 | – | – | 350 |
| CdE | 158 | 147 | 201 | 158 | 184 | 17 | 42 | 47 | 58 | – | – | – |
| CdF | 164 | – | 191 | 137 | – | 16 | 43 | 55 | – | – | – | – |
| CdG | 144 | 149 | 180 | 142 | 172 | – | 39 | – | – | – | – | – |
| CdH | 159 | 132 | 165 | 135 | 155 | 17 | 53 | – | 74 | – | – | – |
| CdI | 159 | 130 | 154 | 125 | 148 | 16 | 57 | – | – | – | – | – |
| CdJ | 154 | 124 | 150 | 119 | 141 | 24 | 49 | – | – | – | – | – |
| CdK | 151 | 116 | 140 | 118 | 133 | 26 | 52 | – | – | – | – | – |
| CdL | 149 | 109 | 132 | 108 | 134 | 37 | 37 | – | – | – | – | – |
| CdM | 138 | 95 | 129 | 101 | 131 | 19 | 44 | – | – | – | – | – |
| CdN | 141 | 91 | 125 | 91 | 126 | 24 | 48 | – | – | – | – | – |
| CdO | 143 | – | – | 87 | 124 | – | 54 | – | – | – | – | – |
| CdP | 133 | 86 | 116 | 86 | 122 | 30 | 35 | – | – | – | – | – |
| CdQ | 136 | 82 | – | 81 | 121 | 31 | 41 | – | – | – | – | – |
| CdR | 138 | 82 | 114 | 82 | 117 | 30 | 52 | – | – | – | – | – |
| CdS | 129 | 75 | – | 76 | 104 | 24 | 49 | – | – | – | – | – |

Abbreviations: CL, centrum length; ACH, anterior centrum height (excluding chevron facets); ACW, anterior centrum width; PCH, posterior centrum height (excluding chevron facets); PCW, posterior centrum width; DFA, distance from anterior end of centrum to anterior end of neural arch; DFP, distance from posterior end of centrum to posterior end of neural arch; NAH, neural arch height (measured from the dorsal surface of the centrum up to the postzygapophyses); NSL, neural spine anteroposterior length (measured along base of spine); NSW, neural spine mediolateral width (measured along base of spine at the posterior margin); PRL, prezygapophysis length; CRL, caudal rib length (transverse width between distal ends of ribs).
Measurements are in millimetres.

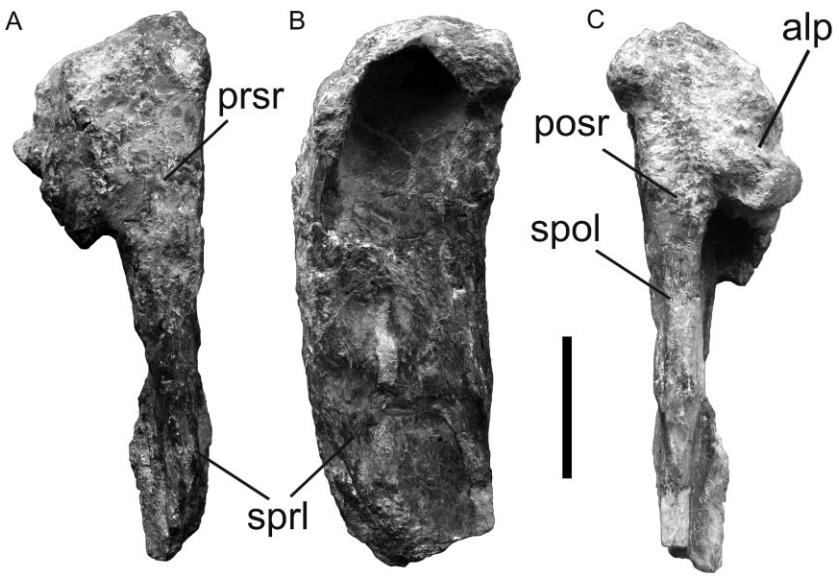


**Figure 3.** *Lusotitan atalaiensis*. Photographs of dorsal neural spine in (A) anterior, (B) left lateral, and (C) posterior views. Abbreviations: alp, aliform process; posr, postspinal ridge; prsr, prespinal ridge; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; Scale bar = 100 mm.

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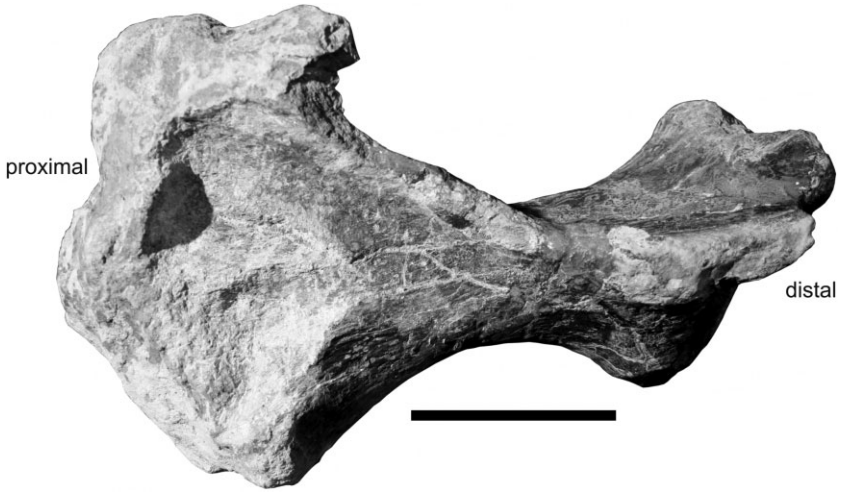


**Figure 4.** *Lusotitan atalaiensis*. Photograph of left sacral rib in dorsal view. Scale bar = 100 mm.

tion. The proximal end also has a lower convex expansion that would have articulated with the centrum. A posterodorsal projection is present on the proximal surface that is ultimately continuous with the plate-like ridge that extends along the dorsal surface of the rib. The iliac articulation is also expanded relative to the midshaft of the rib but is not as expanded or as robust as the proximal end. The distal end surface has an irregular 'D'-shaped outline with the straight margin of this 'D' facing anterodorsally. The point where this straight margin meets the rounded posterodorsal surface represents the distal end of the ridge on the dorsal surface of the rib. The distal articular surface is rugose and mildly convex, except for a deep excavation occupying the anterodorsal portion running along the straight margin of the 'D'-shaped profile. It is not clear from this sacral rib whether there were any foramina between the sacral vertebrae, sacral plate, and/or ilium.

*Caudal vertebrae:* In the MG collections we were able to locate 19 anterior-to-middle caudal vertebrae (see Table 1 for measurements), two fewer than mentioned by Lapparent & Zbyszewski (1957: 40). These authors described them as three anterior caudal vertebrae and an uninterrupted series of 18 caudal vertebrae, with a probable gap of three to four vertebrae in between. Here we describe the existing caudal vertebrae as CdA–S, referring to their mention and illustration in Lapparent & Zbyszewski (1957) where appropriate. The majority of the vertebrae do not preserve neural spines, with most comprising only centra and the bases of the neural arches.

CdA preserves the centrum, arch, and base of the neural spine (Fig. 5), although the right transverse process (= caudal rib) has been broken off since its original description. Lapparent & Zbyszewski (1957: 40 and pl. 23, figs 76–77) considered CdA (MG 4985-2) to be the most anterior caudal vertebra preserved, and thought it likely to represent the second or third element of the tail. No chevron facets are present, which appears to be a genuine feature, supporting the view that this represents one of the anterior-most caudal vertebrae. The transversely convex ventral surface lacks either lateroventral ridges or a midline sulcus, corresponding to the morphology seen in non-titanosaurs and non-diplodocids (McIntosh, 1990; Upchurch, 1995, 1998; Wilson, 2002; Curry Rogers, 2005). The anterior face of the centrum is mildly concave, whereas the posterior face is predominantly flat, differing from the procoelous condition of titanosaurs, flagellicaudatans, and some non-neosauropods (McIntosh, 1990; Upchurch, 1995; Salgado *et al*., 1997). There is no pneumatic fossa or foramen on the lateral surface of the centrum, but small, shallow vascular foramina pierce this surface (Fig. 5B; also observed on CdB). The dorsally projecting neural arch has a slight anterior bias with regard to the centrum length and the neural canal has an elliptical outline, with its long axis orientated dorsoventrally (Fig. 5A). There is a depression between the bases of the prezygapophyses, which is separated from the top of the neural canal by a dorsoventrally tall, convex region. Only the right prezygapophysis is completely preserved. Ventrally, each prezygapophysis is supported by a thin, unbifurcated centroprezygapophyseal lamina (CPRL). The prezygapophyses project anterodorsally beyond the anterior margin of the centrum, and their 'D'-shaped, flat articular facets face dorsomedially. Both postzygapophyses are preserved as laterally facing facets at the base of the neural spine (Fig. 5B). Ventrally, they converge to

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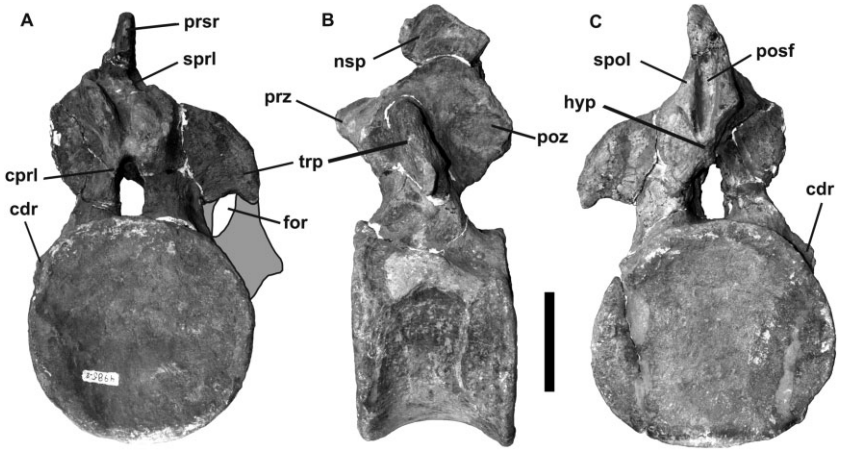


**Figure 5.** *Lusotitan atalaiensis*. Photographs of anterior caudal vertebra CdA in (A) anterior, (B) left lateral, and (C) posterior views. Abbreviations: cdr, caudal rib; cprl, centroprezygapophyseal lamina; for, foramen; hyp, hyposphene; nsp, neural spine; posf, postspinal fossa; poz, postzygapophysis; prsr, prespinal ridge; prz, prezygapophysis; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; trp, transverse process. An interpretative reconstruction of the missing portions of the caudal rib and possible foramen is shown in grey on (A). Scale bar = 100 mm.

meet on the midline at the top of a dorsoventrally short, hyposphenal plate (Fig. 5C). A hyposphenal ridge is present in the anterior caudal vertebrae of most sauropods (Upchurch, 1998), but is absent in some titanosauriforms [e.g. *Tastavinsaurus* (Canudo *et al*., 2008) and *Rapetosaurus* (Curry Rogers, 2009)] and most rebbachisaurids (Mannion, Upchurch & Hutt, 2011a; Mannion *et al*., 2012). As in most titanosauriforms, the hyposphenal ridge in *Lusotitan* is prominent and 'block'-like, differing from the slender ridge seen in many non-macronarians [e.g. *Shunosaurus* (ZDM specimens: P. Upchurch, pers. observ., 1995) and *Apatosaurus* (Gilmore, 1936)] and also *Giraffatitan* (Taylor, 2009). In between the postzygapophyses, there is a slot-like postspinal fossa (Fig. 5C), which has a rugose surface (postspinal rugosity). Much of the neural spine is broken away, but at its base it appears to have been a transversely compressed, anteroposteriorly elongate plate, comparable to taxa such as *Cedarosaurus* (Tidwell, Carpenter & Brooks, 1999: fig. 3) and *Giraffatitan* (Janensch, 1950: pl. 2). At its base, the neural spine is supported by SPRL and SPOL ridges (Fig. 5A, C). The anterior margin of the preserved part of the neural spine is damaged, but there is some evidence for a thin, sheet-like, vertical prespinal ridge (Fig. 5A). The laterally projecting transverse process extends from the level of the base of the prezygapophysis to a point just above the base of the neural arch. Its lateral margin is potentially unusual: whereas in other sauropods this margin is straight or concave in anterior view, in *Lusotitan* this margin is convex. We tentatively regard this feature as an autapomorphy of *Lusotitan*. The true caudal rib (i.e. the lower half) is represented only by a raised area on the dorsal third of the lateral surface of the centrum. The ventral margin of the upper plate appears to represent an unbroken surface, suggesting that it did not contact the dorsal surface of the rib; thus, it is probable that a foramen passed through from the anterior to the posterior surface of the transverse process (Fig. 5A). If correctly interpreted, this feature would be particularly unusual, as perforated or deeply excavated caudal ribs are otherwise only known in diplodocids and rebbachisaurids, respectively (Calvo & Salgado, 1995; Upchurch, Tomida & Barrett, 2004b; Upchurch & Mannion, 2009; Mannion, Upchurch & Hutt, 2011a). None of the caudal vertebrae of *Lusotitan* display any evidence for distinct, ridge-like diapophyseal laminae, which differs from the anteriormost caudal vertebrae of several macronarians that possess a prezygodiapophyseal lamina [e.g. *Aragosaurus* (MPG specimens: P. D. Mannion & P. Upchurch pers. observ., 2009), *Abydosaurus*, *Brachiosaurus*, and *Giraffatitan* (Chure *et al*., 2010)], and several diplodocoids that display a partial or full suite of diapophyseal laminae (Wilson, 1999, 2002; Mannion *et al*., 2011a; Whitlock, 2011b). However, the relevant region of CdA is poorly preserved and this feature is often restricted to the anterior-most vertebrae of the caudal sequence. CdB (MG 4985-3) is represented only by a centrum and does not provide any additional anatomical information.

CdC (MG 4985-4) was figured by Lapparent & Zbyszewski (1957: pl. 29, fig. 111). It is the first caudal vertebra with chevron facets preserved (Fig. 6A–C): prominent posterior facets are clearly visible and there is evidence for less well-defined anterior facets. The

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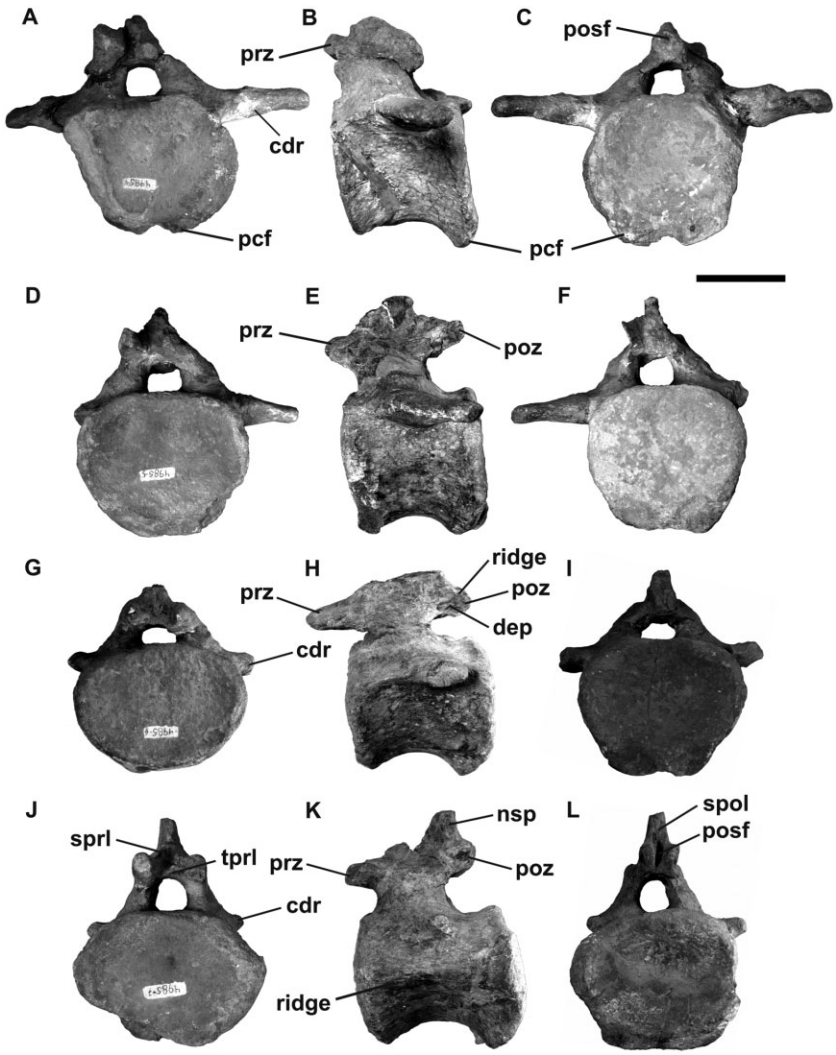


**Figure 6.** *Lusotitan atalaiensis*. Photographs of anterior caudal vertebrae: CdC in (A) anterior, (B) left lateral, and (C) posterior views; CdD in (D) anterior, (E) left lateral, and (F) posterior views; CdE in (G) anterior, (H) left lateral, and (I) posterior views; CdF in (J) anterior, (K) left lateral, and (L) posterior views. Abbreviations: cdr, caudal rib; dep, depression; nsp, neural spine; pcf, posterior chevron facet; posf, postspinal fossa; poz, postzygapophysis; prz, prezygapophysis; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; tprl, intraprezygapophyseal lamina. Scale bar = 100 mm.

posterior facets are well separated from one another along the midline, suggesting that the proximal ends of the chevrons are unbridged; this is the case in all preserved chevron facets along the tail sequence. Unlike CdA–B, both anterior and posterior articular surfaces of the centrum are shallowly concave. The neural arch is situated on the anterior two-thirds of the centrum and the large neural canal is subcircular. Poor preservation means that details of the base of the neural spine and postzygapophyses cannot be fully determined, but the spine probably had a transversely compressed base and there is evidence for a postspinal fossa between the postzygapophyses. Although the postzygapophyseal area is badly eroded, it seems unlikely that a hyposphenal ridge could have been present (Fig. 6C). The caudal ribs are relatively long, dorsoventrally compressed plates that curve strongly laterally and backwards such that their posterior tips are approximately level with the posterior margin of the centrum (Fig. 6B). The latter curvature is a feature of a number of titanosauriforms (Mannion & Calvo, 2011; D'Emic, 2012), although it is absent in *Brachiosaurus*, in which the caudal ribs project laterally (Taylor, 2009).

Cds D and E [MG 4985-5 and -6 (figured by Lapparent & Zbyszewski, 1957: pl. 19, fig. 53); see

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Fig. 6D–I] possess a shallow triangular concavity along the posterior portion of the ventral surface, created in part by very subtle ridges that support the widely separated posterior chevron facets. Prezygapophyses project predominantly anteriorly. The postzygapophyses form transversely compressed, elongate processes that project posteriorly to a point almost level with the posterior margin of the centrum (Fig. 6E, H). *Aragosaurus* also possesses enlarged postzygapophyses in its middle caudal vertebrae (MPG specimens: P. D. Mannion & P. Upchurch, pers. observ., 2009), but these do not form the extended processes seen in *Lusotitan*. This postzygapophyseal morphology is thus regarded here as an autapomorphy of *Lusotitan*. On the lateral surface of these postzygapophyseal plates, a low rounded ridge extends posterodorsally to the dorsal margin of the process, terminating at about midlength (Fig. 6E, H). Below this ridge, where the postzygapophysis merges with the posterior margin of the arch, there is a small depression that probably received the tip of the succeeding prezygapophysis (Fig. 6E, H). It is clear that a hyposphenal ridge is absent (Fig. 6F, I). As in CdC, the caudal ribs project strongly posterolaterally, terminating at or just beyond the posterior margin of the centrum (Fig. 6E, H).

CdF (MG 4985-7) (Fig. 6J–L) marks the point at which the caudal ribs begin to be reduced to small processes, located at about midlength of the centrum. There is now a distinct horizontal ridge on the lateral surface of the centrum (Fig. 6K) that divides it into an upper (laterally and slightly dorsally facing) region and a lower (ventrally and slightly laterally facing) region that merges smoothly into the ventral surface. On the posterior articular surface of the centrum, the central region bears a transversely elongate depression (Fig. 6L; see below). The prezygapophyses are joined by a thin intraprezygapophyseal lamina that forms the roof of the anterior neural canal opening (Fig. 6J). From the dorsomedial surface of each prezygapophysis, a thin SPRL extends posteriorly and medially to the base of the neural spine. The posterior portions of the postzygapophyses are damaged but they clearly project as processes beyond the posterior margins of both the spine and neural arch (Fig. 6K). Rounded lateral ridges and associated depressions for reception of the prezygapophyses are again present. Most of the neural spine is missing but a portion is preserved just above the postzygapophyses. The broken surface suggests that the spine was transversely thickest close to its anterior and posterior margins but had a transversely thin central portion. A well-developed postspinal fossa is located between single SPOLs (Fig. 6L).

Cds G and H (MG 4985-8 and -9) show similar features to CdF, but lack the lateral ridge and the depression on the posterior surface of the centrum. The prezygapophyses of CdH also project anterodorsally (Fig. 7A), differing from the predominantly horizontal orientation of the preceding vertebrae. It is possible that these differences indicate that CdF is actually posterior to CdG–H in the tail sequence, but we retain their current sequence for the purposes of this description.

The morphology of the centrum of CdI (MG 4985-10; Lapparent & Zbyszewski, 1957: pl. 23, fig. 80) is

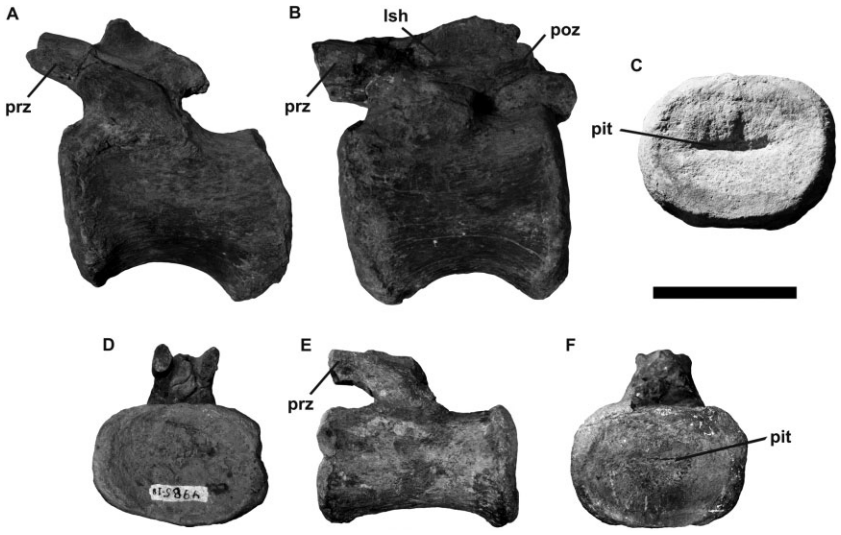


**Figure 7.** *Lusotitan atalaiensis*. Photographs of middle-posterior caudal vertebrae: A, CdH in left lateral view; B, CdI in left lateral view; C, CdM in posterior view; CdR in (D) anterior, (E) left lateral, and (F) posterior views. Abbreviations: lsh, lateral shelf; poz, postzygapophysis; prz, prezygapophysis. Scale bar = 100 mm.

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similar to the preceding vertebrae, although the posterior surface of the centrum is more deeply concave than the anterior one and bears a transversely elongate pit at approximately midheight. Caudal ribs are barely discernible. At the point where the posterior margin of the neural arch meets the dorsal surface of the centrum, there is a posterolaterally directed, rounded bulge, which merges anteriorly into a roughened horizontal ridge. Lateral to the base of the neural spine, in between the prezygapophyses and postzygapophyses, there is a transversely broad area with a mildly excavated dorsal surface (Fig. 7B); this is distinct from the lateroventrally sloping surface of the neural arch. This shoulder-like region can also be seen in Cds E, F, and H, although in these preceding vertebrae it is less well developed. This feature is regarded as diagnostic of *Lusotitan*. Although only the base of the neural spine is preserved, it is probable that the short and poorly developed SPRLs converged on the midline. The SPOLs appear to have been very short and the posterior surface of the spine seems to have been formed by a transversely rounded midline ridge that overhangs the postspinal fossa.

The centrum of CdJ has nearly vertical lateral surfaces and a transversely, mildly convex ventral surface. The lateral and ventral surfaces meet each other at approximately 90°, although this junction is rounded rather than acute. On the lateral surface, the junction between centrum and arch is marked by a low, roughened ridge. The posterior articular surface has a central pit, but it is no longer transversely elongate. Subsequent centra do not differ substantially from CdJ, although the pit in CdM is transversely elongate (Fig. 7C). Beginning with CdL (MG 4985-13), the anterior articular surfaces of centra also bear a deep, pit-like area in their central regions, just above midheight. Both anterior and posterior pits are reduced in Cds O–Q, but become prominent and transversely elongate once more in Cds R–S (Cd7D, F). Similar pits are present on the articular surfaces of caudal centra of other sauropod taxa (e.g. *Gobititan*; You, Tang & Luo, 2003), but these tend to be present only in the more posterior section of the tail or are more irregularly distributed. As such, we consider the relatively consistent presence of these slot-like pits, and their appearance in the anterior part of the tail, a probable autapomorphy of *Lusotitan*. Caudal centra also become increasingly dorsoventrally compressed from approximately CdL onwards (Fig. 7C), and the anterior articular surfaces flatten. Beginning with CdM, the lateral surfaces of the centra become increasingly convex dorsoventrally, such that by CdR (MG 4985-18) the upper part of the lateral surface faces strongly dorsally and only moderately laterally (Fig. 7E). This is accentuated in CdS, in which the dorsolateral surface meets the lateral surface of the centrum at a notable change of direction, creating an almost ridge-like area extending anteroposteriorly. The preserved prezygapophyses in CdQ show that they projected almost entirely anteriorly. CdS (Lapparent & Zbyszewski, 1957: pl. 22, figs 74–75) preserves part of the neural spine, demonstrating that it was directed strongly posterodorsally; as such, the posterior surface of the spine faces ventrally and overhangs the exposed posterior portion of the dorsal surface of the centrum.

*Chevrons:* Lapparent & Zbyszewski (1957) listed 12 chevrons preserved with the type individual of *Lusotitan*, figuring five of them. Two of the anterior chevrons were studied by us ['Chevron A and B' (Fig. 8; see Table 2 for measurements)], but we could not locate the other ten. The following description will therefore be based largely on these two elements, supplemented with information provided by Lapparent & Zbyszewski (1957).


**Figure 8.** *Lusotitan atalaiensis*. Photographs of chevrons: A, chevron A in left lateral view; B, chevron B in posterior view Scale bar = 100 mm.

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**Table 2.** Measurements of chevrons of *Lusotitan atalaiensis*

| Measurement | Chevron A | Chevron B |
|---|---|---|
| Straight line dorsoventral length | 374 | 317 |
| Dorsoventral height of haemal canal | 176 | 151 |
| Anteroposterior width of proximal articulation | 53 | 48 |
| Mediolateral width across proximal end | – | 91 |
| Mediolateral width across one proximal articular facet | 44 | 34 |
| Anteroposterior width of shaft immediately below haemal canal | 51 | 36 |
| Mediolateral width of shaft immediately below haemal canal | 40 | 45 |
| Anteroposterior width of distal end | 57 | 36 |
| Mediolateral width of distal end | 11 | 7.5 |

Measurements are in millimetres.

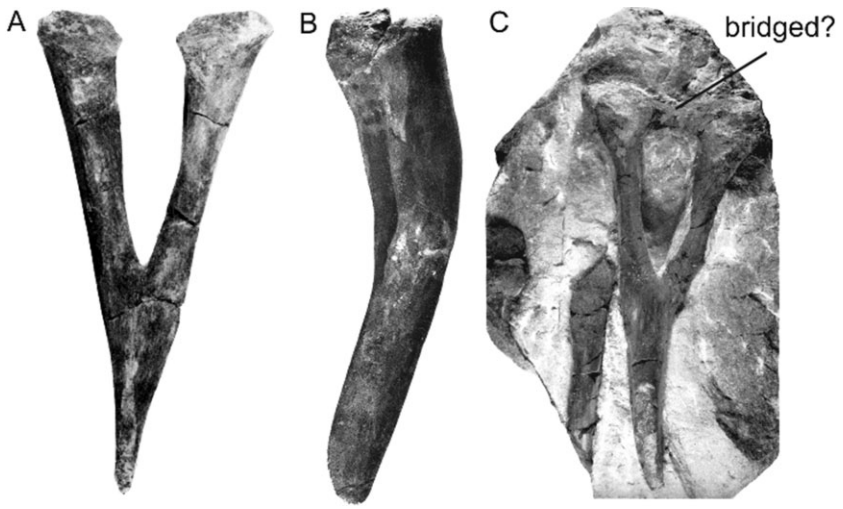


**Figure 9.** *Lusotitan atalaiensis*. Photographs of chevrons reproduced from Lapparent & Zbyszewski (1957): A, chevron in posterior view; B, chevron in right lateral view; C, dorsally bridged (?) chevron in posterior view. No scale bar available.

The chevrons have an elongate 'Y'-shaped profile in anterior view, with open proximal ends (Figs 8, 9A, B). Lapparent & Zbyszewski (1957: 41) commented that the chevrons of anterior caudal vertebrae were proximally closed by a bar of bone: this is clearly not the case in the elements that we examined, but there is evidence for this in one of the figured chevrons in Lapparent & Zbyszewski (1957: pl. 17, fig. 46) (Fig. 9C). Nearly all macronarians possess proximally open chevrons throughout the caudal series (Upchurch, 1995), with the exception of several Chinese taxa and some *Camarasaurus* specimens (Mannion & Calvo, 2011, and references therein), including *Camarasaurus* ('*Cathetosaurus*') *lewisi* (McIntosh *et al*., 1996a); consequently, this would be an unusual and noteworthy feature in *Lusotitan*. The 'bridged' *Lusotitan* chevron is apparently 315 mm long (Lapparent & Zbyszewski, 1957: 41), making it shorter than the two studied elements (Table 2) and indicating that it is from further along the tail sequence. Although it is feasible that *Lusotitan* displayed variation in chevron proximal morphology, it is also possible that the 'bridging' is merely matrix. This possibility is further supported by the wide separation of posterior chevron facets on all caudal vertebrae (see above). However, pending the relocation of these putatively bridged chevrons, this feature must remain ambiguous.

The proximal articular surfaces of at least the anterior-most preserved chevron are anteroposteriorly convex, with equidimensional anterior and posterior facets, as is the case in several titanosauriforms (Canudo *et al*., 2008; Mannion & Calvo, 2011). Haemal canal depth is a little under 50% of total chevron length in the two anterior chevrons, and exceeds 50% in a chevron from further along the tail sequence (Lapparent & Zbyszewski, 1957: pl. 22, fig. 73). This high ratio is generally thought to be a

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feature restricted to titanosaurs (Wilson, 2002), with *Cedarosaurus* convergently acquiring autapomorphically deep haemal canals (Tidwell *et al.*, 1999; Mannion & Calvo, 2011).

The shaft of the chevron, below the haemal canal, is transversely compressed and in the larger, more anterior element ('Chevron A'), it expands slightly anteroposteriorly too. Just distal to the haemal canal, there is a moderately deep midline excavation on the anterior surface. This rapidly disappears distally and is replaced by a midline ridge. In lateral view, each chevron curves strongly posteriorly towards its distal end (see also Lapparent & Zbyszewski, 1957: pl. 32, fig. 138).

*Internal vertebral tissue structure:* There is some evidence for a camellate internal structure in the cervical and anterior dorsal vertebrae figured by Lapparent & Zbyszewski (1957: pl. 25, fig. 85) (Fig. 1), but it is not possible to observe the tissue structure in the middle-posterior dorsal centrum. A camellate structure in presacral vertebrae would be in keeping with a titanosauriform position for *Lusotitan* (see 'Evolution of postcranial pneumaticity' in the Discussion), but at the moment this must remain equivocal. Caudal vertebrae display a solid internal structure.

*Appendicular skeleton*

*Scapula and sternal plate:* Lapparent & Zbyszewski (1957) mentioned the existence of the distal end of a scapula and a portion of sternal plate belonging to the type individual of *Lusotitan*. These elements were not figured in the original description and could not be located for study. Consequently, the only information available on these two elements is the extremely brief description in Lapparent & Zbyszewski (1957: p. 41; translated from the original French by M. T. Carrano): 'The distal end of a scapula is 52 cm wide; the rest of this bone was not found. A fragment of flat bone 15 cm wide and ornamented on the two edges opposing the articular surfaces is referred to a right sternum. Compared to the sternum of *Diplodocus*, it is of proportionally smaller dimensions.'

*Humerus:* Only the proximal halves of the right and left humeri are preserved (Lapparent & Zbyszewski, 1957; see Fig. 10 and Table 3 for measurements). The strongly rugose proximal end surface is transversely convex in anterior view, merging smoothly into the lateral margin (Fig. 10A), as in most other non-somphospondylans (Upchurch, 1999; Wilson, 2002; Mannion & Calvo, 2011). The medial projection of the proximal end is also smoothly convex in anterior view. In dorsal view, the midpoint of the proximal end expands and overhangs the posterior surface of the humerus, extending distally for a short distance (Fig. 10B–E). Immediately medial to this posterior bulge, on the posterior surface, there is a moderately deep concavity.

The proximolateral portion of the humerus forms a low, transversely rounded ridge. Distally, this ridge expands to form the anteriorly directed deltopectoral crest (Fig. 10A, B). The latter crest is reduced, as in other sauropods (Wilson & Sereno, 1998), and does not expand medially across the anterior face of the humerus, differing from titanosaurs (Wilson, 2002) and some basal titanosauriforms (Mannion & Calvo, 2011), including *Giraffatitan* (Janensch, 1961: Beilage A, fig. 1a). There are no ridges or grooves on the lateral surface of the deltopectoral crest. The anterior surface of the proximal end is mildly concave transversely, partly because of the presence of the deltopectoral crest, but also because the surface of the medial part projects a little anteriorly. The cross-

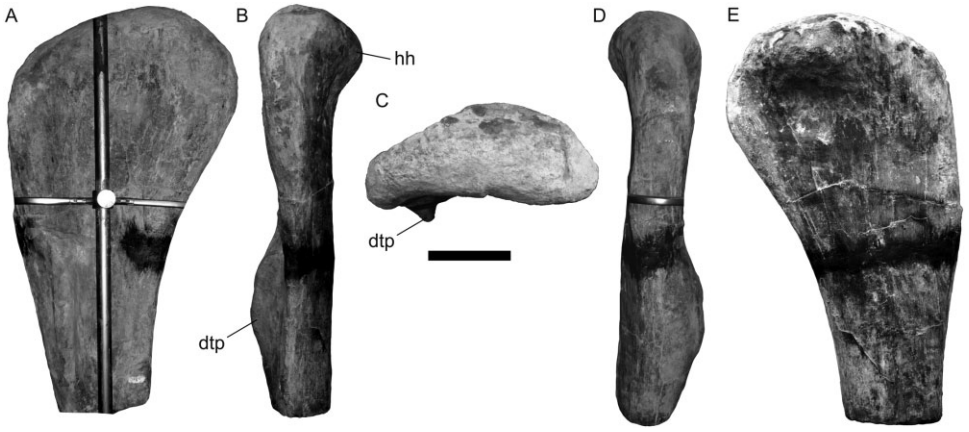


**Figure 10.** *Lusotitan atalaiensis*. Photographs of right humerus (proximal half) in (A) anterior (slightly oblique as a result of mounted position), (B) medial, (C) proximal, (D) lateral, and (E) posterior views. Abbreviations: dtp, deltopectoral crest; hh, humeral head. Scale bar = 200 mm.

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**Table 3.** Measurements of appendicular elements of *Lusotitan atalaiensis*

| Measurement | Humerus | Radius | Pubis | Tibia | Astragalus |
|---|---|---|---|---|---|
| Proximodistal length | 994* | 1145 | 748 | 1079 | – |
| Mediolateral width of proximal end | 545 | 275 | – | 383 | 295 |
| Anteroposterior width of proximal end | 199 | 175 | – | 348 | 160 |
| Estimated length of ischiadic articulation | – | – | 388 | – | – |
| Distance from proximal end to most prominent point of deltopectoral (dtp) crest | 774 | – | – | – | – |
| Projection of dtp crest from anterior surface | 94 | – | – | – | – |
| Distance from proximal end to lateral tip of cnemial crest | – | – | – | 241 | – |
| Distance that cnemial crest projects laterally from tibial surface | – | – | – | 121 | – |
| Mediolateral width at midshaft (at preserved distal end of humerus) | – | 138 | – | 174 | – |
| Anteroposterior width at midshaft (measured at preserved distal end of humerus) | – | 64 | – | 91 | – |
| Mediolateral width of distal end | – | 251 | – | 412 | – |
| Mediolateral width of medial malleolus | – | – | – | 201 | – |
| Anteroposterior width of distal end | – | 152 | – | 238 | – |
| Dorsoventral height of lateral margin | – | – | – | – | 157 |
| Posterodorsal to anteroventral thickness of medial margin | – | – | – | – | 51 |

An asterisk denotes a measurement taken on an incomplete element. Humerus and radius measurements are based on the right elements. Measurements are in millimetres.

sectional area through the shaft may have been affected by crushing, but appears to have an anteroposteriorly compressed trapezoidal outline, comparable to most sauropods (Mannion *et al*., 2012).

*Radius:* The right radius is complete except for a portion of the medial margin missing from the distal third (see Fig. 11 and Table 3 for measurements). The distal end of the left radius is also preserved, but was originally misidentified as the distal end of the right ulna (Lapparent & Zbyszewski, 1957: pl. 28, fig. 109). The following description is based on the more complete and better preserved right element. Its flat proximal end surface has an oval-shaped outline, with a well-developed medial projection. The slender radial shaft is generally anteroposteriorly compressed and transversely widened. The midshaft has an elliptical cross-section, which gradually widens both transversely and anteroposteriorly towards the distal end.

At approximately one-third of the radius length from the distal end, a bulge-like area occurs close to the lateral margin of the posterior surface and gives rise to a nearly vertical, distally directed interosseous ridge (Fig. 11B). This ridge does not extend up to the proximal third of the radius, differing from the radii of several derived titanosaurs (Curry Rogers, 2005), as well as *Aragosaurus* (MPG specimen: P. D. Mannion & P. Upchurch, pers. observ., 2009), *Cedarosaurus* and '*Pleurocoelus*' (Tidwell *et al*., 1999: 27), *Paluxysaurus* (Rose, 2007: 25), *Tastavinsaurus* (Royo-Torres *et al*., 2012), and *Wintonotitan* (Hocknull *et al*., 2009: 22). In *Lusotitan*, close to the point where this ridge fades out into the posterolateral margin of the radius, another, less well-defined vertical ridge appears in a more medial position. This ridge extends distally along the posterior face of the shaft, although it fades out before reaching the distal end.

The rugose distal end surface is convex, as a result of a ventrally facing medial portion and laterally facing lateral portion. In anterior view, this gives the distal end a morphology that is close to the strongly bevelled condition (Fig. 11) seen in some titanosaurs (Wilson, 2002: an angle of at least 20° to the horizontal). In distal end view, the radius has a subrectangular profile, as in most sauropods (Wilson & Sereno, 1998), but with strongly rounded medial and lateral margins; the posterior margin is relatively straight.

*Ulna:* The proximal portion of a right ulna is preserved, but could not be located; as such the following description is based on the information and photograph presented by Lapparent & Zbyszewski (1957: pl. 25, fig. 88) (Fig. 12). It has a triradiate proximal end, as in all sauropods (Wilson & Sereno, 1998). The anteromedial process slopes strongly downwards, at an angle close to 45° to the horizontal (Fig. 12). This is a much steeper angle than in other sauropods, e.g. *Giraffatitan* (Janensch, 1961: Beilage A, fig. 2), but strongly resembles the condition seen in the macron-

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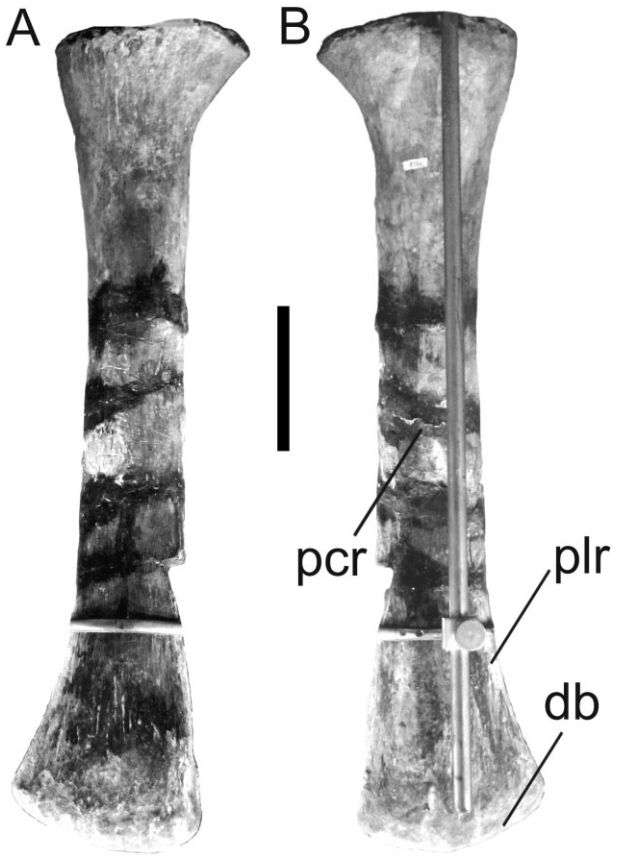


**Figure 11.** *Lusotitan atalaiensis*. Photographs of right radius in (A) anterior, and (B) posterior views. Abbreviations: db, distal bevelling; pcr, posterior central ridge; plr, posterolateral ridge. Scale bar = 200 mm.

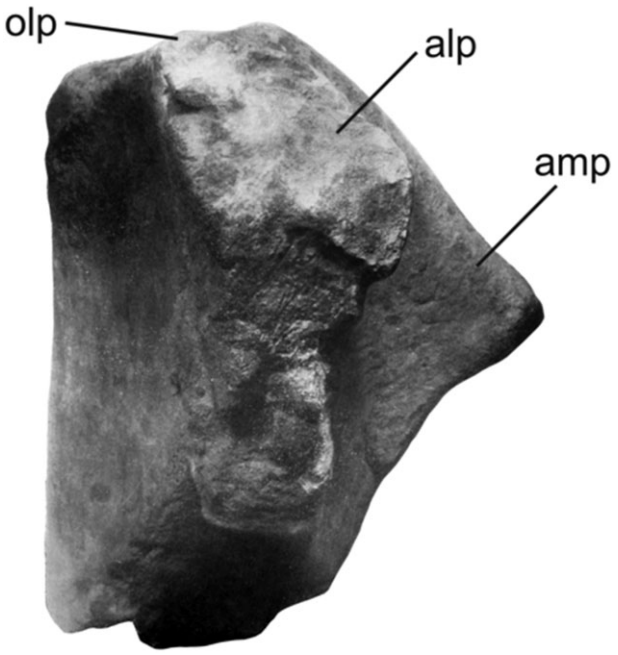


**Figure 12.** *Lusotitan atalaiensis*. Photograph of right ulna (proximal portion only) reproduced from Lapparent & Zbyszewski (1957) in anterior view. Abbreviations: alp, anterolateral process; amp, anteromedial process; olp, olecranon process. No scale bar available.

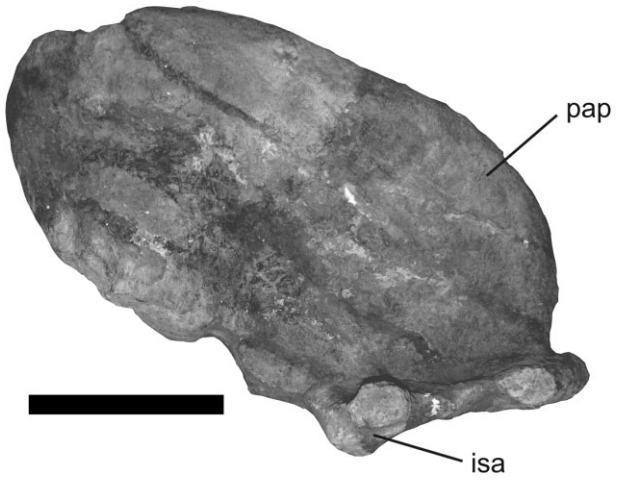


**Figure 13.** *Lusotitan atalaiensis*. Photograph of left ilium (posterior two-thirds only) in lateral view. Abbreviations: isa, ischial articulation; pap, postacetabulum. Scale bar = 200 mm.

arians *Aragosaurus* (MPG specimen: P. D. Mannion & P. Upchurch, pers. observ., 2009) and *Tehuelchesaurus* (Carballido *et al*., 2011b: fig. 16). The articular surface of the anteromedial process is flat, lacking the concave profile seen in titanosaurs (Upchurch, 1995) and some basal titanosauriforms, e.g. *Giraffatitan* (Janensch, 1961: Beilage A, fig. 2). The anterolateral process is incomplete. There is some indication of the presence of an incipient olecranon process (Fig. 12), although this is not the prominent structure observed in some titanosaurs (Wilson & Sereno, 1998), but is closer to the condition found in taxa such as *Cedarosaurus* (Tidwell *et al*., 1999: fig. 9d), *Giraffatitan* (Janensch, 1961: Beilage A, fig. 2), and *Paluxysaurus* (Rose, 2007: fig. 24).

*Ilium:* The posterior two-thirds of a left ilium are preserved, lacking the preacetabular and pubic processes (Fig. 13). The postacetabular process is rounded in medial view and the dorsal margin of the ilium is convex, a feature of all sauropods (Gauthier, 1986). The ischial articulation cannot be clearly observed, although it appears to be greatly reduced as in other neosauropods (Upchurch, 1998), based on Antunes & Mateus (2003: fig. 8). The damaged anterior margin of the ilium curves strongly medially to form two projections in anterior view: these might be the remnants of a sacral rib.

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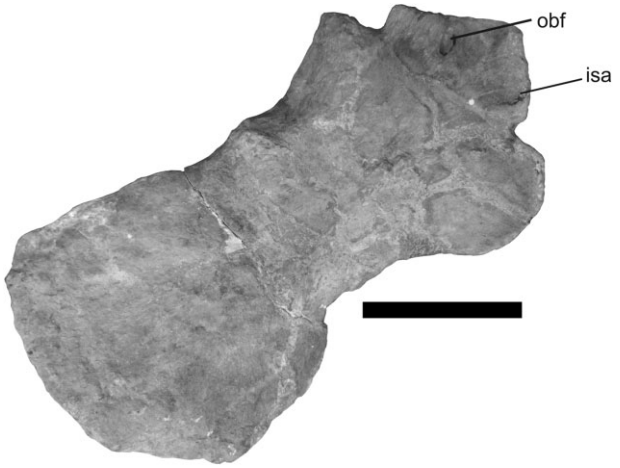


**Figure 14.** *Lusotitan atalaiensis*. Photograph of left pubis in lateral view. Abbreviations: isa, ischial articulation; obf, obturator foramen. Scale bar = 200 mm.

*Pubis:* The left pubis (Fig. 14) is missing the proximal-most part of the iliac peduncle, and the ischial articulation and small portions of the distal end are damaged (see Table 3 for measurements); overall the preservation is also quite poor. The acetabular region faces laterodorsally, and there is no ambiens process. The obturator foramen is present (Fig. 14; contra Antunes & Mateus, 2003), but is only clearly visible on the medial surface – it is oval shaped, with its long axis orientated in the same plane as that of the pubis, as is the case in most titanosauriforms (Mannion & Calvo, 2011). The anterior surface of the proximal end of the pubis forms a transversely broadened triangular area; this anterior margin rapidly contracts in transverse width distally. There are two subtle rugosities on the anterior margin, one above the other, situated just above the point where the pubic blade expands anteroposteriorly. A similar rugosity is also present on the posterior margin, at approximately the same level. Towards the distal end of the pubis, the posterior margin is deflected anteromedially towards what was probably the symphysis with the other pubis. The pubis does not seem to form the anteriorly expanded distal boot observed in some titanosauriforms, e.g. *Giraffatitan* (Naish & Martill, 2001) and *Tastavinsaurus* (Canudo *et al*., 2008).

*Ischium:* All but the distal end of a left ischium is preserved, but this element could not be located; as such the following description is based on photographs presented by Lapparent & Zbyszewski (1957: pl. 28, fig. 106) and Antunes & Mateus (2003: fig. 8) (see Figs 15, 16). The iliac peduncle is extremely elongate anteroposteriorly, similar to several brachiosaurids [e.g. *Cedarosaurus* (DMNH 39045: P. D. Mannion, pers. observ., 2008) and *Qiaowanlong* (You & Li, 2009)], and appears to be strongly compressed transversely. There also seems to be a slight posterior projection at the posterodorsal corner of the iliac peduncle, but it is possible that this is merely a preservational artefact. The anteroventral margin is emarginated distal to the pubic articulation, as in other non-titanosaurs (Wilson, 2002). The long axis of the ischial shaft, if projected upwards, passes through the lower part of the acetabular margin, i.e. it has a less steeply inclined ischial shaft than that of *Giraffatitan* (Upchurch *et al*., 2004a).

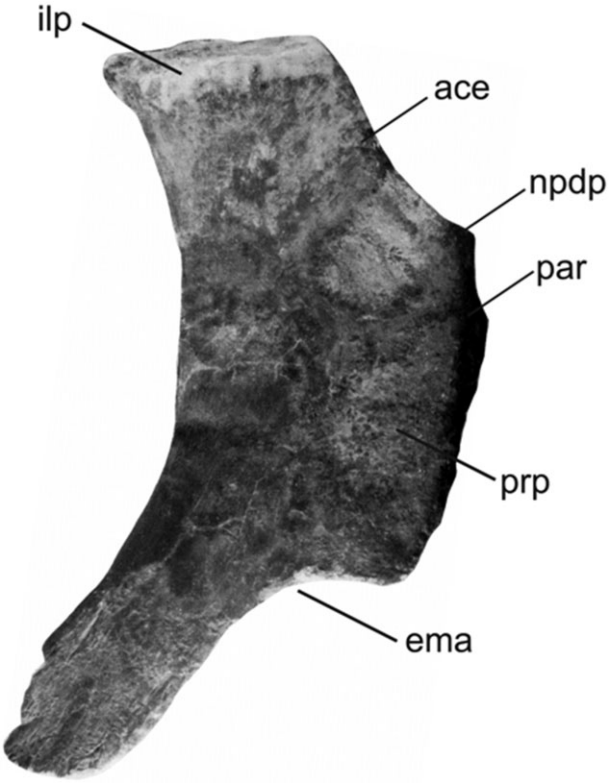


**Figure 15.** *Lusotitan atalaiensis*. Photograph of left ischium reproduced from Lapparent & Zbyszewski (1957) in lateral view. Abbreviations: ace, acetabulum; ema, emargination; ilp, iliac peduncle; npdp, no posterodorsal projection; par, pubic articulation; prp, proximal plate. No scale bar available.

*Tibia:* The complete left tibia (see Fig. 17 and Table 3 for measurements) is strongly bowed laterally. Although this bowing does seem to be more pronounced than in other sauropods, it may have been accentuated by deformation; however, following Antunes & Mateus (2003), we tentatively include it in our emended diagnosis of *Lusotitan*. The tibia has a

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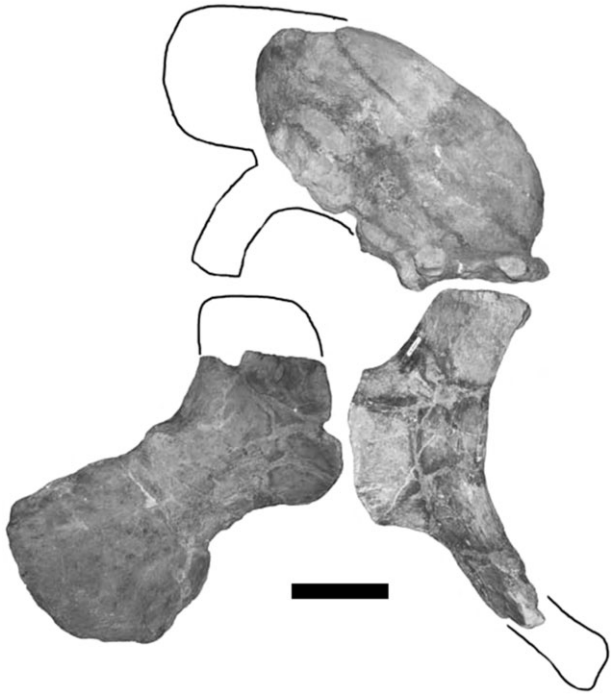

**Figure 16.** *Lusotitan atalaiensis*. Photographs and reconstruction of the left pelvis in lateral view, reproduced from Antunes & Mateus (2003). Scale bar = 200 mm.

rugose proximal end surface that becomes mildly concave centrally and slopes downwards laterally. A stout cnemial crest projects mainly laterally (Fig. 17A, B), as is the case in most eusauropods (Wilson & Sereno, 1998), although the crests of several titanosauriform taxa project anterolaterally, e.g. *Tastavinsaurus* (Canudo *et al*., 2008), *Ligabuesaurus* (Bonaparte, González Riga & Apesteguía, 2006; MCF-PHV 233: P. D. Mannion, pers. observ., 2009), and *Saltasaurus* (Powell, 2003: pl. 45). A small depression is present on the anterolateral margin of the proximal end, posterior to the base of the cnemial crest. Posterior to this, the lateral bulge of the proximal end forms an additional projection. This proximolateral projection (Fig. 17B) is also present in several other sauropods, e.g. *Giraffatitan* (Janensch, 1961: Beilage K, fig. 1d), *Diplodocus* (Hatcher, 1901: fig. 18), *Janenschia* (the 'second cnemial crest' of Bonaparte *et al*., 2000: 37; SMNS 12144: P. D. Mannion, pers. observ., 2011), and *Phuwiangosaurus* (Martin, Suteethorn & Buffetaut, 1999: fig. 39), but is absent in taxa such as *Apatosaurus* (Gilmore, 1936: fig. 23c), *Euhelopus* (Wiman, 1929: pl. 4, fig. 9), and *Paluxysaurus* (Rose, 2007: fig. 28.5). The proximolateral bulge extends distally as a vertical ridge in *Lusotitan* but disappears close to the level where the cnemial crest fades into the anterior surface of the shaft.

The midshaft of the tibia is compressed along its anteromedial–posterolateral axis. At its distal end, the anterior face of the tibia bears the typical subtriangular flattened surface seen in other sauropods (Upchurch *et al*., 2004a). The distal end is strongly expanded mediolaterally and compressed anteroposteriorly, a morphology typical of many titanosauriforms (Salgado *et al*., 1997; Upchurch, 1999; Upchurch *et al*., 2004a; Mannion & Calvo, 2011), although differing from the almost equidimensional distal end of the tibia of the somphospondylans *Antarctosaurus* (Mannion & Otero, 2012) and *Paluxysaurus* (Rose, 2007). The lateral malleolus of the distal end is prominent, whereas the medial malleolus is reduced (Fig. 17C), as in other sauropods (Wilson & Sereno, 1998). Although the lateral and medial malleoli are clearly separated from each other, there is no vertical groove between them ascending the shaft along the posterolateral margin (Fig. 17C), a feature we regard as diagnostic of *Lusotitan*. The anteromedial corner of the distal end is rounded, whereas the anterior and posteromedial surfaces meet at an acute angle.

*Fibula:* The proximal half of a left fibula was mentioned and figured by Lapparent & Zbyszewski (1957: pl. 26, fig. 91) (Fig. 18), although it could not be located for study. Little anatomical information can be gleaned from the original publication except that the proximal end is mediolaterally compressed, as in other sauropods (Upchurch *et al*., 2004a), and it lacks the anteromedial crest seen in several somphospondylans (Wilson & Upchurch, 2009; D'Emic, 2012), e.g. *Euhelopus* (Wilson & Upchurch, 2009) and *Tastavinsaurus* (Canudo *et al*., 2008: fig. 15e), and also *Diplodocus* (Hatcher, 1901: fig. 18).

*Astragalus:* In dorsal view, the complete left astragalus (see Fig. 19 and Table 3 for measurements) has straight anterior and lateral margins that meet at approximately 90°, as well as a long, curving posteromedial margin. In anterior view, the ventral surface is mildly convex mediolaterally and the astragalus tapers in dorsoventral height towards its medial end, both features characteristic of neosauropods (Upchurch, 1995, 1998). The rugose anterior and ventral surfaces merge smoothly into each other to form a strongly anteroposteriorly convex surface. The astragalus is mediolaterally expanded in relation to its proximodistal height, lacking the pyramidal shape of some titanosaur astragali (Wilson, 2002).

The ascending process is located at the lateral end of the astragalus and its anterior surface lacks either a pit or foramina (Fig. 19A), as in other sauropods (Wilson & Sereno, 1998). The lateral surface of the ascending process is mildly concave and faces mainly

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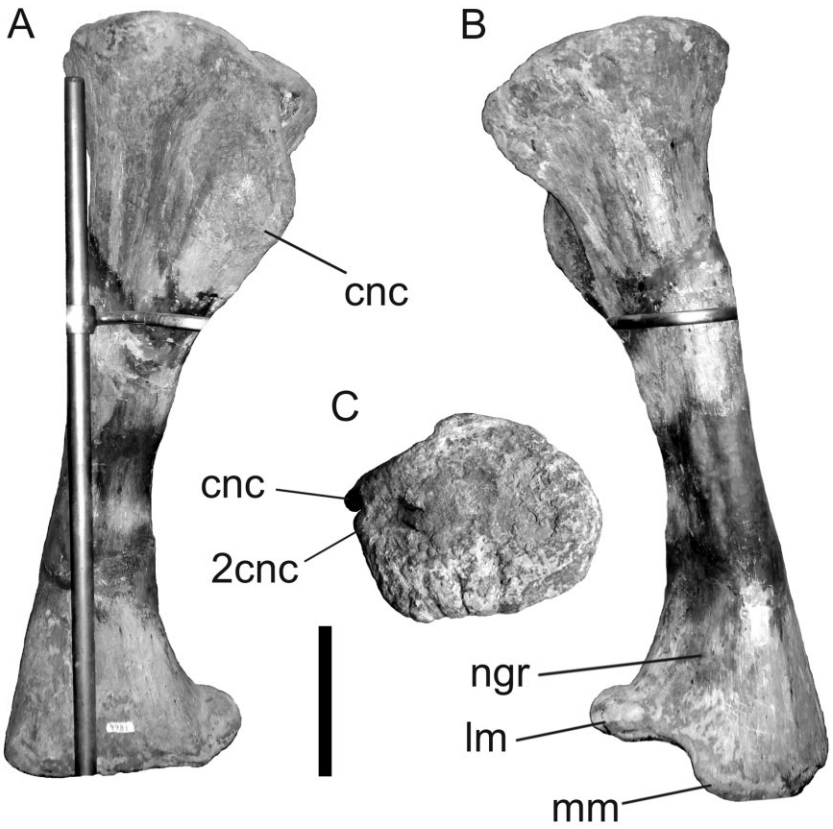


**Figure 17.** *Lusotitan atalaiensis*. Photographs of left tibia in (A) anterior, (B) posterior, and (C) proximal views. Abbreviations: cnc, cnemial crest; lm, lateral malleolus, mm, medial malleolus, ngr, no groove; 2cnc, 'second cnemial crest'. Scale bar = 200 mm.

laterally; there is no strongly developed, laterally directed ventral shelf to underlie the distal end of the fibula (Fig. 19). Such a shelf is present in most sauropods, but is absent in several titanosauriforms, e.g. *Euhelopus* (Wilson & Upchurch, 2009), *Giraffatitan* (HMN MBR specimens: P. D. Mannion, pers. observ., 2011), and *Gobititan* (IVPP V12579: P. D. Mannion & P. Upchurch, pers. observ., 2007). With the flat and rugose dorsal surface of the ascending process orientated horizontally, the posterior margin of the ascending process lies vertically above the posterior margin of the main astragalus body, as is the case in other neosauropods (Wilson & Sereno, 1998). The posterior surface of the astragalus, including the ascending process, is concave both dorsoventrally and mediolaterally. As in other eusauropods (Wilson & Sereno, 1998), a posteromedially orientated ridge descends from the posteromedial corner of the ascending process. This forms a convex 'tongue'-like projection posteromedial to the ascending process, which is separated from the latter by a groove (Fig. 19B). This is the plesiomorphic state in most sauropods, but the projection is lost in many titanosauriforms (D'Emic, 2012; this study). Immediately anteromedial to the posteromedial ridge is a deep foramen (Fig. 19B). The rest of the medial part of the proximal surface is relatively flat and faces proximally and a little posteromedially. A second ridge forms along the posterolateral margin of the astragalus (Fig. 19B), separating the posterior surface of the ascending process from the lateral surface of the astragalus.

### Taxonomic status of material referred to *Lusotitan atalaiensis*

Lapparent & Zbyszewski (1957) referred a number of remains to *Lusotitan* from several additional localities in Lourinhã. These elements comprise the proximal half of a femur and caudal vertebrae from a total of five localities. Only two of the caudal vertebrae were figured by Lapparent & Zbyszewski (1957), and we were only able to locate the femur for study.

The proximal end of a femur was discovered at the Praia de Areia Branca locality (Lapparent & Zbyszewski, 1957: pl. 21, figs 64–65) and displays a relatively well-developed lateral bulge, whose surface is vertically striated. The presence of this lateral bulge would traditionally be viewed as indicating

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**Figure 18.** *Lusotitan atalaiensis*. Photograph of left fibula reproduced from Lapparent & Zbyszewski (1957) in medial view. No scale bar available.

titanosauriform affinities for the specimen (Salgado *et al.*, 1997), but see Discussion regarding the wider distribution of this feature. In anterior view, above the bulge, the lateral surface ascends a short distance before meeting the rugose greater trochanter at a distinct obtuse angle. There are no ridges or processes on either the anterior or posterior surface of the femur. At the broken distal end, the femoral shaft is strongly compressed anteroposteriorly (mediolateral to anteroposterior width ratio = 2.4), comparable to some derived titanosaurs (Wilson & Carrano, 1999) and some more basal titanosauriforms (this study). An anterior caudal vertebra was also listed from this same locality, although it was not figured and no information was provided; furthermore, it is not clear whether the femur and vertebra were found in association. Based on the lack of information on the vertebra and the absence of a femur in the type individual of *Lusotitan*, the femur should be considered as belonging to an indeterminate titanosauriform and the vertebra as Sauropoda indet.

An anterior and a middle caudal centrum from Porto Novo (Maceira) and Cambelas, respectively, were figured by Lapparent & Zbyszewski (1957: pl. 26, figs 94, 95). The first of these centra is amphiplatyan/amphicoelous, and possesses small vascular foramina on the lateral surface. Similar excavations are present in the anterior-most caudal vertebrae of *Lusotitan* (see above) and Mannion & Calvo (2011) noted that these foramina occur in the anterior-middle caudal centra of several titanosaurs; however, they are also present in some taxa that were recovered outside of Macronaria in our phylogenetic analysis (see below). Little anatomical information can be gleaned from the incomplete middle caudal centrum, although the preserved articular surface appears to be mildly concave. Lastly, a middle and posterior caudal vertebra were listed from Alcobaça and Praia das Almoinhas, respectively. All four of these isolated caudal vertebrae should be regarded as indeterminate sauropods pending their location in museum collections and study.

## Phylogenetic analysis of basal titanosauriforms

### *Data sets*

We created a data matrix of 279 characters for 63 sauropod terminal taxa (seven outgroups and 56 putative ingroup titanosauriforms) using MESQUITE (Maddison & Maddison, 2011). Our outgroup taxa are *Shunosaurus*, *Omeisaurus*, *Mamenchisaurus*, *Camarasaurus*, *Nigersaurus*, *Apatosaurus*, and *Diplodocus*. These taxa were selected as they represent relatively complete and well-known genera, including a basal macronarian (the more inclusive clade including Titanosauriformes), three representatives of Diplodocoidea (the sister group to Macronaria), and three non-neosauropods; they also span three continents. The ingroup taxa include some unnamed forms that potentially represent distinct taxa and/or unusual character state combinations. Many ingroup taxa are extremely incomplete; however, excluding them merely on the basis of their completeness is problematic as they might preserve important data and unique character combinations that could have a significant impact on our results (see also discussion on incorporation of incomplete specimens in Kearney & Clark, 2003; Carrano, Benson & Sampson, 2012; and Wiens & Tiu, 2012). Table 4 lists all taxa included in the analysis, as well as our basis (i.e. references and/or personal observations) for coding taxa. Many have never been incorporated into a phylogenetic analysis prior to this study. Coding for *Brachiosaurus*

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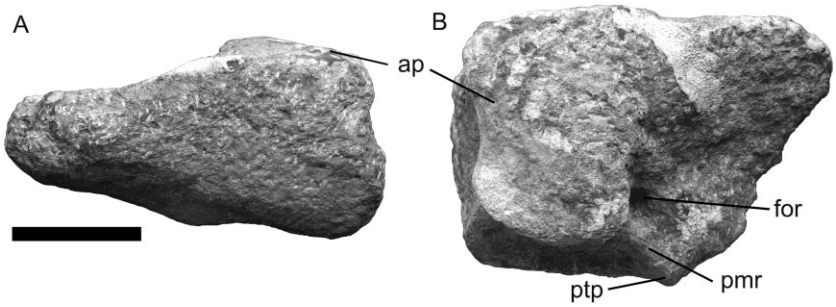


**Figure 19.** *Lusotitan atalaiensis*. Photographs of left astragalus in (A) anterior and (B) dorsal views. Abbreviations: ap, ascending process; for, foramen; pmr, posteromedial ridge; ptp, posterior tongue-like process. Scale bar = 100 mm.

*altithorax* was based only on the type specimen FMNH P25107 (Riggs, 1903). We included FMNH PR 977 [originally described as '*Pleurocoelus* sp.' (Gallup, 1989)] in our coding of *Cedarosaurus*, following its referral by D'Emic (2013). The 'Cloverly titanosauriform' is restricted to the associated skeleton YPM 5449 (Ostrom, 1970). Although we did not disagree a priori with a recent referral of this material and *Paluxysaurus* to *Sauroposeidon* (D'Emic & Foreman, 2012; D'Emic, 2013), we retained these three taxa as separate OTUs to test this hypothesis (note that the material comprising *Sauroposeidon* and the 'Cloverly titanosauriform' both overlap with that of *Paluxysaurus*). The 'French *Bothriospondylus*' refers only to the individual described by Lapparent (1943). Material included in *Janenschia* is restricted to the type and all elements from Quarry P (see Bonaparte *et al*., 2000), although we also included a pubis [Janensch, 1961: pl. 19, fig. 4 (HMN MB.R.2090.2)] and ischium (HMN MB.R.2090.4: P. D. Mannion, pers. observ., 2011) that were recovered from site B [the same locality as the type material (Bonaparte *et al*., 2000) and distinguishable from *Tornieria*: P. D. Mannion, pers. observ., 2011]. We excluded the isolated manus recovered from site Nr. 5 as there are no shared autapomorphies between this and the only remaining overlapping elements from Quarry P. Unlike the recent analysis of Carballido *et al*. (2011b), we also did not include the caudal series HMN MB.R.2091.1–30, as there is currently no basis for its referral to *Janenschia*; instead it was treated here as a separate OTU. *Lapparentosaurus* consists only of the material discussed by Ogier (1975; see Mannion, 2010). We excluded the tentatively referred tooth in our coding of *Xianshanosaurus*, as this element was not found in association with the holotype skeleton (Lü *et al*., 2009a). Although the focus of this study was the relationships of basal titanosauriforms, we included a number of relatively complete and widely accepted derived titanosaurs (*Alamosaurus*, *Malawisaurus*, *Opisthocoelicaudia*, *Rapetosaurus*, and *Saltasaurus*) to help understand character evolution at the base of Titanosauria. Furthermore, these taxa have been included in most previous sauropod analyses, thereby enabling direct comparisons with our results, and several are clade specifiers. We followed previous authors by including referred remains in our *Alamosaurus* OTU (e.g. Upchurch *et al*., 2004a; D'Emic, 2012, 2013; see Table 4), although note that some of these referrals are currently based on non-overlapping material (see D'Emic, Wilson & Williamson, 2011). Supplementary information on scoring was incorporated from Wilson (2002), Upchurch *et al*. (2004a), and D'Emic (2012), and data on the slenderness index (SI) values of teeth were augmented from the supporting information provided by Chure *et al*. (2010).

The majority of characters used in this analysis were derived from Upchurch (1995, 1998), Salgado *et al*. (1997), Wilson & Sereno (1998), and Wilson (2002). These were revised and modified, including removal of problematic gaps between plesiomorphic and derived character states (see also Mannion *et al*., 2012, for a similar treatment of diplodocoid characters). This core data set was supplemented with characters from subsequent phylogenetic analyses (i.e. Upchurch *et al*., 2004a; Curry Rogers, 2005; Canudo *et al*., 2008; Remes *et al*., 2009; Chure *et al*., 2010; Ksepka & Norell, 2010; Carballido *et al*., 2011b; Whitlock, 2011b; D'Emic, 2012, 2013; Mannion *et al*., 2012), new characters based on descriptions and revisions (e.g. Wedel, Cifelli & Sanders, 2000a; Apesteguía, 2005a, b; Bonaparte, González Riga & Apesteguía, 2006; Rose, 2007; Taylor, 2009; Wilson & Upchurch, 2009; D'Emic *et al*., 2011; Mannion, 2011; Mannion & Calvo, 2011), and entirely novel characters presented here, based on personal observations and an extensive review of the literature. We did not exclude characters based on a priori assumptions about their level of homoplasy. Where possible, we attempted to quantify, or at least more precisely define, characters and state boundaries to remove ambiguity (see similar attempts by Harris, 2006). The complete character list, including references, as well

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**Table 4.** Taxa, geological age, geographical distribution, and references used for phylogenetic analysis (see text for further details)

| Taxon | Age and distribution | Reference/source |
|---|---|---|
| Outgroup taxa | | |
| *Shunosaurus lii* | Bathonian–Callovian (MJ); China | Zhang (1988); Chatterjee & Zheng (2002); P. Upchurch, pers. observ. (1995: ZDM specimens) |
| *Omeisaurus* spp. | Bathonian–Callovian (MJ); China | He, Li & Cai (1988); Tang *et al.* (2001a); P. Upchurch, pers. observ. (1995: ZDM specimens) |
| *Mamenchisaurus* spp. | LJ; China | Young (1958); Young & Zhao (1972); Ouyang & Ye (2002); P. Upchurch, pers. observ. (2010) and P. D. Mannion, pers. observ. (2011: IVPP specimens) |
| *Camarasaurus* spp. | Kimmeridgian–Tithonian (LJ); USA | Osborn & Mook (1921); Gilmore (1925); Ostrom & McIntosh (1966); Madsen, McIntosh & Berman (1995); McIntosh *et al.* (1996b); P. D. Mannion, pers. observ. (2008: CM & YPM specimens) |
| *Nigersaurus taqueti* | Aptian–Albian (EK); Niger | Sereno *et al.* (1999, Sereno *et al.* 2007); Sereno & Wilson (2005); P. D. Mannion, pers. observ. (2010) |
| *Apatosaurus* spp. | Kimmeridgian–Tithonian (LJ); USA | Gilmore (1936); Ostrom & McIntosh (1966); Berman & McIntosh (1978); Upchurch *et al.* (2004b); Whitlock (2011b); P. D. Mannion, pers. observ. (2008: CM & YPM specimens and UWGM 15556) |
| *Diplodocus* spp. | Kimmeridgian–Tithonian (LJ); USA | Hatcher (1901); Holland (1906, 1910, 1924); Mook (1917a); McIntosh & Berman (1975); Whitlock (2011b); P. D. Mannion, pers. observ. (2008: CM specimens) |
| Ingroup taxa | | |
| *Abydosaurus mcintoshi* | Late Albian (EK); USA | Chure *et al.* (2010); D'Emic (2012) |
| *Alamosaurus sanjuanensis* | Maastrichtian (LK); USA | Gilmore (1922, 1946); Kues, Lehman & Rigby (1980); Lehman & Coulson (2002); D'Emic *et al.* (2011); Fronimos (2011); P. D. Mannion & P. Upchurch, pers. observ. (2008: USNM specimens) |
| *Andesaurus delgadoi* | Early Cenomanian (LK); Argentina | Calvo & Bonaparte (1991); Mannion & Calvo (2011); P. D. Mannion, pers. observ. (2009) |
| *Angolatitan adamastor* | Late Turonian (LK); Angola | Mateus *et al.* (2011); P. D. Mannion & P. Upchurch, pers. observ. (2009) |
| *Aragosaurus ischiatus* | Valanginian–early Barremian (EK); Spain | Sanz (1982); Sanz *et al.* (1987); P. D. Mannion & P. Upchurch, pers. observ. (2009) |
| *Astrophocaudia slaughteri* | Early Albian (EK); USA | Langston (1974); D'Emic (2013) |
| *Atlasaurus imelakei* | Bathonian–Callovian (MJ); Morocco | Monbaron *et al.* (1999); D'Emic (2012) |
| *Australodocus bohetii* | Tithonian (LJ); Tanzania | Remes (2007); Whitlock (2011a); P. D. Mannion, pers. observ. (2011) |
| *Baotianmansaurus henanensis* | Cenomanian–Turonian (LK); China | Zhang *et al.* (2009); P. D. Mannion & P. Upchurch, pers. observ. (2012) |
| *Brachiosaurus altithorax* | Kimmeridgian–Tithonian (LJ); USA | Riggs (1903, 1904); Taylor (2009); P. D. Mannion, pers. observ. (2008) |
| *Brontomerus mcintoshi* | Aptian–Albian (EK); USA | Taylor *et al.* (2011) |
| *Cedarosaurus weiskopfe* | Aptian–Albian (EK); USA | Tidwell *et al.* (1999); D'Emic (2013); P. D. Mannion, pers. observ. (2008) |
| *Chubutisaurus insignis* | Aptian–Cenomanian (EK–LK); Argentina | Salgado (1993); Carballido *et al.* (2011a); R. N. Barnes, pers. observ. (2009) |
| 'Cloverly titanosauriform' | Late Albian (EK); USA | Ostrom (1970); D'Emic & Foreman (2012); P. D. Mannion, pers. observ. (2008) |
| *Daxiatitan binglingi* | Aptian (EK); China | You *et al.* (2008) |
| *Diamantinasaurus matildae* | Middle Cenomanian–early Turonian (LK); Australia | Hocknull *et al.* (2009); P. D. Mannion & P. Upchurch, pers. observ. (2012) |

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| | | |
|---|---|---|
| *Dongbeititan dongi* | Barremian (EK); China | Wang *et al.* (2007); R. N. Barnes, pers. observ. (2011) |
| *Dongyangosaurus sinensis* | Cenomanian–Santonian (LK); China | Lü *et al.* (2008) |
| *Erketu ellisoni* | Cenomanian–Santonian (LK); Mongolia | Ksepka & Norell (2006, 2010) |
| *Euhelopus zdanskyi* | Barremian–Aptian (EK); China | Wiman (1929); Young (1935); Wilson & Upchurch (2009); P. D. Mannion & P. Upchurch, pers. observ. (2007) |
| *Europasaurus holgeri* | Middle Kimmeridgian (LJ); Germany | Sander *et al.* (2006); Carballido *et al.* (2011b); P. D. Mannion, pers. observ. (2007) |
| 'French *Bothriospondylus*' | Late Oxfordian (LJ); France | Lapparent (1943); P. D. Mannion, pers. observ. (2011: only some elements) |
| *Fukuititan nipponensis* | Barremian (EK); Japan | Azuma & Shibata (2010) |
| *Fusuisaurus zhaoi* | Aptian (EK); China | Mo *et al.* (2006); photographs (P. M. Barrett and Mo J.-Y.) |
| *Galveosaurus herreroi* | Tithonian–middle Berriasian (LJ–EK); Spain | Sánchez-Hernández (2005); Barco *et al.* (2006); Barco (2009) |
| *Giraffatitan brancai* | Kimmeridgian–Tithonian (LJ); Tanzania | Janensch (1935‐36, 1950); Taylor (2009); P. D. Mannion, pers. observ. (2011) |
| *Gobititan shenzhouensis* | Albian (EK); China | You, Tang & Luo (2003); P. D. Mannion & P. Upchurch, pers. observ. (2007 and 2012) |
| HMN MB.R.2091.1-30 | Tithonian (LJ); Tanzania | Bonaparte *et al.* (2000); P. D. Mannion, pers. observ. (2011–2012) |
| *Huanghetitan liujiaxiaensis* | Aptian (EK); China | You *et al.* (2006) |
| *'Huanghetitan' ruyangensis* | Cenomanian–Santonian (LK); China | Lü *et al.* (2007); P. D. Mannion & P. Upchurch, pers. observ. (2012) |
| *Janenschia robusta* | Tithonian (LJ); Tanzania | Janensch (1961); Bonaparte *et al.* (2000); P. D. Mannion, pers. observ. (2011–2012) |
| *Jiangshanosaurus lixianensis* | Albian (EK); China | Tang *et al.* (2001b) |
| *Lapparentosaurus madagascariensis* | Bathonian (MJ); Madagascar | Ogier (1975); Bonaparte (1986); P. Upchurch, pers. observ. (1992); P. D. Mannion, pers. observ. (2011) |
| *Ligabuesaurus leanzai* | Late Aptian–Albian (EK); (Argentina) | Bonaparte, González Riga & Apesteguía (2006); P. D. Mannion & R. N. Barnes, pers. observ. (2009) |
| *Liubangosaurus hei* | Aptian (EK); China | Mo *et al.* (2010); photographs (P. M. Barrett) |
| *Lusotitan atalaiensis* | Late Kimmeridgian–early Tithonian (LJ); Portugal | Lapparent & Zbyszewski (1957); this study |
| *Malarguesaurus florenciae* | Late Turonian–early Coniacian (LK); Argentina | González Riga *et al.* (2009) |
| *Malawisaurus dixeyi* | Aptian (EK); Malawi | Haughton (1928); Jacobs *et al.* (1993); Gomani (1999, 2005); Gomani, Jacobs & Winkler (1999); P. D. Mannion, pers. observ. (2008: SAM 7405) |
| *Mongolosaurus haplodon* | Aptian–Albian (EK); China | Mannion (2011); P. D. Mannion, pers. observ. (2008) |
| *Opisthocoelicaudia skarzynskii* | Maastrichtian (LK); Mongolia | Borsuk-Bialynicka (1977) |
| *Paluxysaurus jonesi* | Aptian–Albian (EK); USA | Rose (2007) |
| *'Pelorosaurus' becklesii* | Berriasian–Valanginian (EK); UK | Upchurch *et al.* (2011b); P. D. Mannion & P. Upchurch, pers. observ. (2010) |
| *Phuwiangosaurus sirindhornae* | Barremian–Aptian (EK); Thailand | Martin, Buffetaut & Suteethorn (1994); Martin *et al.* (1999); Suteethorn *et al.* 2009, 2010); D'Emic (2012); M. D. D'Emic, pers. comm. (2012) |
| *Qiaowanlong kangxii* | Aptian–Albian (EK); China | You & Li (2009) |

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**Table 4.** *Continued*

| Taxon | Age and distribution | Reference/source |
|---|---|---|
| *Rapetosaurus krausei* | Maastrichtian (LK); Madagascar | Curry Rogers & Forster (2004); Curry Rogers (2009); P. D. Mannion, pers. observ. (2008); R. N. Barnes, pers. observ. (2010) |
| *Ruyangosaurus giganteus* | Cenomanian–Santonian (LK); China | Lü *et al.* (2009b); P. D. Mannion & P. Upchurch, pers. observ. (2012) |
| *Saltasaurus loricatus* | Late Campanian–Maastrichtian(LK); Argentina | Powell (2003); Salgado & Powell (2010) |
| *Sauroposeidon proteles* | Aptian–Albian (EK); USA | Wedel *et al.* (2000a, b); M. J. Wedel, pers. comm. (2011) |
| *Sonorasaurus thompsoni* | Late Albian–early Cenomanian (EK–LK); USA | Ratkevich (1998); Curtice (2000); D'Emic (2012); M. D. D'Emic, pers. comm. (2011) |
| *Tangvayosaurus hoffeti* | Aptian–Albian (EK); Laos | Allain *et al.* (1999); Suteethorn *et al.* (2010); R. Allain, pers. comm. (2012); photographs (R. Allain) |
| *Tastavinsaurus sanzi* | Early Aptian (EK); Spain | Canudo *et al.* (2008); Royo-Torres (2009); Royo-Torres *et al.* (2012); P. D. Mannion & P. Upchurch, pers. observ. (2009) |
| *Tehuelchesaurus benitezii* | Kimmeridgian–Tithonian (LJ); Argentina | Rich *et al.* (1999); Carballido *et al.* (2011b) |
| *Tendaguria tanzaniensis* | Tithonian (LJ); Tanzania | Bonaparte *et al.* (2000); P. D. Mannion, pers. observ. (2011–2012) |
| *Venenosaurus dicrocei* | Barremian (EK); USA | Tidwell *et al.* (2001); P. D. Mannion, pers. observ. (2008) |
| *Wintonotitan wattsi* | Middle Cenomanian–early Turonian (LK); Australia | Hocknull *et al.* (2009); P. D. Mannion & P. Upchurch, pers. observ. (2012) |
| *Xianshanosaurus shijiagouensis* | Cenomanian–Santonian (LK); China | Lü *et al.* (2009a); P. D. Mannion & P. Upchurch, pers. observ. (2012) |

Abbreviations: MJ, Middle Jurassic; LJ, Late Jurassic; EK, Early Cretaceous; LK, Late Cretaceous.
Museum abbreviations are provided for personal observations when there might be some ambiguity as to which specimens are being referred to (see text for further details).
Geological ages are based on information provided in the descriptive papers listed below, and recent data sets (e.g. Mannion *et al.*, 2011b; Mannion & Calvo, 2011; Upchurch *et al.*, 2011a; Mannion & Otero, 2012), including The Paleobiology Database.
Additional information on the ages of the Hekou Group (*Daxiatitan* and *Huanghetitan liujiaxiaensis*), Gaogou Formation (*Baotianmansaurus*), Napai Formation (*Fusuisaurus* and *Liubangosaurus*), and Winton Formation (*Diamantinasaurus* and *Wintonotitan*) comes from Chen *et al.* [2006 (age inferred based on the presence of the fish *Sinamia*)], Suarez (2008), Liang *et al.* (2009), Amiot *et al.* (2011), and Tucker *et al.* (2013).

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as our data matrices, is provided in Appendices 1–3. The MESQUITE versions of the data matrices are also presented as Supporting Information Appendices S1–S3 and their TNT equivalents are available from the first or second authors on request.

Reductive (or 'contingent') coding was used here, rather than absence coding. Although problems exist with the former method, simulation studies suggest that it is the best solution when there is no logical interpretation of a character for a given taxon (Strong & Lipscomb, 1999; Brazeau, 2011). For example, our character number 127 (C127) relates to the absence or presence of postzygapophyseal epipophyses on cervical vertebrae, whereas C128 relates to the posterior extent of these epipophyses. However, a taxon scored as zero for C127 (i.e. that lacks epipophyses) cannot be scored for either the basal state (epipophyses do not extend beyond the postzygapophyses) or derived state (epipophyses extend beyond the postzygapophyses) for C128. In absence coding, our taxon would be scored as '0' for C128, designating it as the basal condition without any actual evidence for this decision, whereas in reductive coding we scored this character as a '?'.

There are two versions of the data matrix, known here as the '*Lusotitan* standard discrete matrix' (LSDM) and the '*Lusotitan* continuous + discrete matrix' (LCDM). These matrices differ in the way they deal with quantitative characters, such as the relative proportions of skeletal elements. In both matrices, characters 1–74 represent quantitative characters, whereas characters 75–279 score discrete variation (mostly binary characters such as the absence/presence of a feature). Thus, the numbers referring to characters in the character list (see Appendix 1) apply to both the LSDM and LCDM, even though the treatment of characters 1–74 is different in the two matrices. In the LSDM, the quantitative characters have been 'discretized' by dividing the observed variation in the ratio between two measurements into two or more discrete states (with state boundaries determined from previous studies and/or based on our outgroup taxa). For example, C2 in the character list (see Appendix 1) is: 'External naris, greatest diameter to greatest diameter of orbit ratio: greater than 1.0 (0); 1.0 or less (1)'. This is the standard method for dealing with quantitative morphological characters and it has been used by virtually all previous phylogenetic analyses of dinosaur relationships (although see, for example, Maidment *et al*., 2008). We applied this standard approach in order to make our results more easily comparable with previous analyses of sauropod relationships, all of which have discretized their quantitative characters. However, there are several problems with the treatment of quantitative characters in this way, one of which is that the discretization of continuous variation is somewhat arbitrary (Wiens, 2001). In many cases, the relative proportions of two skeletal elements vary in a continuous fashion across the known taxa: that is, variation does not fall neatly into two or more separate clusters with gaps between them. This means that different systematists might find evidence to support alternative tree topologies because they have defined the boundaries between states at different points in a character's continuous variation. For example, Wilson & Sereno (1998) noted that macronarian sauropods have a derived condition in which the ratio of the length of the longest metacarpal to the length of the radius is 0.45 or higher (C52 in our study). Consequently, taxa such as *Apatosaurus louisae* and *Mamenchisaurus youngi*, with metacarpal to radius length ratios of approximately 0.40 (Table 5), are scored with the plesiomorphic state. However, metacarpal to radius length ratios in sauropods cover a wide range of values (Table 5), with no clear gaps in this variation that might be used to produce a more objective division into plesiomorphic and derived states. For example, it would be equally legitimate to define the division between states 0 and 1 as a ratio of 0.4 (as implemented by Upchurch *et al*., 2004a, and in this study), so that *Apatosaurus* and *Mamenchisaurus* would be scored with state 1. A second drawback with discretization of quantitative characters is that it might fail to capture some of the potentially phylogenetically informative signal in the data. For example, Table 5 suggests that additional derived states in longest metacarpal to radius length ratios could be recognized: titanosaurs such as *Aeolosaurus* and *Argyrosaurus* have very high values of 0.53–0.6, whereas other taxa have values in the range of 0.45–0.50 (e.g. *Camarasaurus* and *Rapetosaurus*). At present, this variation is obscured by assigning state 1 to all taxa with a ratio of 0.4/0.45 or higher (see Wiens, 2001, for further discussion of this issue). These problems can be circumvented by representing quantitative characters by continuous data: that is, by using the ratios between two parameters as the character states themselves, as proposed by Goloboff, Mattoni & Quinteros (2006) and as can be implemented in TNT (Goloboff, Farris & Nixon, 2008). For example, in the case of C2 in our data set, the LCDM scored *Shunosaurus* with state 1.26, *Diplodocus* with state 0.71, and *Giraffatitan* with state 1.15. This means that relatively larger changes between character states (i.e. the values of the ratio) required by a given tree topology will cost more (in terms of parsimony) than a relatively smaller shift. In effect, treatment of quantitative characters as continuous data means that the cost of evolutionary transformation of a character (on a given tree topology) is proportional to the required change in the value of the character

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**Table 5.** The ratio of the longest metacarpal length to radius length for an array of sauropod dinosaurs. Taxa are listed in order of increasing metacarpal to radius length ratio

| Taxon/specimen | Ratio | Reference/source |
|---|---|---|
| *Shunosaurus lii* | 0.30 | Zhang (1988) |
| *Diplodocus* spp. | 0.30–0.35 | Bedell & Trexler (2005); McIntosh (2005) |
| *Barosaurus lentus* | 0.32 | McIntosh (2005) |
| *Omeisaurus tianfuensis* | 0.32–0.35 | He *et al*. (1988) |
| *Apatosaurus* spp. | 0.37–0.40 | Gilmore (1936); Upchurch *et al*. (2004b) |
| *Aragosaurus ischiatus* | 0.37 | MAPA and MPG specimens (P. D. Mannion & P. Upchurch, pers. observ., 2009) |
| *Atlasaurus imelakei* | 0.38 | Monbaron *et al*. (1999) |
| *Ferganasaurus verzilini* | 0.38 | Alifanov & Averianov (2003) |
| *Turiasaurus riodevensis* | 0.38 | CPT-1195–1210 (P. D. Mannion & P. Upchurch, pers. observ., 2009) |
| *Mamenchisaurus youngi* | 0.41 | Ouyang & Ye (2002) |
| 'French *Bothriospondylus*' | 0.44 | Lapparent (1943) |
| *Camarasaurus* spp. | 0.44–0.48 | Gilmore (1925); Ikejiri, Tidwell & Trexler (2005) |
| *Opisthocoelicaudia skarzynskii* | 0.46 | Borsuk-Bialynicka (1977) |
| *Angolatitan adamastor* | 0.49 | Mateus *et al*. (2011) |
| *Fukuititan nipponensis* | 0.49 | Azuma & Shibata (2010) |
| *Hudiesaurus sinojapanorum* | 0.50 | IVPP V. 11121-1 (P. D. Mannion & P. Upchurch, pers. observ., 2007) |
| *Rapetosaurus krausei* | 0.50 | Curry Rogers (2009) |
| *Alamosaurus sanjuanensis* | 0.51 | Gilmore (1946) |
| *Cedarosaurus weiskopfe* | 0.51 | Tidwell *et al*. (1999) |
| *Giraffatitan brancai* | 0.51 | Janensch (1961) |
| *Venenosaurus dicrocei* | 0.52 | Tidwell *et al*. (2001) |
| *Aeolosaurus rionegrinus* | 0.53 | Powell (2003) |
| *Wintonotitan wattsi* | 0.53 | Hocknull *et al*. (2009) |
| *Chubutisaurus insignis* | 0.54 | Salgado (1993) |
| *Epachthosaurus sciuttoi* | 0.55 | Martínez *et al*. (2004) |
| *Sonorasaurus thompsoni* | 0.56 | M. D. D'Emic, pers. comm. (2010) |
| *Argyrosaurus superbus* | 0.60 | Mannion & Otero (2012) |

states (Goloboff *et al*., 2006). Thus, treating quantitative characters as continuous data eliminates the need to define arbitrary state boundaries in order to discretize the observed variation (Wiens, 2001; Goloboff *et al*., 2006), which otherwise imposes artificial and potentially subjective divisions onto a quantitative data series that might result in the a priori biasing of an analysis (Maidment *et al*., 2008). A further benefit is that future analyses do not need to modify the state boundary, or reverse the polarity, when using the same character for revised data sets or analyses focused at different taxonomic levels (e.g. an analysis examining all sauropods, rather than just titanosauriforms). However, continuous coding sometimes means that less information can be gleaned from a description or personal examination of a specimen. For example, if an author states that one dimension of an element is greater than another (e.g. 'wider than tall') but does not provide the actual value, or if an element is incomplete such that its exact dimensions are unknown but it is clear that one value is greater than the other, then the character cannot be coded for the continuous data matrix but often can for the discrete matrix (in the current study, 30 vs. 32% of the quantitative character data matrix could be scored for the continuous and discrete data sets, respectively). Additionally, the use of continuous characters makes it more difficult to identify synapomorphies because characters represent a spectrum of morphological variation. Different but analogous treatments of quantitative characters have been implemented in a small number of other palaeontological studies (e.g. Maidment *et al*., 2008; Angielczyk & Rubidge, 2010; Ketchum & Benson, 2010; Kammerer, Angielczyk & Fröbisch, 2011), and the method used here has been implemented in palaeontological studies of mammalian and trilobite phylogeny (Prevosti, 2010; Hopkins, 2011), and in one preliminary study of sauropodomorphs (Upchurch, 2009).

One important issue raised by the treatment of quantitative characters as continuous data is that of

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'scaling' (Goloboff *et al*., 2006). The range of values covered by each quantitative character is likely to vary, resulting in characters having different weights. For example, suppose that character x has state values that range from 0.5 to 0.8, whereas character y has values that range from 0.5 to 3.5. The range of values covered by x is 0.3 whereas that for y is 3.0. This means that the weight of character y is ten times greater than that assigned to x: all things being equal, y is more likely to have a stronger influence on final tree topology than x (see Goloboff *et al*., 2006 for further discussion and examples). Most systematists who apply parsimony have preferred to commence their analyses with the assumption that all characters are equally weighted (see also our LSDM analysis). Thus, the treatment of quantitative characters as continuous data means that we need a method that deals with the scaling issue. One such approach is 'implied weights', (Goloboff, 1993; Goloboff *et al*., 2006). This approach weights each character in proportion to its fit to a given tree topology, and is calculated as follows:

$$\text{fit} = k/(h + k)$$

where $k$ is a constant (defined by the user) and $h$ is a measure of the homoplasy of the character (i.e. the number of steps required by the character on a given tree minus the minimum number of steps required by that character when it displays no homoplasy). Thus, implied weights provide a means for identifying and down-weighting homoplastic characters and, unlike other methods (such as rescaled weighting), is implemented during a tree search rather than afterwards (Goloboff *et al*., 2006). One byproduct of implied weighting is that homoplasy in a relatively scaled-up quantitative character (e.g. y above) is penalized more strongly than the same amount of homoplasy in a relatively scaled-down one (e.g. x above). The result of applying implied weights is that the differential weighting of quantitative characters is reduced, at least partially, and it has been recommended as a method for dealing with the scaling issues created by the treatment of quantitative characters as continuous data (Goloboff *et al*., 2006). Here, therefore, we analyse the LCDM using implied weighting with the default $k$-value of 3 in TNT (Goloboff *et al*., 2006), although we note that different $k$-values can produce alternative topologies (Goloboff, 1993).

All tree searches, identification of 'wild card' taxa, and tests of topological robustness were carried out in TNT (Goloboff *et al*., 2008). Character mapping and tree drawing were carried out in MESQUITE (Maddison & Maddison, 2011). PAUP 4.0 (Swofford, 2002) was used to implement Templeton's tests.

## ANALYSES AND RESULTS

### THE *LUSOTITAN* STANDARD DISCRETE MATRIX (LSDM)

*Tree searches*

In all analyses of the LSDM, characters 11, 14, 15, 27, 104, 122, 147, 148, 177, 205, and 259 were treated as ordered multistate characters. Safe taxonomic reduction was applied to this data set using the program TAXEQ3 (Wilkinson, 1995), but no redundant taxa were identified. The full LSDM was then analysed using the 'Stabilise Consensus' option in the 'New Technology Search' in TNT vs. 1.1 (Goloboff *et al*., 2008). In these analyses, searches were carried out using sectorial searches, drift, and tree fusing, with the consensus stabilized five times. This yielded 142 trees of length 1070 steps. In order to search for additional topologies, these 142 trees were used as the starting trees for a 'Traditional Search' using tree bisection-reconstruction (TBR). This produced 24 192 most parsimonious trees (MPTs) of length 1069 steps [consistency index (CI) = 0.275, retention index (RI) = 0.532, rescaled consistency index (RCI) = 0.147]. The strict consensus tree is shown in Figure 20. The pruned trees option in TNT was then used to identify the most unstable OTUs in the MPTs. This analysis indicated that the greatest increase in strict consensus tree resolution could be achieved through the a posteriori deletion of *Australodocus* and *Malarguesaurus*, resulting in the strict reduced consensus tree (see Wilkinson, 1994) shown in Figure 21.

The agreement subtree (i.e. the largest fully resolved topology common to all MPTs) was then calculated in TNT, requiring the a posteriori pruning of a further ten OTUs (see Fig. 22). These OTUs are: *Abydosaurus*, *Angolatitan*, *Astrophocaudia*, *Cedarosaurus*, *Chubutisaurus*, 'Cloverly titanosauriform', *Europasaurus*, *Fukuititan*, *Fusuisaurus*, and *Ligabuesaurus*. The relationships of each of the 12 pruned OTUs were then investigated individually by sequentially deleting 11 of them from the 24 192 MPTs and then constructing a strict reduced consensus tree for each. These studies indicated that: (1) *Abydosaurus* and *Cedarosaurus* are derived brachiosaurids, forming a polytomy with *Giraffatitan* and *Venenosaurus*; (2) *Australodocus* is a member of Titanosauria, but detailed relationships are difficult to assess; (3) *Angolatitan*, *Chubutisaurus*, 'Cloverly titanosauriform', and *Malarguesaurus* are non-titanosaurian somphospondylans, more closely related to Titanosauria than the euhelopodid clade; (4) *Astrophocaudia* is a basal somphospondylan that occupies positions within Euhelopodidae in some of the MPTs, and basal to this clade in others; (5) *Europasaurus* is a basal brachiosaurid, in a polytomy with forms such as *Brachiosaurus* and the 'French *Bothriospondylus*'; (6)

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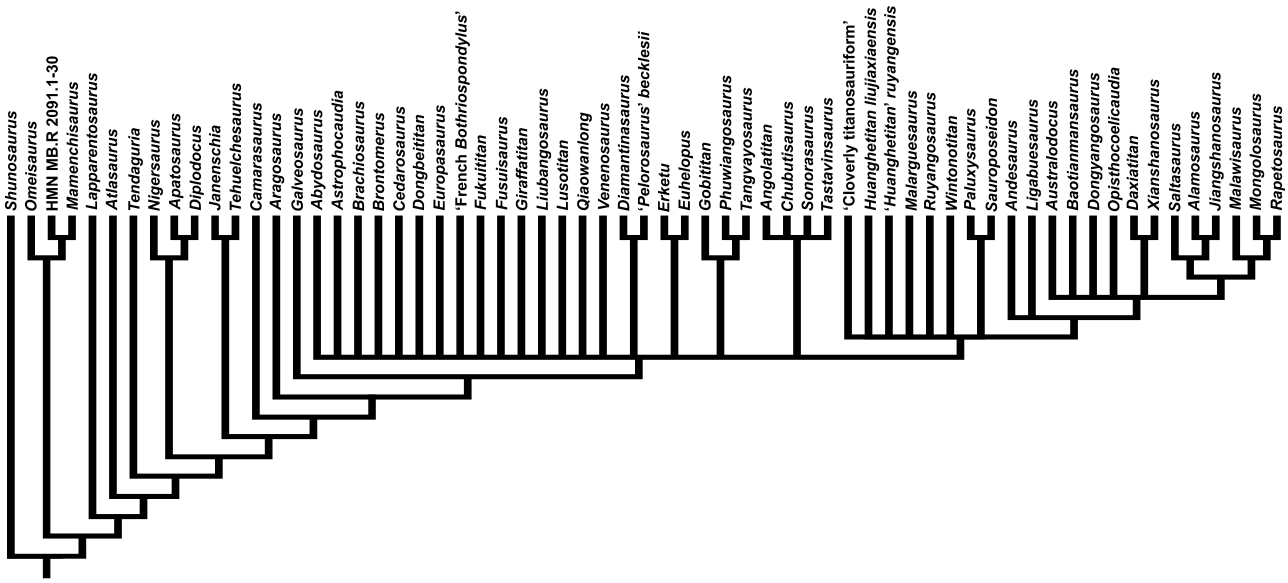


**Figure 20.** The strict consensus cladogram of the 24 192 most parsimonious trees found by analysis of the *Lusotitan* standard discrete matrix.

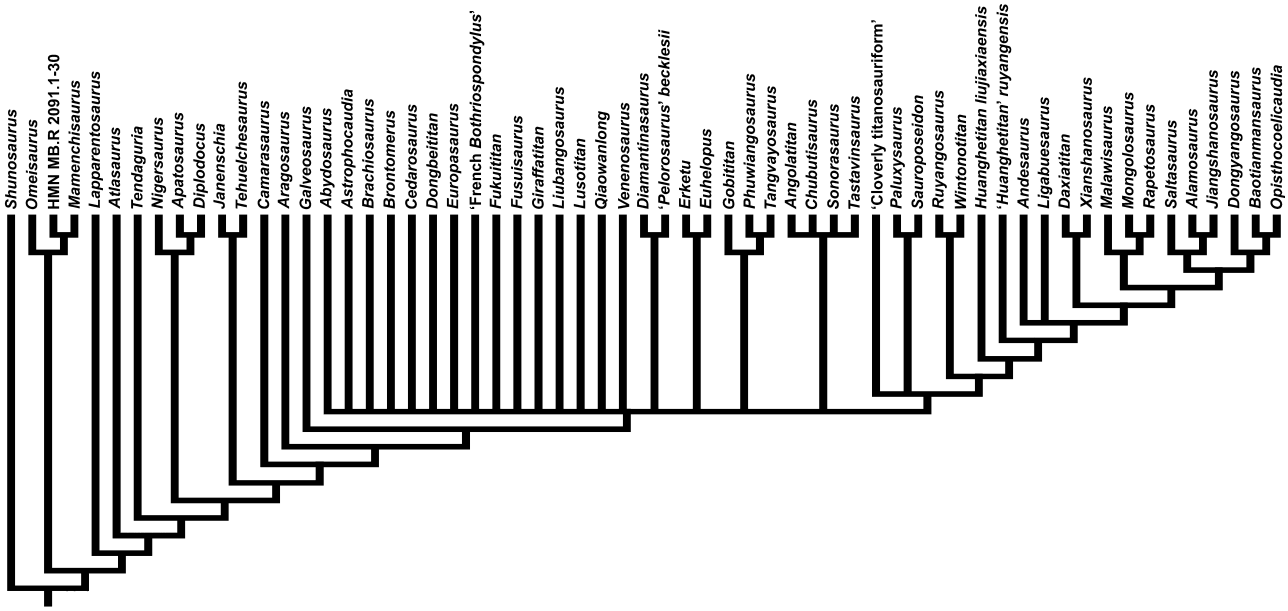


**Figure 21.** The strict reduced consensus cladogram produced by a posteriori deletion of two operational taxonomic units (*Australodocus* and *Malarguesaurus*) from the 24 192 most parsimonious trees found by analysis of the *Lusotitan* standard discrete matrix.

**Figure 22.** The time-calibrated agreement subtree generated from the 24 192 most parsimonious trees (MPTs) yielded by the analysis of the *Lusotitan* standard discrete matrix. This fully resolved topology was common to all MPTs once 12 operational taxonomic units (*Abydosaurus*, *Angolatitan*, *Astrophocaudia*, *Australodocus*, *Cedarosaurus*, *Chubutisaurus*, 'Cloverly titanosauriform', *Europasaurus*, *Fukuititan*, *Fusuisaurus*, *Ligabuesaurus*, and *Malarguesaurus*) were pruned a posteriori. A phylogenetic diversity estimate of titanosauriform diversity through time is plotted at the bottom of the figure.

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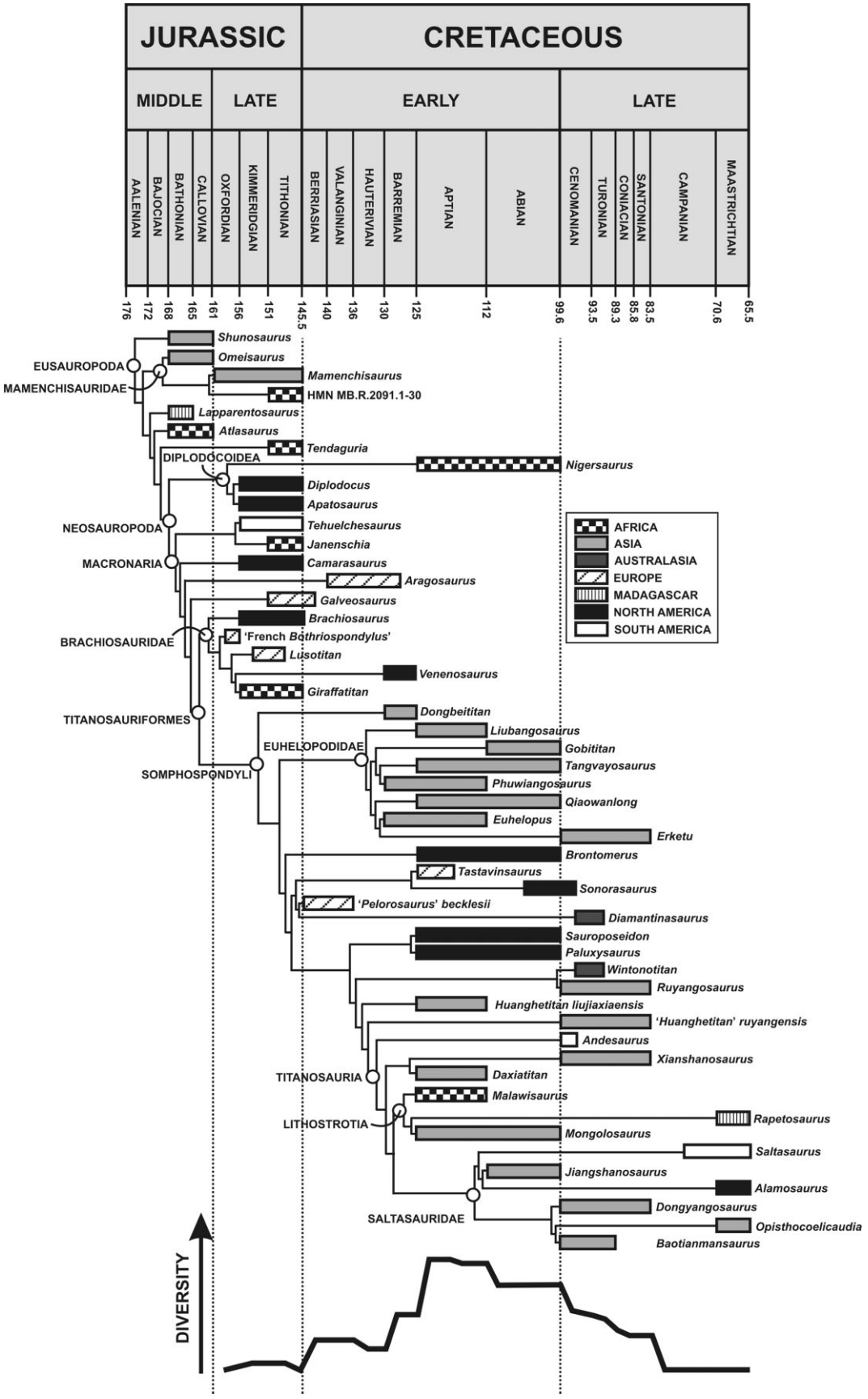


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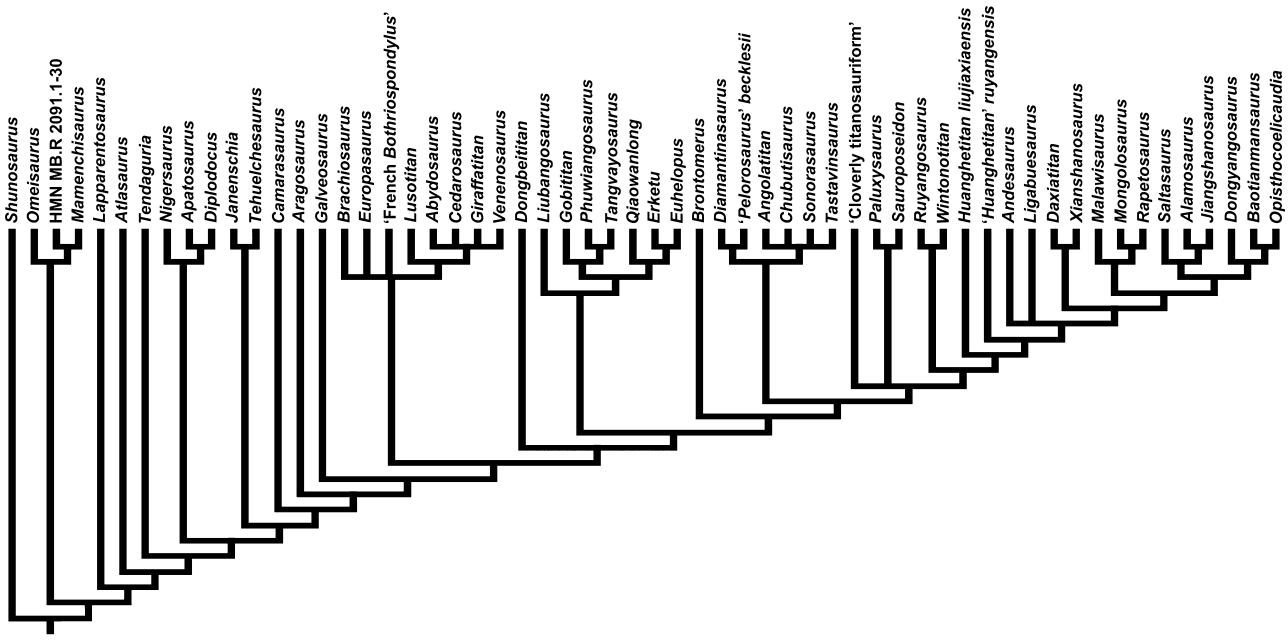


**Figure 23.** The strict reduced consensus cladogram produced by the a priori pruning of the five least stable operational taxonomic units (*Astrophocaudia*, *Australodocus*, *Fukuititan*, *Fusuisaurus*, and *Malarguesaurus*) from the 24 192 most parsimonious trees found by analysis of the *Lusotitan* standard discrete matrix.

*Fukuititan* and *Fusuisaurus* are very unstable non-titanosaurian titanosauriforms that occupy positions within Brachiosauridae and basal Somphospondyli in the MPTs; and (6) *Ligabuesaurus* is either a basal titanosaur or the sister-taxon to Titanosauria, in a trichotomy with *Andesaurus* and a clade of all other titanosaurs. Based on these results, a reduced strict consensus cladogram (Fig. 23) was generated via the a priori pruning of the five least stable OTUs (*Astrophocaudia*, *Australodocus*, *Fukuititan*, *Fusuisaurus*, and *Malarguesaurus*).

*Robustness tests*

The support for the relationships produced by the LSDM was evaluated using symmetric resampling. Bremer supports were not calculated because collection of suboptimal trees indicated that the limit of 99 999 topologies was reached when trees of just one extra step were retained (i.e. trees with lengths of 1069 and 1070 steps). This means that Bremer supports could not be evaluated because of the limits on memory in TNT.

Symmetric resampling is similar to bootstrapping and jack-knifing, but the probability of down-weighting a given character is equal to the probability of up-weighting it (Goloboff *et al*., 2003). Following Goloboff *et al*. (2003), symmetric resampling was used here to generate the relative, rather than absolute, frequencies of groups of taxa in the trees produced by multiple replicate analyses. This was because these authors demonstrated that absolute frequencies (i.e. the number of times a clade occurs, divided by the total number of resampled replicate trees) often under- or over-estimate support. Relative frequency (termed the 'GC value' by Goloboff *et al*., 2003) is defined as the frequency of a given group of taxa minus the frequency of the most common contradictory group. GC values can thus vary from 1 to –1, where 1 indicates maximum support, 0 indicates indifferent support, and –1 indicates maximum contradiction. Symmetric resampling was applied to the LSDM using 5000 replicates in TNT. All tree searches were carried out using 'Traditional Search' with TBR. The resulting GC values are shown in Figure 24A (note that in all Figures, GC values are multiplied by 100). As noted by Wilkinson (1996), support values can be lowered by OTU instability. For example, a clade containing five OTUs (e.g. A to E) can appear weakly supported, but this can arise from the combination of a strongly supported clade of four OTUs (e.g. A–D) and the instability of one OTU (e.g. E). In order to investigate this phenomenon in the LSDM trees, the 12 OTUs excluded from the agreement subtree (Fig. 22) were pruned from the replicate trees generated by symmetric resampling, and the GC values were recalculated (see Fig. 24B).

*LSDM with implied weights*

We also analysed the LSDM using implied weighting in TNT with a *k*-value of 3 (see 'Data sets' above).

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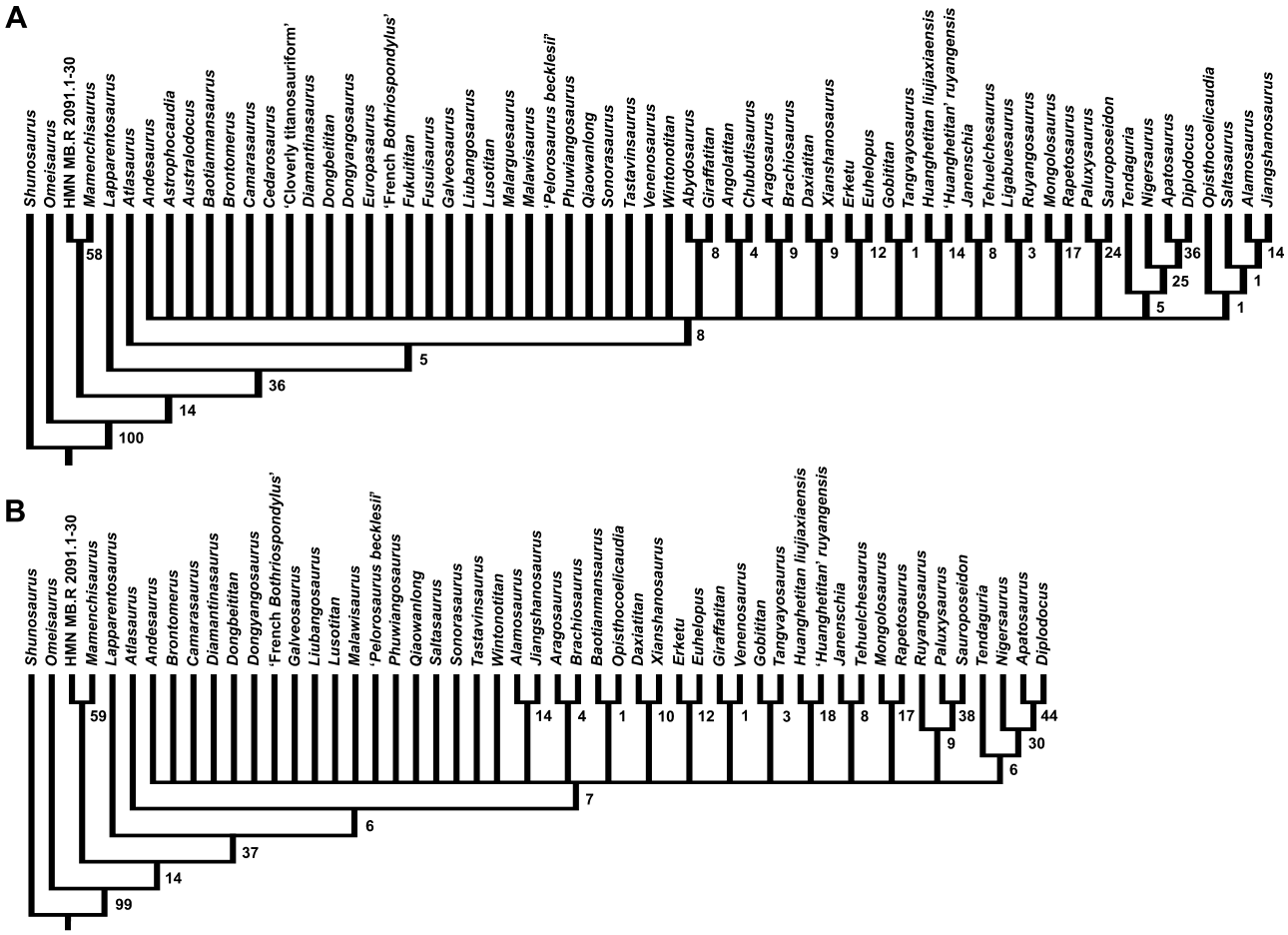


**Figure 24.** A, GC values (relative clade frequencies) for the *Lusotitan* standard discrete matrix (LSDM), generated from 5000 replicates using symmetric resampling; B, GC values for the LSDM [with the 12 operational taxonomic units pruned from the agreement subtree (see Fig. 22) also pruned from the resampled replicate trees], generated from 5000 replicates using symmetric resampling. GC values have been multiplied by 100, and collapsed nodes indicate values of zero or less than zero. See main text for details.

These analyses are here referred to as $LSDM_{iw}$. The purpose of these analyses was to enable determination of the relative contributions of implied weighting and the alternative treatments of continuous data to the LSDM and LCDM results. Differences between the LSDM and $LSDM_{iw}$ topologies indicate the impact of applying implied weighting, whereas differences between the $LSDM_{iw}$ and LCDM indicate the effects of treating continuous data as such.

The $LSDM_{iw}$ was analysed using the same protocols as the LSDM (i.e. an initial 'New Technology Search' in which the consensus was stabilized five times, followed by the use of the resulting MPTs as the starting trees for two consecutive rounds of TBR). These analyses produced 45 MPTs of length 111.22035 steps. The strict consensus cladogram of these 45 MPTs is shown in Figure 25 and the agreement subtree, following the a posteriori pruning of eight OTUs (*Abydosaurus*, *Angolatitan*, *Baotianmansaurus*, *Brachiosaurus*, *Cedarosaurus*, *Europasaurus*, '*Pelorosaurus*' *becklesii*, and *Xianshanosaurus*), is shown in Figure 26.

## THE *LUSOTITAN* CONTINUOUS + DISCRETE MATRIX (LCDM)

### *Tree searches*

In all analyses described below, characters 104, 122, 147, 148, 177, 205, and 259 were ordered. The LCDM was analysed in TNT using the 'New Technology Search' followed by 'Traditional Search' with TBR, as described above for the LSDM. However, for the LCDM, implied weights were used with a *k*-value of 3, as was implemented for our $LSDM_{iw}$. These searches yielded three MPTs of length 102.79682 steps. The non-integer step length reflects the presence of 74

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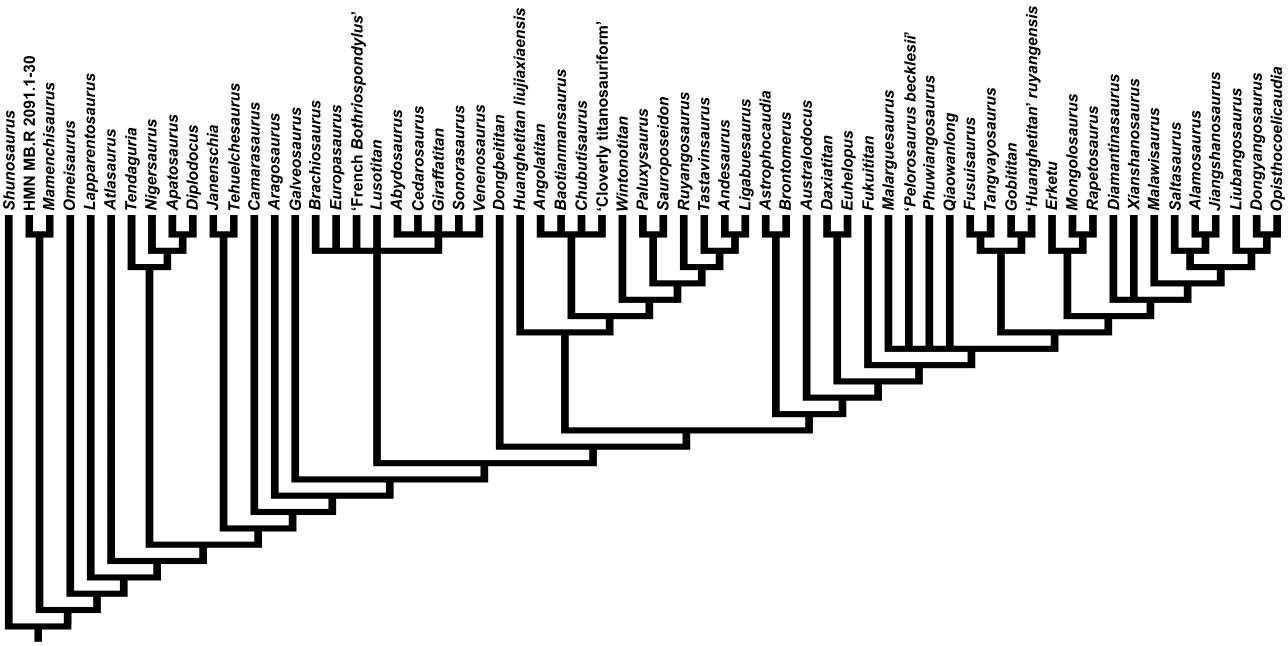


**Figure 25.** The strict consensus cladogram of the 45 most parsimonious trees found by the analysis of the *Lusotitan* standard discrete matrix (LSDM) using implied weights ($LSDM_{iw}$ analysis).

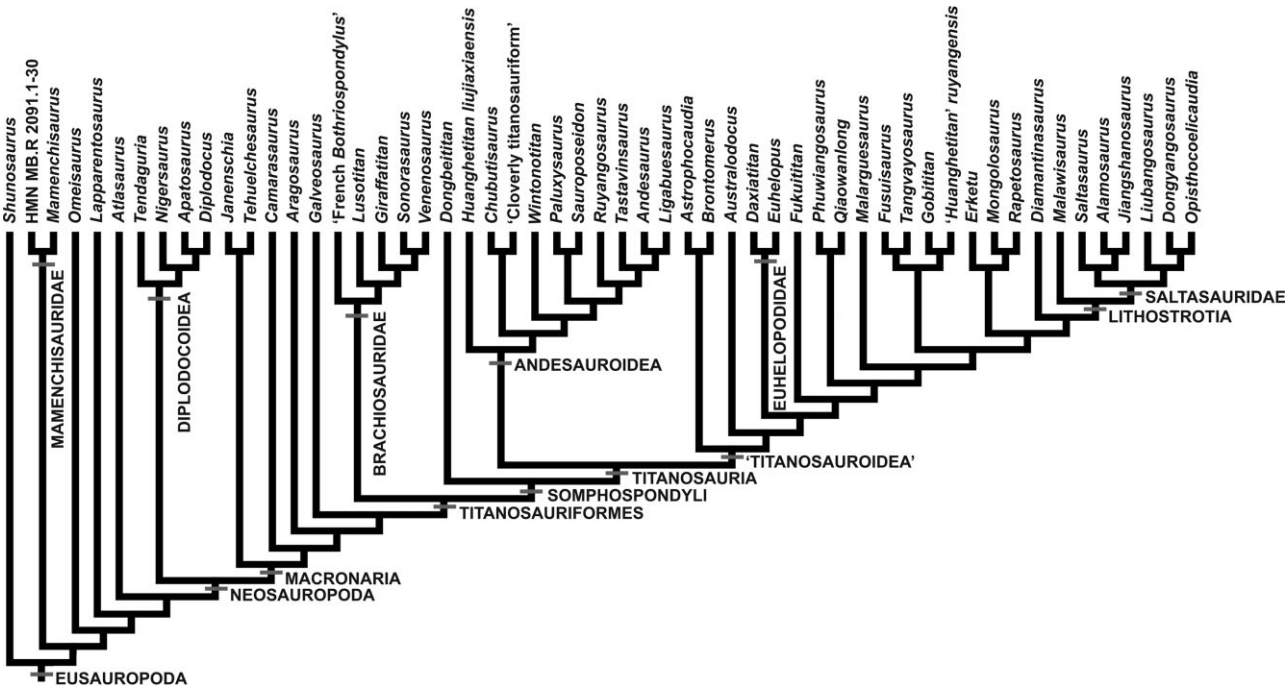


**Figure 26.** The agreement subtree generated from the 45 most parsimonious trees (MPTs) yielded by the analysis of the *Lusotitan* standard discrete matrix with implied weights ($LSDM_{iw}$). This fully resolved topology was common to all MPTs once eight operational taxonomic units (*Abydosaurus*, *Angolatitan*, *Baotianmansaurus*, *Brachiosaurus*, *Cedarosaurus*, *Europasaurus*, '*Pelorosaurus*' *becklesii*, and *Xianshanosaurus*) are pruned a posteriori.

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quantitative characters in which states are expressed directly as continuous data, combined with the down-weighting of homoplastic characters produced by the application of implied weights. The latter is also responsible for the fact that tree length is substantially lower than the total number of characters. The strict consensus tree of the three MPTs is shown in Figure 27.

*Robustness tests*

Symmetric resampling and Bremer support were applied to the LCDM. The GC values produced by symmetric resampling (5000 replicates; see above for methodology) are shown in Figure 28A. Bremer support values were generated in TNT by applying the 'New Traditional Search' using TBR [with implied weights ($k = 3$)] and collecting suboptimal topologies. In the case of the LCDM, only relative Bremer supports were calculated because it is not clear how additional fractional steps should be interpreted in the context of absolute Bremer supports. Relative Bremer support values (termed the relative fit difference, RFD) are calculated as follows:

$$\mathrm{RFD} = (F - C)/F$$

where $F$ is the sum of the fits of characters that fit the MPTs better than suboptimal trees, and $C$ is the sum of the fits of characters that fit suboptimal trees better than MPTs (Goloboff & Farris, 2001). RFD therefore varies from 0 to 1, so that a value of 0 indicates that a clade has no support, and a value of 1 indicates that the clade is entirely uncontradicted (Goloboff & Farris, 2001). For example, if twice as many binary characters support a given node as contradict it, the RFD value is 0.5. The RFD values for the LCDM are shown in Figure 28B (as before, the GC and RFD values are multiplied by 100 in the figures).

### Templeton's tests

The LSDM, $\mathrm{LSDM_{iw}}$, and LCDM analyses produced MPTs that have many relationships in common, as well as some important differences (compare sets of Figures 20–23, 25–26, and 27). Whereas the points of agreement can be interpreted as relatively well-supported aspects of titanosauriform phylogeny (because they are robust to radically different treatments of the characters and homoplasy), the differences cannot be evaluated without first determining whether the LSDM, $\mathrm{LSDM_{iw}}$, and LCDM MPTs are statistically significantly different from each other. The 24 992, 45, and three MPTs generated by the LSDM, $\mathrm{LSDM_{iw}}$, and LCDM, respectively, were imported into PAUP 4.0 (Swofford, 2002) and compared using a series of pairwise Templeton's tests. According to the LSDM character matrix, the LCDM MPTs are 34 steps longer than the LSDM MPTs. This tree length difference is statistically significant ($P = 0.023$–$0.028$). The $\mathrm{LSDM_{iw}}$ MPTs are 24 steps longer than the LSDM trees ($P = 0.112$–$0.160$). Finally, the LCDM MPTs are ten steps longer than the $\mathrm{LSDM_{iw}}$ trees ($P = 0.132$).

## DISCUSSION

### Robustness of titanosauriform phylogenetic relationships

Before we examine the phylogenetic results for implications concerning titanosauriform classification and evolutionary history, it is important to consider the robustness of the MPT topologies. In general, support values are relatively low for most nodes, although increases can be achieved if less stable taxa are pruned from replicate or suboptimal tree topologies a posteriori.

In the LSDM MPTs, GC values are positive for 22 nodes (we excluded the second most basal node as its support is fixed by designation of *Shunosaurus* as the outgroup) (Fig. 24A). The most strongly supported node is that uniting *Mamenchisaurus* and HMN MB.R.2091.1–30. Amongst titanosauriform taxa, the nodes with the highest GC values include those that unite *Sauroposeidon* with *Paluxysaurus*, and *Rapetosaurus* with *Mongolosaurus*. The total number of nodes with positive GC values decreased to 20 when wild card taxa were pruned from the replicate trees a posteriori (Fig. 24B), but the support values for some nodes (e.g. *Paluxysaurus* + *Sauroposeidon*) increased markedly.

In the case of the LCDM, support values are lower, with only 13 nodes in Figure 28A displaying GC values higher than zero. Again, the node uniting *Mamenchisaurus* and HMN MB.R.2091.1–30 received relatively strong support, and the best supported node overall is that uniting *Apatosaurus* and *Diplodocus*. With regard to titanosauriform relationships, the node uniting *Rapetosaurus* and *Mongolosaurus* again received the strongest support in Figure 28A. Most nodes in the LCDM MPTs have positive RFD support values (Fig. 28B), with seven nodes within Titanosauriformes receiving RFD values of 0.44 or higher (N.B. limitations on the number of suboptimal trees that can be stored in TNT meant that a RFD value of $> 0.44$ represents the highest support that can be detected: actual RFD values might be somewhat higher if longer suboptimal topologies could be collected). These results provide some indication of areas of relative strength and weakness in the LCDM topologies. In particular, the best supported portions of the LCDM MPTs include (1) macronarian mono-

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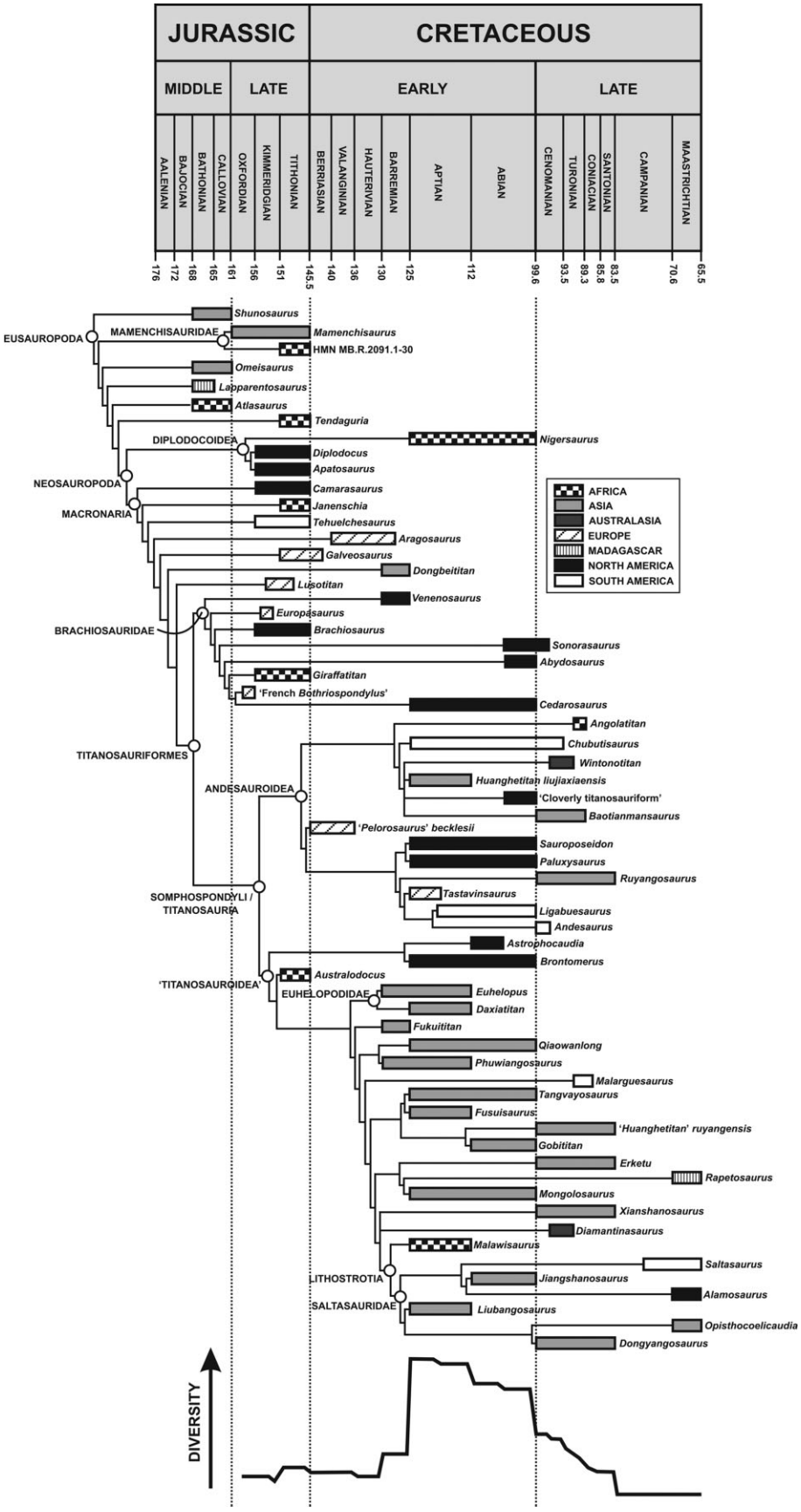


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**Figure 27.** The strict consensus cladogram of the three most parsimonious trees found by analysis of the *Lusotitan* continuous + discrete matrix. A phylogenetic diversity estimate of titanosauriform diversity through time is plotted at the bottom of the figure.

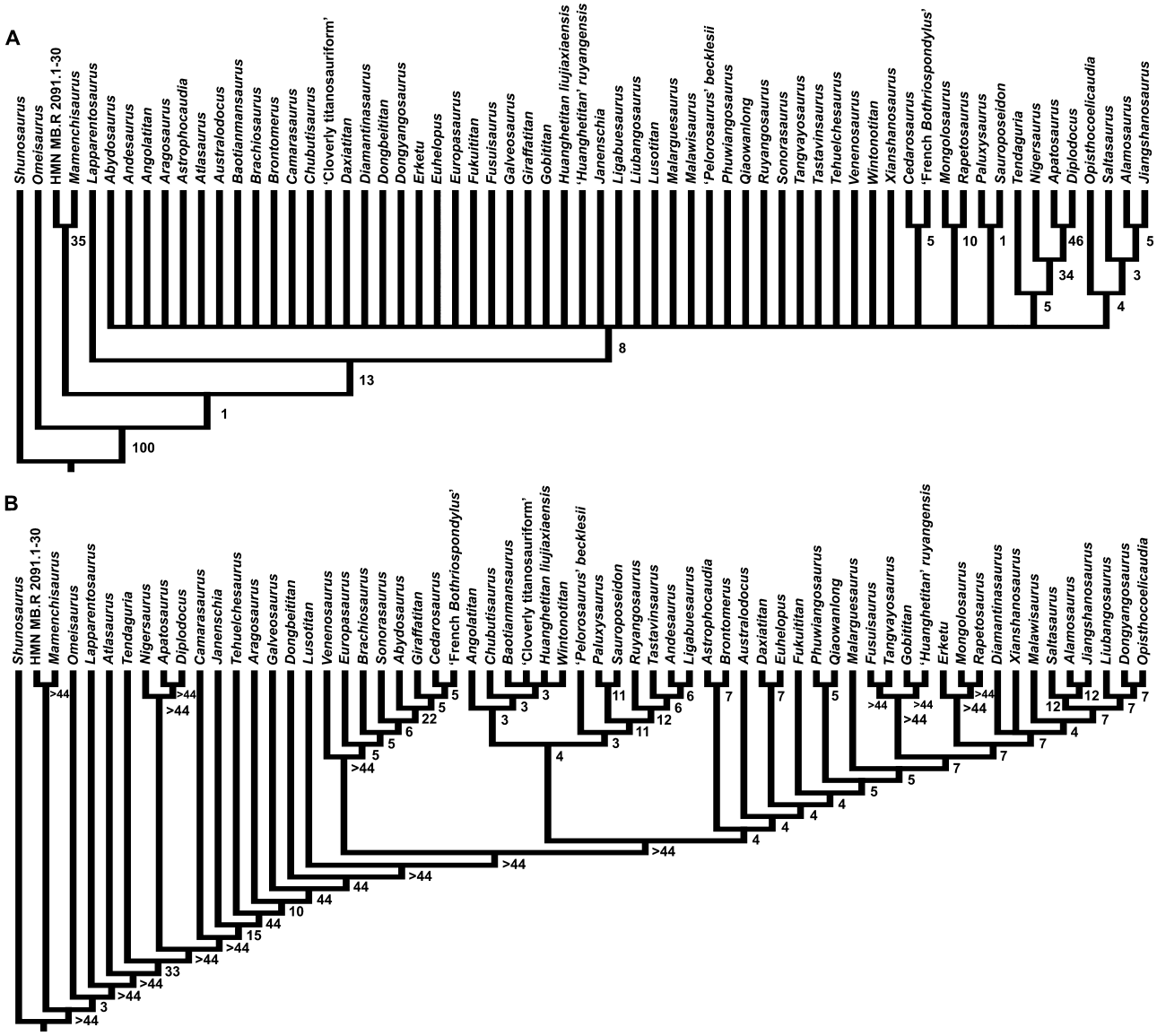


**Figure 28.** A, GC values (relative clade frequencies) for the *Lusotitan* continuous + discrete matrix (LCDM), generated from 5000 replicates using symmetric resampling. GC values have been multiplied by 100, and collapsed nodes indicate values of zero or less than zero; B, relative Bremer support values (RFDs) for the LCDM. RFD values have been multiplied by 100. Limits on memory meant that we could only collect the 99 999 suboptimal topologies that are closest, in terms of tree length, to the original most parsimonious trees (MPTs). This means that the strongest nodes in the MPTs might have higher RFD values, but we could not test this without collecting more and longer trees. As a result, we could only deduce that the strongest nodes have RFDs that are higher than 44. See main text for details.

phyly; (2) the monophyly of Titanosauriformes and its two constituent clades (Brachiosauridae and Somphospondyli); (3) the clade containing *Fusuisaurus*, *Gobititan*, *'Huanghetitan' ruyangensis*, and *Tangvayosaurus*; and (4) the clade comprising *Erketu*, *Mongolosaurus*, and *Rapetosaurus*.

Low support values for many nodes in both LSDM and LCDM MPTs probably arise from complex inter-

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actions amongst three critical factors. First, large quantities of missing data increase taxon instability. Many of the titanosauriform OTUs are known from only very incomplete specimens (Table 7); consequently, the two data sets comprise approximately 67% missing data. Second, homoplasy is very common. This is reflected in the low CI and RCI values for the LSDM MPTs (see above) and also the low tree length values for the $LSDM_{iw}$ and LCDM MPTs resulting from the presence of highly homoplastic characters that were strongly down-weighted when implied weights were used. Third, estimation of support values when analysing relatively large and complex data sets is also problematic because of reasons relating to the efficacy of tree searches. When the LSDM and LCDM were analysed in order to find the most parsimonious trees, a battery of sophisticated search algorithms were applied (e.g. sectorial searches, drift, tree fusing, TBR, etc.), and considerable processing time (hours or even days) was used to obtain the results. Such efficient and intensive searching for the most parsimonious trees, however, is often not feasible when producing thousands of replicate analyses or suboptimal trees for the purposes of estimating clade supports. Consequently, clades present in the original MPTs are less likely to be present in the populations of replicate and suboptimal trees than would be the case if the tree searches had been carried out using more efficient and time-consuming methods (for further discussion of this issue see Goloboff & Farris, 2001; Goloboff *et al*., 2003).

To some extent these problems are intractable. For example, it is unlikely that future discoveries of new taxa (or better preserved specimens of existing ones) will substantially decrease the amount of homoplasy in the data set. However, 23 of the OTUs considered here were scored solely on the basis of the published literature (or photographs): in some cases, the available descriptions are relatively brief and sparsely illustrated. Thus, it is probable that first-hand examination of many titanosauriforms will yield new characters and state scores that could help to reduce taxon instability and increase the support values in future studies. Pending such further work, the relationships discussed below should be treated with caution, and the interpretation of titanosauriform evolutionary history should be regarded as a set of provisional hypotheses that require considerable further testing.

## Taxonomic and phylogenetic implications

Based on our LSDM, $LSDM_{iw}$, and LCDM MPTs, below we discuss the phylogenetic relationships of *Lusotitan*, the composition of the two titanosauriform clades (Brachiosauridae and Somphospondyli), and the affinities of those putative ingroup taxa recovered outside Titanosauriformes (see Table 7 for a summary of the affinities and previous assignments of all putative ingroup taxa, and Appendices 4 and 5 for synapomorphies of the main macronarian clades). $LSDM_{iw}$ results are only reported when they deviate from the LSDM.

### *Brachiosauridae*

#### *Lusotitan*

As noted in the Introduction, *Lusotitan* was originally described as a new species of *Brachiosaurus*: '*Brachiosaurus atalaiensis*' (Lapparent & Zbyszewski, 1957). Very little was subsequently written about this taxon, with McIntosh (1990) including it within *Brachiosaurus* without further comment, before Antunes & Mateus (2003) and Upchurch *et al*. (2004a) expressed doubt as to the referral. Both sets of authors regarded it as a brachiosaurid distinct from *Brachiosaurus*, and Antunes & Mateus (2003) created the new combination *Lusotitan atalaiensis*, which has been adopted by subsequent workers (e.g. Taylor, 2009). In its first inclusion in a phylogenetic study, both our analyses support the generic separation of *Lusotitan* from *Brachiosaurus* (and also *Giraffatitan*), but differ in its placement. Whereas the LSDM recovers it as a brachiosaurid, the LCDM places *Lusotitan* as the sister taxon to Titanosauriformes.

#### Other brachiosaurids

Titanosauriformes is the least inclusive clade including *Brachiosaurus altithorax* and *Saltasaurus loricatus* (Salgado *et al*., 1997) and comprises the sister clades Brachiosauridae and Somphospondyli (see Table 6). Brachiosauridae is defined as the most inclusive clade that includes *Brachiosaurus altithorax* but excludes *Saltasaurus loricatus* (Wilson & Sereno, 1998). Common to both our LSDM and LCDM analyses, we recovered *Abydosaurus*, *Brachiosaurus*, and *Giraffatitan* as brachiosaurids, as in all previous phylogenetic studies (Table 7). Furthermore, our analyses support Taylor's (2009) generic separation of the Late Jurassic North American *Brachiosaurus altithorax* and African *Giraffatitan* (*Brachiosaurus*) *brancai* species (see also D'Emic, 2012, 2013 and 'Note on the taxonomy of *Brachiosaurus*' below). We recovered *Brachiosaurus* in a more basal position than *Giraffatitan*, the reverse of that reported by D'Emic (2012, 2013). We found agreement with D'Emic (2012, 2013) in the placement of the Kimmeridgian-aged German dwarf sauropod *Europasaurus* (Sander *et al*., 2006) as a member of Brachiosauridae, differing from previous identifications as a non-titanosauriform macronarian (Sander *et al*., 2006; Ksepka & Norell, 2010; Carballido *et al*., 2011a, b). In its first inclusion in a phylogenetic analysis, the Oxfordian 'French

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**Table 6.** Phylogenetic definitions of clade names used in this study

| Clade name/author | Phylogenetic definition | Defined by |
|---|---|---|
| Andesauroidea Salgado (2003) | The most inclusive clade that includes *Andesaurus delgadoi* but excludes *Saltasaurus loricatus* | Salgado (2003) |
| Brachiosauridae Riggs (1904) | The most inclusive clade that includes *Brachiosaurus altithorax* but excludes *Saltasaurus loricatus* | Wilson & Sereno (1998) |
| Diplodocoidea Marsh (1884) | The most inclusive clade that includes *Diplodocus longus* but excludes *Saltasaurus loricatus* | Wilson & Sereno (1998) |
| Euhelopodidae Romer (1956) | The most inclusive clade that includes *Euhelopus zdanskyi* but excludes *Neuquensaurus australis* | D'Emic (2012) |
| Eusauropoda Upchurch (1995) | The least inclusive clade containing *Shunosaurus lii* and *Saltasaurus loricatus* | Upchurch *et al*. (2004a) |
| Lithostrotia Wilson & Upchurch (2003) | The least inclusive clade containing *Malawisaurus dixeyi* and *Saltasaurus loricatus* | Wilson & Upchurch (2003); Upchurch *et al*. (2004a) |
| Macronaria Wilson & Sereno (1998) | The most inclusive clade that includes *Saltasaurus loricatus* but excludes *Diplodocus longus* | Wilson & Sereno (1998) |
| Mamenchisauridae Young & Zhao (1972) | The most inclusive clade that includes *Mamenchisaurus constructus* but excludes *Saltasaurus loricatus* | Naish & Martill (2007) |
| Neosauropoda Bonaparte (1986) | The least inclusive clade containing *Saltasaurus loricatus* and *Diplodocus longus* | Wilson & Sereno (1998) |
| Saltasauridae Bonaparte & Powell (1980) | The least inclusive clade that includes *Opisthocoelicaudia skarzynskii* and *Saltasaurus loricatus* | Sereno (1998); Wilson & Upchurch (2003) |
| Somphospondyli Wilson & Sereno (1998) | The most inclusive clade that includes *Saltasaurus loricatus* but excludes *Brachiosaurus altithorax* | Wilson & Sereno (1998); Upchurch *et al*. (2004a) |
| Titanosauria Bonaparte & Coria (1993) | The least inclusive clade that includes *Andesaurus delgadoi* and *Saltasaurus loricatus* | Wilson & Upchurch (2003) |
| Titanosauriformes Salgado *et al*. (1997) | The least inclusive clade including *Brachiosaurus altithorax* and *Saltasaurus loricatus* | Salgado *et al*. (1997) |

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**Table 7.** Summary of conclusions concerning the phylogenetic classification of the 56 ingroup taxa considered in this study

| Taxon | Classification | Comment | CCM |
|---|---|---|---|
| *Abydosaurus** | Brachiosauridae | Agrees with Chure *et al.* (2010), Ksepka & Norell (2010), and D'Emic (2012, 2013) | 24 |
| *Alamosaurus* | Saltasauridae | Regarded as a derived lithostrotian or saltasaurid in all previous analyses (e.g. Wilson, 2002; Upchurch *et al.*, 2004a; Curry Rogers, 2005) | 66 |
| *Andesaurus* | Titanosauria | Clade specifier | 31 |
| *Angolatitan** | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to LSDM, and titanosaurian according to LCDM; Mateus *et al.* (2011) identified it as a non-titanosaurian somphospondylan, whereas D'Emic (2012) suggested lithostrotian affinities | 13 |
| *Aragosaurus* | Non-titanosauriform macronarian | Several authors have suggested titanosauriform affinities (e.g. Barco *et al.*, 2006; Mannion & Calvo, 2011; D'Emic, 2012), whereas Royo-Torres (2009) supported the basal macronarian position | 34 |
| *Astrophocaudia** | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to the LSDM, and non-lithostrotian titanosaurian according to the LCDM; D'Emic (2013) recovered it as a non-titanosaurian somphospondylan | 23 |
| *Atlasaurus* | Non-neosauropod eusauropod | Considered 'brachiosaurid-like' by Monbaron *et al.* (1999); recovered as a non-titanosauriform macronarian by Upchurch *et al.* (2004a), and as a non-neosauropod by all other authors (e.g. Royo-Torres *et al.*, 2006; Wilson & Upchurch, 2009; D'Emic, 2012; Royo-Torres & Upchurch, 2012) | 22 |
| *Australodocus** | Non-lithostrotian titanosaurian | Originally referred to Diplodocidae (Remes, 2007), but shown to represent a titanosauriform by Whitlock (2011a, b; see also D'Emic, 2012; Mannion *et al.*, 2012) | 6 |
| *Baotianmansaurus* | Titanosauria *incertae sedis* | Saltasaurid according to the LSDM, and non-lithostrotian titanosaurian according to the LCDM; referred to Titanosauriformes by Zhang *et al.* (2009), with suggestion of somphospondylan affinities [see also D'Emic 2012 (euhelopodid)] | 12 |
| *Brachiosaurus* | Brachiosauridae | Clade specifier | 28 |
| *Brontomerus* | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to LSDM, and non-lithostrotian titanosaurian according to LCDM; Taylor *et al.* (2011) referred it to Camarasauromorpha *incertae sedis*, and D'Emic (2012) regarded it as an indeterminate titanosauriform | 8 |
| *Cedarosaurus* | Brachiosauridae | Recovered as a brachiosaurid in most previous studies (e.g. Tidwell *et al.*, 1999; Upchurch *et al.*, 2004a; Ksepka & Norell, 2010; D'Emic, 2012, 2013), but as a basal titanosaur in Canudo *et al.* (2008), a basal somphospondylan in Rose (2007) and some analyses of Royo-Torres *et al.* (2012), and as a basal macronarian in Royo-Torres (2009) | 39 |
| *Chubutisaurus** | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to LSDM, and non-lithostrotian titanosaurian according to LCDM; included within Brachiosauridae by McIntosh (1990) and recovered as a non-titanosaurian somphospondylan by most authors (Salgado *et al.*, 1997; Bonaparte *et al.*, 2006; González Riga *et al.*, 2009; Royo-Torres, 2009; Carballido *et al.*, 2011a; D'Emic, 2012), but placed outside Titanosauriformes by Carballido *et al.* (2011b) | 33 |
| 'Cloverly titanosauriform'* | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to LSDM, and non-lithostrotian titanosaurian according to LCDM; originally described as a titanosaur by Ostrom (1970), but regarded as a non-titanosaurian somphospondylan by D'Emic & Foreman (2012), who referred it to *Sauroposeidon* (see also D'Emic, 2012) | 15 |
| *Daxiatitan* | Non-lithostrotian titanosaurian | Regarded as a basal titanosaur by You *et al.* (2008) and as a non-titanosaurian somphospondylan (euhelopodid) by D'Emic (2012) | 24 |
| *Diamantinasaurus* | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to the LSDM, and non-lithostrotian titanosaurian according to the LCDM; recovered as a lithostrotian by Hocknull *et al.* (2009) and Zaher *et al.* (2011), with saltasaurid affinities suggested by D'Emic (2012) | 27 |
| *Dongbeititan* | Macronaria *incertae sedis* | Basal-most somphospondylan according to the LSDM, and non-titanosauriform macronarian according to the LCDM; considered a somphospondylan by Wang *et al.* (2007) and D'Emic (2012), and a titanosaur by Mannion & Calvo (2011) | 35 |
| *Dongyangosaurus* | Saltasauridae | Regarded as a titanosaur by Lü *et al.* (2008), and non-titanosaurian somphospondylan (euhelopodid) by D'Emic (2012) | 17 |
| *Erketu* | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan (euhelopodid) according to the LSDM, and non-lithostrotian titanosaurian according to the LCDM; previously considered a non-titanosaurian somphospondylan [Ksepka & Norell, 2006, 2010; D'Emic, 2012 (euhelopodid)] | 15 |
| *Euhelopus* | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to the LSDM, and non-lithostrotian titanosaurian according to the LCDM; regarded as a basal somphospondylan by Wilson & Upchurch (2009; see also for a review of previous taxonomic assignments) and most other authors (e.g. D'Emic, 2012), but as a basal macronarian by Royo-Torres (2009) and Carballido *et al.* (2011b) | 59 |
| *Europasaurus** | Brachiosauridae | Previously identified as a non-titanosauriform macronarian (Sander *et al.*, 2006; Ksepka & Norell, 2010; Carballido *et al.*, 2011a, b); D'Emic (2012, 2013) agreed with a brachiosaurid position | 70 |
| 'French *Bothriospondylus*' | Brachiosauridae | Lapparent (1943) and subsequent workers have all considered it to represent a brachiosaurid (see Mannion, 2010; D'Emic, 2012) | 27 |
| *Fukuititan** | Titanosauriformes *incertae sedis* | Non-titanosaurian titanosauriform according to LSDM, and non-lithostrotian titanosaur according to the LCDM; Azuma & Shibata (2010) identified it as a basal titanosauriform; D'Emic (2012) could not assign it beyond Macronaria | 11 |

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| | | | |
|---|---|---|---|
| *Fusuisaurus** | Titanosauriformes *incertae sedis* | Non-titanosaurian titanosauriform according to the LSDM, and titanosaurian according to the LCDM; previously assigned to Titanosauriformes *incertae sedis* by Mo *et al.* (2006; see also D'Emic, 2012) | 9 |
| *Galveosaurus* | Non-titanosauriform macronarian | Position agrees with Barco *et al.* (2006) and Carballido *et al.* (2011a, b); other workers have considered it a basal eusauropod (see Royo-Torres & Upchurch, 2012) or titanosauriform (D'Emic, 2012) | 28 |
| *Giraffatitan* | Brachiosauridae | Supports previous analyses that have treated *Brachiosaurus* and *Giraffatitan* as separate operational taxonomic units (Taylor, 2009; Ksepka & Norell, 2010; D'Emic, 2012, 2013) | 96 |
| *Gobititan* | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan (euhelopodid) according to the LSDM, and non-lithostrotian titanosaurian according to the LCDM; originally described as a basal titanosaur (You *et al.*, 2003), although subsequently suggested to represent a non-titanosaurian titanosauriform (Mannion & Otero, 2012); D'Emic (2012) regarded it as a somphospondylan | 19 |
| HMN MB.R.2091.1-30 | Mamenchisauridae | Originally referred to *Janenschia* and considered a titanosaur (Janensch, 1929); Bonaparte *et al.* (2000) questioned its titanosaurian affinities and removed it from *Janenschia* | 14 |
| *Huanghetitan liujiaxiaensis* | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to the LSDM, and non-lithostrotian titanosaurian according to the LCDM; recovered as a non-titanosaurian somphospondylan by You *et al.* (2006) and Hocknull *et al.* (2009); considered a somphospondylan by D'Emic (2012) | 12 |
| *'Huanghetitan' ruyangensis* | Somphospondyli *incertae sedis* | Non-titanosauriform somphospondylan according to the LSDM, and non-lithostrotian titanosaurian according to the LCDM; Lü *et al.* (2007) regarded it as a basal titanosauriform, whereas D'Emic (2012) considered it as a somphospondylan | 14 |
| *Janenschia* | Non-titanosauriform macronarian | Previously regarded as a titanosaur by most workers (e.g. Janensch, 1929; Upchurch, 1995; Curry Rogers, 2005), a titanosauriform by D'Emic (2012), or closely related to *Camarasaurus* (Bonaparte *et al.*, 2000); Carballido *et al.* (2011b) recovered it in a non-titanosauriform macronarian position | 24 |
| *Jiangshanosaurus* | Saltasauridae | Previously regarded as a titanosaur (Tang *et al.*, 2001b; Upchurch *et al.*, 2004a), with saltasaurid affinities suggested by D'Emic (2012) | 15 |
| *Lapparentosaurus* | Non-neosauropod eusauropod | Bonaparte (1986) also considered it to represent a basal eusauropod, whereas McIntosh (1990) and Upchurch (1995, 1998) referred it to Brachiosauridae; the analysis of Upchurch *et al.* (2004a) recovered it as Titanosauriformes *incertae sedis* | 51 |
| *Ligabuesaurus** | Somphospondyli *incertae sedis* | Recovered in a trichotomy with *Andesaurus* and other titanosaurs according to the LSDM, and as a non-lithostrotian titanosaur according to the LCDM; recovered as a non-titanosaurian somphospondylan by most authors (Bonaparte *et al.*, 2006; González Riga *et al.*, 2009; Carballido *et al.*, 2011a; D'Emic, 2012, 2013), but as a titanosaur by Carballido *et al.* (2011b) | 33 |
| *Liubangosaurus* | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan (euhelopodid) according to the LSDM, and saltasaurid according to the LCDM; Mo *et al.* (2010) recovered it as a non-neosauropod eusauropod | 8 |
| *Lusotitan* | Macronaria *incertae sedis* | Brachiosaurid according to the LSDM, and sister taxon to Titanosauriformes according to the LCDM; considered a brachiosaurid by all previous workers (Lapparent & Zbyszewski, 1957; McIntosh, 1990; Upchurch, 1995; Antunes & Mateus, 2003; Upchurch *et al.*, 2004a; D'Emic, 2012) | 27 |
| *Malarguesaurus** | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to the LSDM, and non-lithostrotian titanosaur according to the LCDM; recovered as a non-titanosaurian somphospondylan by González Riga *et al.* (2009), but as a titanosaur by Carballido *et al.* (2011a); D'Emic (2012) regarded it as a titanosauriform | 12 |
| *Malawisaurus* | Lithostrotia | Clade specifier | 65 |
| *Mongolosaurus* | Titanosauria *incertae sedis* | Lithostrotian according to the LSDM, and non-lithostrotian titanosaur according to the LCDM; recovered as a titanosaur by Mannion (2011), with some indication of a derived position within Lithostrotia (see also Wilson, 2005a); D'Emic (2012) suggested non-titanosaurian somphospondylan affinities | 10 |
| *Opisthocoelicaudia* | Saltasauridae | Clade specifier | 60 |
| *Paluxysaurus* | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to the LSDM, and non-lithostrotian titanosaurian according to the LCDM; recovered as a brachiosaurid by most previous authors (Rose, 2007; Ksepka & Norell, 2010; Carballido *et al.*, 2011b), but D'Emic (2012, 2013) placed it in a non-titanosaurian somphospondylan position and referred it to *Sauroposeidon* (supported here) | 61 |
| *'Pelorosaurus' becklesii* | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to the LSDM, and non-lithostrotian titanosaur according to the LCDM; regarded as a basal titanosaur in previous studies (Upchurch, 1995; Upchurch *et al.*, 2004a, 2011b), and considered Titanosauriformes *incertae sedis* by D'Emic (2012) | 9 |

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**Table 7.** *Continued*

| Taxon | Classification | Comment | CCM |
|---|---|---|---|
| *Phuwiangosaurus* | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to the LSDM (euhelopodid), and non-lithostrotian titanosaurian according to the LCDM; previous studies have recovered it as either a basal titanosaur (e.g. Upchurch, 1998; Curry Rogers, 2005; Canudo *et al.*, 2008; Carballido *et al.*, 2011a; Zaher *et al.*, 2011), or a non-titanosaurian somphospondylan [e.g. Rose, 2007; González Riga *et al.*, 2009; Wilson & Upchurch, 2009; Suteethorn *et al.*, 2010; Carballido *et al.*, 2011b; D'Emic, 2012 (euhelopodid)], although Royo-Torres, (2009) positioned it as a brachiosaurid | 62 |
| *Qiaowanlong* | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to the LSDM (euhelopodid), and non-lithostrotian titanosaurian according to the LCDM; described as a brachiosaurid by You & Li (2009); recovered as a non-titanosaurian somphospondylan by Ksepka & Norell (2010) and D'Emic [2012 (euhelopodid)] | 13 |
| *Rapetosaurus* | Titanosauria *incertae sedis* | Lithostrotian according to the LSDM, and non-lithostrotian titanosaur according to the LCDM; all previous studies have recovered *Rapetosaurus* as a derived titanosaur (e.g. Wilson, 2002; Curry Rogers, 2005) | 81 |
| *Ruyangosaurus* | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to the LSDM, and non-lithostrotian titanosaurian according to the LCDM; regarded as a basal titanosaur ('Andesauridae') by Lü *et al.* (2009b), a non-titanosaurian somphospondylan by Mannion & Calvo (2011), and a somphospondylan by D'Emic (2012) | 9 |
| *Saltasaurus* | Saltasauridae | Clade specifier | 58 |
| *Sauroposeidon** | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to the LSDM, and non-lithostrotian titanosaurian according to the LCDM; considered a brachiosaurid in previous studies (Wedel *et al.*, 2000a, b; Upchurch *et al.*, 2004a), whereas D'Emic (2012, 2013) recovered it in a non-titanosaurian somphospondylan position | 7 |
| *Sonorasaurus* | Titanosauriformes *incertae sedis* | Non-titanosaurian somphospondylan according to the LSDM, and brachiosaurid according to the LCDM; described as a brachiosaurid by Ratkevich (1998; see also D'Emic, 2012), and recovered as a basal macronarian by Royo-Torres (2009) | 11 |
| *Tangvayosaurus** | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to the LSDM (euhelopodid), and non-lithostrotian titanosaur according to the LCDM; considered a titanosaur by Allain *et al.* (1999) and Zaher *et al.* (2011), a non-titanosaurian somphospondylan by Suteethorn *et al.* (2010) and D'Emic [2012 (euhelopodid)], and non-titanosauriform macronarian by Royo-Torres (2009) | 35 |
| *Tastavinsaurus* | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to the LSDM, and non-lithostrotian titanosaurian according to the LCDM; Canudo *et al.* (2008) and D'Emic (2012) recovered it as a non-titanosaurian somphospondylan, whereas Royo-Torres *et al.* (2012) found evidence to support either a brachiosaurid or non-titanosaurian somphospondylan position; Royo-Torres (2009) and Carballido *et al.* (2011a, b) recovered it as a non-titanosauriform macronarian | 47 |
| *Tehuelchesaurus* | Non-titanosauriform macronarian | Previously placed as a non-neosauropod eusauropod (Rich *et al.*, 1999; Upchurch *et al.*, 2004a), whereas Rauhut *et al.* (2005) Carballido *et al.* (2011a, b) and D'Emic (2012, 2013) recovered it as a non-titanosauriform macronarian | 30 |
| *Tendaguria* | Eusauropoda *incertae sedis* | Sister taxon to Neosauropoda according to the LSDM and LCDM, but basal diplodocoid according to the $LSDM_{iw}$; regarded as Sauropoda *incertae sedis* by Bonaparte *et al.* (2000) and Upchurch *et al.* (2004a); Carballido *et al.* (2011b) recovered it as either a non-neosauropod or a non-titanosauriform macronarian; Mannion & Calvo (2011) suggested possible titanosaurian affinities | 10 |
| *Venenosaurus* | Brachiosauridae | Rose (2007) and Canudo *et al.* (2008) recovered it as a non-titanosaurian somphospondylan (see also some analyses of Royo-Torres *et al.*, 2012); D'Emic (2012, 2013) recovered it as a brachiosaurid (see also Wilson, 2002, and some analyses of Royo-Torres *et al.*, 2012); Royo-Torres (2009) and Carballido *et al.* (2011a) recovered it as a non-titanosauriform macronarian; Upchurch *et al.* (2004a) suggested titanosaurian affinities | 32 |
| *Wintonotitan* | Somphospondyli *incertae sedis* | Non-titanosaurian somphospondylan according to the LSDM, and non-lithostrotian titanosaurian according to the LCDM; recovered as a non-titanosaurian somphospondylan by Hocknull *et al.* (2009) and Carballido *et al.* (2011a), and as a non-titanosauriform macronarian by Carballido *et al.* (2011b); D'Emic (2012) regarded it as Titanosauriformes *incertae sedis* | 23 |
| *Xianshanosaurus* | Non-lithostrotian titanosaurian | Lü *et al.* (2009a) referred it to Neosauropoda, Mannion & Calvo (2011) suggested possible titanosaurian affinities, and D'Emic (2012) regarded it as a lithostrotian | 13 |

The phylogenetic definitions of higher taxa are given in Table 6.
Taxa marked by an asterisk are unstable in one or both sets of most parsimonious trees (MPTs; i.e. they were pruned from the MPTs to create the agreement subtrees).
When the results of the *Lusotitan* standard discrete matrix (LSDM) and *Lusotitan* continuous + discrete matrix (LCDM conflicted, the taxon was assigned to the least inclusive clade agreed upon by both analyses and is marked *incertae sedis*.
Results from the LSDM with implied weights ($LSDM_{iw}$) are only mentioned when they differ from both the LSDM and LCDM.
The percentage of characters scored for each ingroup taxon is provided (rounded to the nearest whole number), based on the character completeness metric (CCM) of Mannion & Upchurch (2010b).

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*Bothriospondylus*' is also positioned as a brachiosaurid, supporting previous proposals (Lapparent, 1943; McIntosh, 1990; Upchurch, 1995; Wilson, 2002; Mannion, 2010). Whereas it is placed as a basal brachiosaurid in our LSDM, it occupies a much more derived position in the LCDM. A basal position would be in keeping with its stratigraphical age, but could relate to the immature age of the individual, with derived features yet to develop (see also Tidwell & Wilhite, 2005 and Carballido *et al*., 2012 regarding the impact of ontogeny on character states in other brachiosaurid specimens). Our scoring of this taxon was based mainly on the brief description and figures provided in Lapparent (1943), and it is in need of first-hand study and revision. *Cedarosaurus* and *Venenosaurus* are both known from the late Early Cretaceous of North America (Tidwell *et al*., 1999; Tidwell, Carpenter & Meyer, 2001). *Cedarosaurus* has been recovered as a brachiosaurid in most previous studies (e.g. Tidwell *et al*., 1999; Upchurch *et al*., 2004a; Ksepka & Norell, 2010; D'Emic, 2012, 2013), but as a basal somphospondylan in Rose (2007), a basal titanosaur in Canudo *et al*. (2008), and a non-titanosauriform macronarian in Royo-Torres (2009). Rose (2007) and Canudo *et al*. (2008) recovered *Venenosaurus* as a non-titanosaurian somphospondylan, whereas the analysis of D'Emic (2012, 2013) placed it within Brachiosauridae (see also Wilson, 2002: table 13), and Upchurch *et al*. (2004a) suggested titanosaurian affinities. In contrast to all of these studies, Royo-Torres (2009) and Carballido *et al*. (2011a) recovered *Venenosaurus* as a non-titanosauriform macronarian. Here, we recovered both *Cedarosaurus* and *Venenosaurus* as brachiosaurids in all our analyses.

No other taxa were recovered as brachiosaurids in our LSDM analysis; however *Sonorasaurus* was placed within this clade in our $LSDM_{iw}$ and LCDM, whereas it was recovered as a basal somphospondylan in our LSDM. This middle Cretaceous North American taxon is known from fragmentary, deformed material and has only received a brief description (Ratkevich, 1998; Curtice, 2000), meaning that we were able to code it for just 11% of characters. Previously described as a brachiosaurid (Ratkevich, 1998; see also D'Emic, 2012), *Sonorasaurus* awaits revision to fully determine its affinities, but based on the current analysis it appears to represent a titanosauriform, contrasting with a basal macronarian placement in its only previous inclusion in a phylogenetic analysis (Royo-Torres, 2009).

### Note on the taxonomy of *Brachiosaurus*

Riggs (1903) erected *Brachiosaurus altithorax* for a partial skeleton from the Late Jurassic Morrison Formation of North America. A second species, from the contemporaneous Tendaguru Formation of Tanzania, was named *Brachiosaurus brancai* (Janensch, 1914). *Brachiosaurus atalaiensis* was named for Late Jurassic Portuguese material by Lapparent & Zbyszewski (1957), and Lapparent (1960: 40–42, and pl. 2, 3, 8, 10) erected a fourth species (*Brachiosaurus nougaredi*) based on material from Zarzaïtine, in eastern Algeria, close to the Libyan border. This locality is from the Upper Jurassic Taouratine Series (Lapparent, 1960; see also Buffetaut *et al*., 2006), and not the middle Cretaceous 'Continental Intercalaire', as has been mistakenly reported in some instances (e.g. Upchurch *et al*., 2004a).

'*Brachiosaurus nougaredi*' has received little attention since its original description, with Upchurch *et al*. (2004a) suggesting that it is probably not referable to *Brachiosaurus*. Antunes & Mateus (2003) removed '*Brachiosaurus atalaiensis*' from *Brachiosaurus* and renamed it *Lusotitan*, a decision that seems to have been subsequently accepted in the literature and has been supported here through its first inclusion in a phylogenetic analysis. More recently, Taylor (2009) demonstrated numerous anatomical differences between *Brachiosaurus altithorax* and *Brachiosaurus brancai* and argued for their generic separation, proposing the new binomial *Giraffatitan brancai* for the African taxon (see also Paul, 1988). However, subsequent authors have argued against this separation based on the sister-taxon relationship of the two species recovered in Taylor's (2009) phylogenetic analysis (Chure *et al*., 2010; Whitlock, 2011a). As noted above, our analyses support the generic separation of the North American taxon *Brachiosaurus altithorax* and the African form *Giraffatitan brancai*, as proposed by Taylor (2009; see also Salgado & Calvo, 1997; D'Emic, 2012, 2013). To retain *Giraffatitan* as a species of *Brachiosaurus* would require the synonymization of several other brachiosaurid genera with *Brachiosaurus* (e.g. *Abydosaurus* and *Cedarosaurus*), a proposal that we consider unrealistic because of the large stratigraphical and geographical ranges that such a taxon would have occupied, as well as the large morphological variation that such a taxon would have to encompass.

A number of North American remains have been referred to *Brachiosaurus* (see Taylor, 2009, for a review), although most of these referrals have been refuted (Taylor, 2009). Of those elements still potentially referable to *Brachiosaurus*, few actually augment our knowledge of the anatomy of this species, and the basis for referral of cervical vertebrae was their similarity to *Giraffatitan* (Wedel, Cifelli & Sanders, 2000b; Taylor, 2009), a reasoning no longer supported following the separation of these two genera within Brachiosauridae. Similarly, USNM 5730, a partial skull from the Morrison Formation,

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was previously described as '*Brachiosaurus* sp.' (Carpenter & Tidwell, 1998). The latter authors documented a number of differences between USNM 5730 and *Camarasaurus*, and also between this specimen and *Giraffatitan*, and described USNM 5730 as 'intermediate' between the two. The quarry that yielded USNM 5730 also contained the sauropods *Apatosaurus*, *Camarasaurus*, *Diplodocus*, and *Haplocanthosaurus*. Whereas the material clearly does not pertain to a diplodocid, the basis for referral to *Brachiosaurus* was on similarities with the skull of the Tanzanian species *Giraffatitan brancai*, not on the presence of overlapping material referable to *Brachiosaurus altithorax*; thus, it cannot currently be referred to *Brachiosaurus* and requires restudy to determine its taxonomic affinities. One possible exception is the juvenile individual known as 'Toni' (Schwarz *et al*., 2007) from the Morrison Formation. Originally described as a diplodocid (Schwarz *et al*., 2007), it was recently reinterpreted as a juvenile brachiosaurid, and considered probably referable to *Brachiosaurus*, although a number of potentially ontogenetic related differences preclude definite assignment to that taxon (Carballido *et al*., 2012). Therefore, currently we recommend restricting *Brachiosaurus altithorax* to its holotype. Similar problems might affect our understanding of *Giraffatitan*, with numerous remains referred to this taxon without autapomorphy-based evidence. This is potentially reflected in two instances of polymorphic character coding in our analyses (C159 and C215), which might merely represent individual or sexual variation, but could also indicate the presence of more than one taxon amongst the remains attributed to *Giraffatitan*. A revision of the Tendaguru material is required to determine this issue, based on a revised diagnosis of the *Giraffatitan* lectotype, with additional material only referred if bearing corresponding autapomorphies.

The fourth '*Brachiosaurus*' species, '*Brachiosaurus nougaredi*', is based on a sacrum, parts of a forelimb (the distal ends of an ulna and radius, a carpal, three metacarpals and a phalanx), a tibia, and some partial metatarsals (Lapparent, 1960). However, these separate regions of the skeleton were not recovered in association: the forelimb was found 'several hundred metres' east of the sacrum, the tibia was found 800 m west of the sacrum, and the metatarsals were found somewhere in between the sacrum and tibia (Lapparent, 1960). As such, there is no reason to expect that they belong to the same individual or even taxon. Most of the sacrum and the elements of the metacarpus were apparently recovered; however, the ulna, radius, and carpal were considered too fragile to collect (Lapparent, 1960). It is unclear whether the tibia and metatarsals were collected, but currently only the third metacarpal can be located in the MNHN collections. Little anatomical information regarding the missing and uncollected elements can be gleaned from Lapparent (1960), with the exception of the sacrum. Lapparent (1960: 40; translated from the original French by M. T. Carrano) wrote: 'Such as could be removed and reconstructed, this sauropod sacrum presents an exceptional size: total length = 130 cm; diameter = 80 cm. The sacral vertebrae number four, fused together. The first offers an enormous anterior disc, 23 cm wide and 22 cm tall. The third sacral is 28 cm long and has a disc diameter of 20 cm; the keel is very marked on the ventral part, and the diameter of the centrum in the middle is only 10 cm. The zygapophyses have wide and strongly twisted stalks; they are extended up to 40 cm to the right and left of the neural canal; at their end, they are widened in the shape of a powerful club and are solidly fused together there'. Based on contemporaneous sauropods, this animal most likely possessed a fifth sacral vertebra; however, even without the addition of this extra sacral, the '*Brachiosaurus nougaredi*' sacrum would have been longer (1300 mm) than nearly all other known sauropod sacra (including taxa with five and six sacral vertebrae), with the exception of the five sacrals comprising the type of *Apatosaurus louisae* [total length = 1325 mm (Gilmore, 1936)] and *Argentinosaurus* [total length of five preserved sacral vertebrae = 1350 mm: MCF-PVPH-1 (P. D. Mannion, pers. observ., 2009)]. As such, assuming the measurement in Lapparent (1960) is at least approximately accurate, this '*Brachiosaurus nougaredi*' individual must clearly have been one of the largest bodied sauropods yet known. Pending its rediscovery in the MNHN collections, we consider this sacrum to represent an indeterminate sauropod.

The left metacarpal III of '*Brachiosaurus nougaredi*' is here described orientated in a horizontal plane, with the anteriorly facing surface in life treated as the dorsal surface. It is nearly complete (see Fig. 29 and Table 8 for measurements), although it is poorly preserved at its proximal end, with the lateral, medial, and ventral margins all weathered. Based on its current state, the proximal end probably had a subrectangular or trapezoidal outline, with a longer lateromedial than dorsoventral axis. Both proximal and distal articular surfaces are strongly rugose. The lateral and medial surfaces of the proximal end are concave, but it is not possible to determine whether this is a genuine feature or the product of weathering. Along its proximal third, the dorsal surface of the metacarpal is mildly concave transversely; it is transversely convex along the middle third and flat distally (Fig. 29A). Excluding the proximal third (which is either flat or too damaged to ascertain its morphology), the ventral surface is transversely concave along most of the metacarpal,

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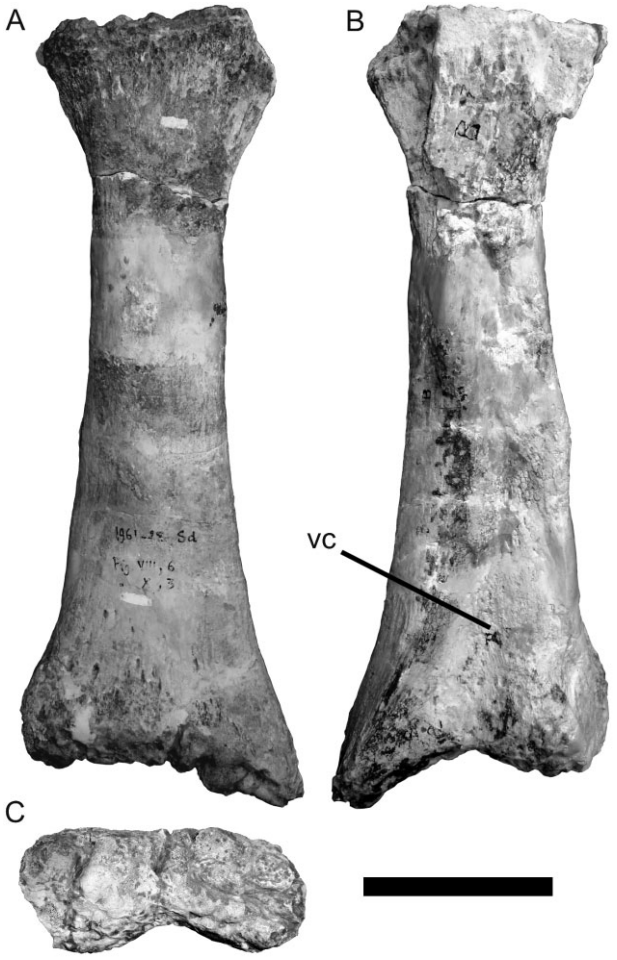


**Figure 29.** '*Brachiosaurus nougaredi*'. Photographs of metacarpal III (MNHN) in (A) dorsal, (B) ventral, and (C) proximal views. Abbreviation: vc, ventral concavity. Scale bar = 100 mm.

**Table 8.** Measurements of the third metacarpal of '*Brachiosaurus nougaredi*' (MNHN)

| Measurement | |
|---|---|
| Proximodistal length | 427 |
| Maximum mediolateral width of proximal end | 123 |
| Maximum dorsoventral height of proximal end | 88 |
| Mediolateral width at midshaft | 76 |
| Dorsoventral height at midshaft | 58 |
| Maximum mediolateral width of distal end | 160 |
| Maximum dorsoventral height of distal end | 81 |

Measurements are in millimetres.

with this concavity bounded by lateroventral and medioventral ridges (Fig. 30B); this concavity deepens close to the distal end. A similar morphology is also present in the middle metacarpals of the Argentinean

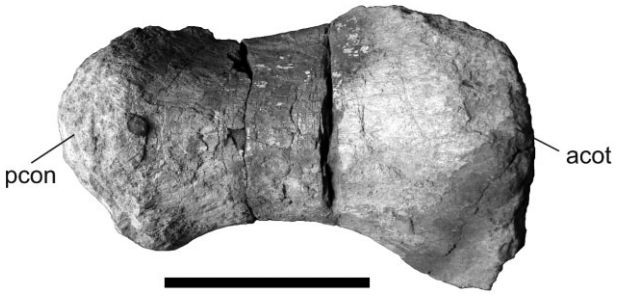


**Figure 30.** Titanosauriformes indet. Photograph of middle caudal centrum (MG 4799) in right lateral view. Abbreviations: acot, anterior cotyle; pcon, posterior condyle. Scale bar = 100 mm.

titanosaur *Argyrosaurus* (Mannion & Otero, 2012), but the distribution of this feature is currently unclear within Sauropoda. However, this feature is absent in the metacarpals of *Giraffatitan* (e.g. HMN MBR 2249: P. D. Mannion, pers. observ., 2011), which suggests that '*Brachiosaurus nougaredi*' is distinct from the Tanzanian species. At its distal end, the metacarpal expands transversely, especially on the lateral margin. The distal end is clearly more expanded transversely than the proximal end, even taking into account the damage to the latter. The distal articular surface is dorsoventrally convex, curving down onto the ventral surface, and is transversely concave (Fig. 29C). The lack of expansion of this distal end onto the dorsal surface is a synapomorphy of Titanosauriformes (D'Emic, 2012; this study); as such, the '*Brachiosaurus nougaredi*' metacarpal should currently be regarded as belonging to an indeterminate member of this clade.

*Somphospondyli*

Somphospondyli is defined as the most inclusive clade that includes *Saltasaurus loricatus* but excludes *Brachiosaurus altithorax* (Wilson & Sereno, 1998; Upchurch *et al*., 2004a), and within this Titanosauria is defined as the least inclusive clade that includes *Andesaurus delgadoi* and *Saltasaurus loricatus* (Wilson & Upchurch, 2003) (see Table 6). Our analyses produced notably different topologies for Somphospondyli: whereas our LSDM recovered a large paraphyletic array of basal somphospondylans leading to a relatively 'traditional' Titanosauria, the $LSDM_{iw}$ and LCDM resulted in either one or zero basal somphospondylans, respectively, and an extremely diverse Titanosauria. In our $LSDM_{iw}$ and LCDM, Titanosauria is composed of an 'andesauroid' clade that is the sister taxon to a clade of titanosaurs containing Lithostrotia (the least inclusive clade containing *Malawisaurus dixeyi* and *Saltasaurus loricatus*; Wilson & Upchurch, 2003; Upchurch *et al*.,

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2004a). This split at the base of Titanosauria into an andesauroid and derived titanosaur clade has only previously been recovered in the analyses of Canudo *et al*. (2008) and Carballido *et al*. (2011b). 'Andesauridae' was originally erected as a family comprising *Andesaurus*, *Argentinosaurus*, and *Epachthosaurus* (Bonaparte & Coria, 1993), but all subsequent phylogenetic analyses have recovered this assemblage as paraphyletic (e.g. Salgado *et al*., 1997; Sanz *et al*., 1999; Curry Rogers, 2005; Calvo *et al*., 2007), and several authors have recommended the disuse of this name (Salgado *et al*., 1997; Salgado, 2003; Wilson & Upchurch, 2003; Mannion & Calvo, 2011). Following our recovery of a clade containing *Andesaurus* and other taxa, we refer to this as Andesauroidea, following Salgado (2003; see Table 6 for the phylogenetic definition). The sister clade to Andesauroidea in our analysis would traditionally be called Titanosauroidea (Upchurch, 1995; Salgado, 2003); however, *Titanosaurus* is indeterminate and thus its co-ordinated rank-taxa must be abandoned (Wilson & Upchurch, 2003). As a result of *Andesaurus* being recovered as the sole representative of Andesauroidea in our LSDM, we refrain from providing a new name for it sister clade, referring to it as 'Titanosauroidea'.

*Dongbeititan* was placed as the basal-most member of Somphospondyli in our LSDM, but as a non-titanosauriform macronarian in our LCDM. Wang *et al*. (2007) described *Dongbeititan*, from the Barremian of China, as a non-titanosaurian somphospondylan, Mannion & Calvo (2011) noted possible titanosaurian affinities, and D'Emic (2012) indicated a placement within Somphospondyli. Its variable position here might reflect the highly deformed nature of the material (R. N. Barnes, pers. observ., 2011).

The LSDM recovered a euhelopodid clade of East Asian basal somphospondylans, forming a sister clade with all other somphospondylans. Euhelopodidae (see Table 6 for phylogenetic definition) comprises five (*Erketu*, *Euhelopus*, *Phuwiangosaurus*, *Qiaowanlong*, and *Tangvayosaurus*) of the six taxa recovered in this clade by D'Emic (2012), as well as two additional taxa not included in the latter analysis (*Gobititan* and *Liubangosaurus*). Our composition primarily differs in that *Daxiatitan* was recovered as a derived titanosaur in the LSDM. However, our $LSDM_{iw}$ and LCDM produced notably different results in the placements of these taxa: all were recovered in the titanosauroid clade, but form a paraphyletic array, rather than a monophyletic clade.

*Liubangosaurus* was recovered as the basal-most euhelopodid in our LSDM, but as a saltasaurid in our $LSDM_{iw}$ and LCDM. Known from five middle-posterior dorsal vertebrae from the Early Cretaceous of China, *Liubangosaurus* was described as a basal eusauropod by Mo, Xu & Buffetaut (2010), recovered in a polytomy with Macronaria and Diplodocoidea at the base of Neosauropoda. If correctly identified, the presence of such a basal taxon would be highly unusual: the Cretaceous sauropod fauna of China is otherwise entirely composed of titanosauriforms (Wilson, 2005a; Wilson & Upchurch, 2009), or at least derived macronarians (based on the placement of *Dongbeititan*: see above). A putative diplodocid (Upchurch & Mannion, 2009) might represent an additional non-titanosauriform presence in the Cretaceous of China, although Whitlock, D'Emic & Wilson (2011) have argued for a probable titanosauriform identification of this specimen. With the exception of Spanish occurrences whose stratigraphical age cannot be constrained more precisely than Tithonian–middle Berriasian (e.g. Royo-Torres *et al*., 2006), there is no other evidence for the survival of non-neosauropods across the Jurassic/Cretaceous (J/K) boundary in any part of the world (Mannion *et al*., 2011b). This is consistent with the results from both of our analyses, which suggest that *Liubangosaurus* is a somphospondylan, rather than a late surviving Cretaceous non-neosauropod as proposed by Mo *et al*. (2010).

The phylogenetic affinity of the Chinese taxon *Euhelopus* has a complex history, with the most recent thorough treatment regarding it as a basal somphospondylan (Wilson & Upchurch, 2009), although it was placed as a basal macronarian by Royo-Torres (2009) and Carballido *et al*. (2011b). Its role as a clade specifier for Euhelopodidae (D'Emic, 2012) makes it a member of this clade by default, but in our $LSDM_{iw}$ and LCDM, *Daxiatitan* is the only other euhelopodid. *Daxiatitan* is an Early Cretaceous Chinese taxon that was recovered as a somphospondylan or basal titanosaur by You *et al*. (2008). However, the exclusion of *Andesaurus* from this, and many other analyses (e.g. Wilson, 2002; Suteethorn *et al*., 2010; Zaher *et al*., 2011), despite its importance as a clade specifier for Titanosauria (see above and Table 6), means that the placement of the titanosaurian node has often been arbitrarily determined. Here we found support for a slightly more derived placement within Titanosauria. *Erketu*, from the early Late Cretaceous of Mongolia [Ksepka & Norell, 2006, 2010 (see the latter reference regarding this younger age, rather than the Early Cretaceous age originally proposed)] has previously been included in three phylogenetic analyses, in which it was recovered as a non-titanosaurian somphospondylan (Ksepka & Norell, 2006, 2010), and an euhelopodid (D'Emic, 2012). Whereas it was recovered as the sister taxon to *Euhelopus* in our LSDM, *Erketu* was placed as a derived titanosauroid in our $LSDM_{iw}$ and LCDM, forming a clade with *Mongolosaurus* + *Rapetosaurus*.

The Early Cretaceous Chinese taxon *Qiaowanlong* was originally described as a brachiosaurid by You &

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Li (2009), but was recovered as a basal somphospondylan in the analysis of Ksepka & Norell (2010), with these authors demonstrating the wider distribution of the features used by You & Li (2009) to support a brachiosaurid position (see also Mannion, 2011). Here, *Qiaowanlong* formed a sister-taxon relationship with *Phuwiangosaurus* in our $LSDM_{iw}$ and LCDM, rather than clustering with *Erketu* + *Euhelopus* as in our LSDM. The Thai taxon *Phuwiangosaurus* has been regarded as either a basal titanosaur (e.g. Upchurch, 1998; Curry Rogers, 2005; Canudo *et al*., 2008; Carballido *et al*., 2011a; Zaher *et al*., 2011) or non-titanosaurian somphospondylan (although see earlier discussion regarding the exclusion of *Andesaurus* from many analyses) in nearly all previous analyses (e.g. Rose, 2007; González Riga *et al*., 2009; Wilson & Upchurch, 2009; Suteethorn *et al*., 2010; Carballido *et al*., 2011b; D'Emic, 2012, 2013). Royo-Torres (2009) provided the only strongly contrasting viewpoint, recovering *Phuwiangosaurus* as a brachiosaurid, but its somphospondylan affinities appear secure.

*Tangvayosaurus*, from the Aptian–Albian of Laos, was originally described as a basal titanosaur, although Allain *et al*. (1999: 610) noted that this was only supported by one feature ('pubis significantly longer than ischium'). A basal titanosaurian position was also supported in the analysis of Zaher *et al*. (2011; although see above regarding the exclusion of *Andesaurus*). Several authors have listed *Tangvayosaurus* as a non-titanosaurian titanosauriform (e.g. Wilson, 2005a; Wilson & Upchurch, 2009; Mannion & Calvo, 2011), whereas Royo-Torres (2009) placed it as the sister taxon to Titanosauriformes, and Suteethorn *et al*. (2010) recovered it as a non-titanosaurian somphospondylan. Here, *Tangvayosaurus* was placed as the sister taxon to *Fusuisaurus* [forming a clade with *Gobititan* + '*Huanghetitan*' *ruyangensis* (see below)] in our $LSDM_{iw}$ and LCDM, rather than as the sister taxon to *Phuwiangosaurus* as in our LSDM (see also D'Emic, 2012). You *et al*. (2003) described *Gobititan*, from the Albian of China, as a basal titanosaur, but this position has been doubted by several subsequent workers, who have suggested a more basal position within Titanosauriformes (Wilson & Upchurch, 2009; Mannion & Calvo, 2011; Mannion & Otero, 2012), including listing it as a somphospondylan (D'Emic, 2012). Euhelopodid or titanosauroid affinities are supported based on our analyses. The Early Cretaceous Chinese taxon *Fusuisaurus* was considered a titanosauriform of uncertain affinities by Mo *et al*. (2006) and according to our LSDM (see above). This instability most likely relates to the incompleteness and brief description of the specimen [character completeness metric (CCM) = 9%; Mannion & Upchurch, 2010b], and we regard it as a titanosauriform of uncertain placement, with probable somphospondylan affinities based on our $LSDM_{iw}$ and LCDM.

The late Early Cretaceous North American genus *Brontomerus* (Taylor, Wedel & Cifelli, 2011) was recovered as the most basal member of the non-euhelopodid somphospondylan clade in our LSDM, and occupies a similar position within the titanosauroid clade of our $LSDM_{iw}$ and LCDM. *Brontomerus* was described by Taylor *et al*. (2011) as a camarasauromorph (i.e. basal macronarian), with some evidence for a somphospondylan position, as supported here, although D'Emic (2012) regarded it as an indeterminate titanosauriform. *Astrophocaudia* was recovered as the sister taxon to *Brontomerus* in our $LSDM_{iw}$ and LCDM, and as a basal somphospondylan in our LSDM. *Astrophocaudia* is known from the early Albian of North America (Langston, 1974; D'Emic, 2013) and has been regarded as either a brachiosaurid or titanosaur by previous workers (see D'Emic, 2013, for a review). However, a recent revision of this material and its first incorporation into a phylogenetic analysis (D'Emic, 2013) positioned it as a non-titanosaurian somphospondylan. Thus, it seems that the somphospondylan affinities of *Brontomerus* and *Astrophocaudia* are secure, but their exact placement within this clade cannot currently be ascertained.

Our LSDM recovered a basal somphospondylan clade comprising ((*Sonorosaurus* + *Tastavinsaurus*) + (*Diamantinasaurus* + '*Pelorosaurus*' *becklesii*)), whereas none of these taxa clustered together in our other analyses. In our $LSDM_{iw}$ and LCDM, *Sonorosaurus* is regarded as a brachiosaurid (see above), and *Tastavinsaurus* is recovered as a derived andesauroid. *Tastavinsaurus* is known from two individuals from the early Aptian of Spain (Canudo *et al*., 2008; Royo-Torres, 2009; Royo-Torres *et al*., 2012). Originally recovered as a non-titanosaurian somphospondylan (Canudo *et al*., 2008; see also D'Emic, 2012), the analyses of Carballido *et al*. (2011a, b) placed it as a non-titanosauriform macronarian. Royo-Torres *et al*. (2012) recovered it as the sister taxon to *Cedarosaurus* in all of their analyses, forming a clade with *Venenosaurus* that these authors called Laurasiformes (see also Royo-Torres, 2009, who found *Aragosaurus* and *Sonorasaurus* to be additional members of this clade). However, the position of Laurasiformes varied in Royo-Torres *et al*. (2012), being recovered as a basal somphospondylan clade in the analyses based on the data matrix of Wilson (2002), and as a brachiosaurid clade in those based on Upchurch *et al*. (2004a), whereas in Royo-Torres (2009) this clade was placed outside Titanosauriformes. Here, we found no evidence to support the monophyletic clustering of these taxa as Laurasiformes (see also D'Emic, 2012): *Tastavinsaurus* is a somphospondylan, *Cedarosaurus* and *Venenosaurus* are brachiosaurids (see above),

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*Sonorasaurus* might represent a brachiosaurid or somphospondylan (see above), and *Aragosaurus* is placed outside Titanosauriformes (see below). The $LSDM_{iw}$ placed '*Pelorosaurus*' *becklesii* within the titanosauroid clade, whereas the LCDM analysis recovered it as a basal member of Andesauroidea. This taxon is known from an upper forelimb and skin impression from the Berriasian–Valanginian of England. It has a complicated taxonomic history (Taylor & Naish, 2007; Upchurch, Mannion & Barrett, 2011b), but has been regarded as a basal titanosaur by some authors (Upchurch, 1995; Upchurch *et al*., 2004a, 2011b; Mannion & Calvo, 2011). Although known only from limited material, '*Pelorosaurus*' *becklesii* represents a distinct and diagnostic somphospondylan, requiring a new generic name (Upchurch *et al*., 2011b), although its titanosaurian affinities cannot currently be confirmed (see also D'Emic, 2012). *Diamantinasaurus*, from the early Late Cretaceous of Australia (Hocknull *et al*., 2009; see Tucker *et al*., 2013, regarding this younger age, rather than the late Albian age traditionally ascribed to the Winton Formation), has previously been recovered as a lithostrotian by Hocknull *et al*., (2009) and Zaher *et al*. (2011). It was placed as the sister taxon to Lithostrotia in our $LSDM_{iw}$ and LCDM analyses.

The late Early Cretaceous North American taxa *Sauroposeidon* and *Paluxysaurus* were both originally described as brachiosaurids (Wedel *et al*., 2000a, b; Rose, 2007), with this position supported in subsequent analyses incorporating *Paluxysaurus* (Ksepka & Norell, 2010; Carballido *et al*., 2011b). However, D'Emic (2013) referred *Paluxysaurus* to *Sauroposeidon* and recovered this combined OTU close to the base of Somphospondyli (see also D'Emic, 2012). The two were recovered as sister taxa in all of our analyses, supporting D'Emic's synonymization, although they were recovered as basal somphospondylans in our LSDM (albeit in a more derived position than in D'Emic, 2012), and andesauroids in our $LSDM_{iw}$ and LCDM. The contemporaneous 'Cloverly titanosauriform' has not previously been included in an analysis by itself, but was originally described as a titanosaur by Ostrom (1970) and referred to *Sauroposeidon* by D'Emic & Foreman (2012). In our LSDM the 'Cloverly titanosauriform' was recovered in a trichotomy with *Sauroposeidon* + *Paluxysaurus* and a clade leading to Titanosauria, whereas it was placed as a distantly related andesauroid in the $LSDM_{iw}$ and LCDM analyses. As such, we find only equivocal support for its referral to *Sauroposeidon*.

*Wintonotitan*, from the early Late Cretaceous of Australia has previously been recovered as a non-titanosaurian somphospondylan (Hocknull *et al*., 2009; Carballido *et al*., 2011a), a non-titanosauriform macronarian (Carballido *et al*., 2011b), and as a basal titanosaur [as *Austrosaurus* (Upchurch *et al*., 2004a) – see below]. Hocknull *et al*. (2009) also noted several morphological features (not included in their phylogenetic analysis) that might indicate a position within Titanosauria. The early Late Cretaceous Chinese sauropod *Ruyangosaurus* was originally described as a basal titanosaur ('Andesauridae') by Lü *et al*. (2009b), but Mannion & Calvo (2011) argued that it showed no clear titanosaurian features and should be considered a non-titanosaurian somphospondylan. In our LSDM, *Wintonotitan* and *Ruyangosaurus* form a clade of derived non-titanosaurian somphospondylans, whereas they are andesauroids in our $LSDM_{iw}$ and LCDM results.

*Huanghetitan liujiaxiaensis*, from the Early Cretaceous of China, was recovered as a non-titanosaurian somphospondylan by You *et al*. (2006) and Hocknull *et al*. (2009). '*Huanghetitan*' *ruyangensis* is an early Late Cretaceous Chinese taxon described as a second species of *Huanghetitan*, with Huanghetitanidae erected as a monogeneric family (Lü *et al*., 2007). However, we found that the two *Huanghetitan* species did not cluster together in our analyses: they are successive outgroups to Titanosauria in our LSDM, whereas in our $LSDM_{iw}$ and LCDM the type species is an andesauroid and the referred species a titanosauroid. As such, we do not support the monophyly of Huanghetitanidae and, pending revision of the two species, suggest that the diagnostic '*Huanghetitan*' *ruyangensis* (Henan Geological Museum specimen 41HIII-0001: P. D. Mannion & P. Upchurch, pers. observ., 2012) is in need of a new generic name.

In our $LSDM_{iw}$ and LCDM analyses, several taxa not yet mentioned were recovered within the andesauroid clade. The Turonian-aged African genus *Angolatitan* was recovered as a basal somphospondylan in its only previous inclusion in a phylogenetic analysis (Mateus *et al*., 2011), although D'Emic (2012) suggested lithostrotian affinities. Our LSDM supports the non-titanosaurian somphospondylan placement of Mateus *et al*. (2011), whereas it was recovered as an andesauroid in our other analyses. Although the middle Cretaceous Argentinean genus *Chubutisaurus* was included within Brachiosauridae by McIntosh (1990), it has been recovered as a non-titanosaurian somphospondylan by most other authors, usually closely related to the titanosaur radiation (Salgado *et al*., 1997; Bonaparte *et al*., 2006; Calvo *et al*., 2007; González Riga *et al*., 2009; Carballido *et al*., 2011a; D'Emic, 2012), but was placed outside Titanosauriformes by Carballido *et al*. (2011b). In all our analyses, *Chubutisaurus* clusters closely with *Angolatitan*. The Late Cretaceous Chinese taxon *Baotianmansaurus* was originally described as a titanosauriform with probable somphospondylan affinities by Zhang *et al*.

(2009), and D'Emic (2012) indicated euhelopodid affinities. In its first incorporation into a phylogenetic analysis, *Baotianmansaurus* was recovered as a titanosaur in all analyses: in our LSDM it was placed within Saltasauridae, as the sister taxon to *Opisthocoelicaudia*, whereas it was recovered as an andesauroid in our $LSDM_{iw}$ and LCDM. *Ligabuesaurus*, from the Aptian–Albian of Argentina (Bonaparte *et al*., 2006), was recovered in a trichotomy with the middle Cretaceous Argentinean taxon *Andesaurus* (Calvo & Bonaparte, 1991; Mannion & Calvo, 2011) and a clade comprising all other titanosaurs in our LSDM, and was recovered as the sister taxon of *Andesaurus* in our $LSDM_{iw}$ and LCDM analyses, in a deeply nested position within the andesauroid clade. *Ligabuesaurus* has been recovered as a non-titanosaurian somphospondylan by most authors (Bonaparte *et al*., 2006; González Riga *et al*., 2009; Carballido *et al*., 2011a), and was placed as the most basal member of this clade in the analysis of D'Emic (2012). However, Carballido *et al*. (2011b) found it to form a clade with *Andesaurus*, a position partly supported here.

*Australodocus* was recovered as a titanosaur in all of our analyses, forming a polytomy with titanosaurs more derived than *Andesaurus* in our LSDM, and placed as a basal titanosauroid in our $LSDM_{iw}$ and LCDM. This Tithonian-aged taxon from the Tendaguru Formation of Tanzania was originally described as a new genus of diplodocid (Remes, 2007), but revision by Whitlock (2011a) demonstrated its titanosauriform affinities (see also D'Emic, 2012), a position supported by phylogenetic analysis (Whitlock, 2011a, b; Mannion *et al*., 2012). These previous analyses were focused on the inter-relationships of diplodocoids and thus *Brachiosaurus* (a composite OTU of *Brachiosaurus* and *Giraffatitan*) and *Sauroposeidon* (Whitlock, 2011a) were the only other titanosauriforms included, limiting further determination of the position of *Australodocus*. However, Whitlock (2011a) recovered a clade of *Australodocus* + *Brachiosaurus*, to the exclusion of *Sauroposeidon*, indicating a closer relationship with Brachiosauridae for *Australodocus*. The recovered position in our analyses demonstrates the spatiotemporally contemporaneous existence of both brachiosaurids (i.e. *Giraffatitan*) and somphospondylans in the Tendaguru Formation, and provides the earliest body fossil evidence for titanosaurs (see 'Jurassic titanosaurs?' below).

*Fukuititan*, from the Barremian of Japan, was regarded as a titanosauriform of uncertain affinities by Azuma & Shibata (2010), and in our LSDM. In our $LSDM_{iw}$ and LCDM it was recovered as a basal titanosauroid. This taxon shares one potentially unusual feature with the putative titanosaur *Borealosaurus* from the Late Cretaceous of China (You *et al*., 2004): both species possess opisthocoelous middle-posterior caudal centra. Future studies incorporating both taxa should assess whether this feature is a synapomorphy or convergently acquired, with the latter presumably the case in the non-neosauropod eusauropod *Turiasaurus* from the latest Jurassic–earliest Cretaceous of Spain (Royo-Torres *et al*., 2006).

*Malarguesaurus*, from the early Late Cretaceous of Argentina (González Riga *et al*., 2009) was placed in a basal position within Titanosauria by Carballido *et al*. (2011a), whereas González Riga *et al*. (2009) recovered *Malarguesaurus* as a non-titanosaurian somphospondylan. D'Emic (2012) listed it as a macronarian. Here it was recovered as a non-titanosaurian somphospondylan of uncertain affinities in our LSDM, but as a titanosauroid in our other analyses.

All remaining taxa were recovered within Titanosauria in all analyses, and we do not discuss in detail the positions of the 'higher titanosaurs' (i.e. *Alamosaurus*, *Malawisaurus*, *Opisthocoelicaudia*, *Rapetosaurus*, and *Saltasaurus*) because they are not the focus of this study. *Xianshanosaurus* is known from the early Late Cretaceous of China and was considered a neosauropod of uncertain affinities by Lü *et al*. (2009a). Mannion & Calvo (2011) suggested possible titanosaurian affinities, and a lithostrotian identification was postulated by D'Emic (2012). *Xianshanosaurus* + *Daxiatitan* (see above) is the sister clade to Lithostrotia in our LSDM, and the former taxon forms a trichotomy with *Diamantinasaurus* (see above) and Lithostrotia in our $LSDM_{iw}$ and LCDM. In our LSDM trees, Lithostrotia is composed of two clades: Saltasauridae, and a clade of *Malawisaurus* + (*Mongolosaurus* + *Rapetosaurus*). However, *Mongolosaurus* + *Rapetosaurus* was recovered outside of Lithostrotia in our $LSDM_{iw}$ and LCDM analyses. *Mongolosaurus*, from the Aptian–Albian of China, has been considered as a diplodocid, euhelopodid, and titanosaur in the past (see Barrett *et al*., 2002; Mannion, 2011; D'Emic, 2012), although its only prior inclusion in a phylogenetic analysis demonstrated probable titanosaurian affinities, with a possible derived position (Mannion, 2011; see also Wilson, 2005a), as supported here.

In all our analyses, *Saltasaurus* + (*Alamosaurus* + *Jiangshanosaurus*) formed a clade. *Jiangshanosaurus*, from the Albian of China, has previously been regarded as a titanosaur (Tang *et al*., 2001b; Upchurch *et al*., 2004a; Wilson, 2005a; Wilson & Upchurch, 2009), and D'Emic (2012) suggested saltasaurid affinities, but this is the first time that this has been tested and received support from phylogenetic analysis. Its position as the sister taxon to *Alamosaurus* has interesting biogeographical implications (see 'East Asian Cretaceous sauropods' below). The sister clade to this grouping includes *Opisthocoelicaudia* and *Dongyangosaurus* in all three analyses, with *Baotianmansaurus* (see above) and *Liubangosaurus* (see

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above) comprising the third member of this clade in our LSDM and $LSDM_{iw}$/LCDM analyses, respectively. The early Late Cretaceous Chinese taxon *Dongyangosaurus* was regarded as a titanosaur by Lü *et al*. (2008), and euhelopodid by D'Emic (2012), but this is its first inclusion in a phylogenetic analysis and the first time that a saltasaurid identification has been proposed.

*Non-titanosauriforms*

A number of taxa included in our analysis have previously been identified as titanosauriforms or macronarians, but are here recovered in more basal positions, either as non-titanosauriforms or placed outside Neosauropoda in all analyses. We discuss each of these taxa below.

HMN MB.R.2091.1–30 is a series of 30 articulated caudal vertebrae from the Tithonian Tendaguru Formation of Tanzania that was originally referred to *Janenschia* (see below) and considered a titanosaur by Janensch (1929), on the basis of the strong procoely of the first ten caudal vertebrae (see also Jacobs *et al*., 1993; Salgado & Calvo, 1997). Bonaparte *et al*. (2000) questioned its titanosaurian affinities (see also McIntosh, 1990) as a result of the wider distribution of caudal procoely in sauropods (see 'Implications for phylogenetic characters' below), and removed it from *Janenschia* based on the lack of overlapping elements. Royo-Torres & Cobos (2009) also suggested that it might represent a non-neosauropod turiasaur. Here, we recovered it as the sister taxon to *Mamenchisaurus* in all analyses (see Table 6 for the phylogenetic definition of Mamenchisauridae). Previous authors have found evidence for clustering of some Middle–Late Jurassic North African and European sauropod taxa with Chinese forms [*Atlasaurus* and *Jobaria* with *Bellusaurus* (Upchurch *et al*., 2004a); *Cetiosauriscus* and *Losillasaurus* with *Mamenchisaurus* and *Omeisaurus* (Rauhut *et al*., 2005; Harris, 2006; Nair & Salisbury, 2012); see also discussion of similarities between the Middle Jurassic North African genus *Spinophorosaurus* and Asian mamenchisaurids in Remes *et al*., 2009], although this is the first time that a taxon from the southern part of Africa has been linked with these Asian species. Most evidence indicates that East Asia was separated from the rest of Pangaea during the Late Jurassic (see Barrett *et al*., 2002; Upchurch, Hunn & Norman, 2002; and Wilson & Upchurch, 2009 for reviews and 'East Asian Cretaceous sauropods' below), which might indicate an earlier and more widespread diversification of mamenchisaurids prior to this geographical isolation. One caveat is that the focus of character and taxon sampling in this study was on basal titanosauriforms; thus, to test fully the position of HMN MB.R.2091.1–30, consideration of other non-neosauropods is required [e.g. *Jobaria* (Sereno *et al*., 1999), *Spinophorosaurus* (Remes *et al*., 2009), and turiasaurs (Royo-Torres *et al*., 2006)]. However, we note that at least one feature [an approximate 200% anteroposterior length increase of middle caudal neural spines from their base to their summit (C199)] appears to be uniquely shared by HMN MB.R.2091.1–30 and the mamenchisaurids *Mamenchisaurus* [*Mamenchisaurus hochuanensis* (Young & Zhao, 1972: pl. 3; IVPP type: P. Upchurch, pers. observ., 2010) and *Mamenchisaurus youngi* (Ouyang & Ye, 2002: pl. I5)] and *Chuanjiesaurus* (Sekiya, 2011: figs 32–35) amongst Sauropoda.

*Lapparentosaurus madagascariensis*, from the Bathonian (Middle Jurassic) of Madagascar, has a complex taxonomic history (Mannion, 2010). Originally described as '*Bothriospondylus madagascariensis*' by Lydekker (1895), with additional material referred by Thevenin (1907) and Ogier (1975), Bonaparte (1986) created the new combination *Lapparentosaurus madagascariensis* to include all of this material. However, in the same paper, Bonaparte (1986) also erected a new genus and species – *Lapparentosaurus madagascariensis* – with the material described by Ogier (1975) elected as the holotype. As such, the latter name is a homonym. Mannion (2010) demonstrated that the type material of '*Bothriospondylus madagascariensis*' represents a non-diagnostic non-neosauropod eusauropod, and thus Bonaparte's (1986) first usage of *Lapparentosaurus madagascariensis* (as a new combination) is a *nomen dubium*. Consequently, the name *Lapparentosaurus* is not available for the Ogier (1975) material and, following International Commission on Zoological Nomenclature (ICZN) rules, this taxon requires a new generic name. However, the name *Lapparentosaurus* has been associated solely with the Ogier (1975) material in subsequent taxonomic works (e.g. McIntosh, 1990; Upchurch, 1995, 1998; Upchurch *et al*., 2004a; Läng & Goussard, 2007; Mannion, 2010; this work), including the only previous inclusions of this taxon in cladistic analyses (Upchurch, 1998; Upchurch *et al*., 2004a). As such, we recommend submitting a case to the ICZN for the conservation of the name *Lapparentosaurus madagascariensis* in its current usage to assist nomenclatural stability (see the recent example of *Cetiosaurus*; Upchurch & Martin, 2003; Upchurch, Martin & Taylor, 2009), and we follow this proposal in the following discussion. Bonaparte (1986) placed *Lapparentosaurus* as a basal member of the Cetiosauridae, a family of non-neosauropod eusauropods, whereas McIntosh (1990) and Upchurch (1995) both suggested brachiosaurid affinities. In the first phylogenetic analysis to include *Lapparentosaurus*, Upchurch (1998) found support for a brachiosaurid position, although in an updated

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analysis its position was modified to Titanosauriformes *incertae sedis* (Upchurch *et al*., 2004a). Here, we found no evidence to support a placement within Titanosauriformes for *Lapparentosaurus*; instead, it was recovered as a non-neosauropod eusauropod in all analyses. Upchurch (1995) noted that the lack of lateral pneumatic fossae in the cervical and dorsal vertebrae might support the basal position proposed by Bonaparte (1986); however, the cervical centra do possess shallow lateral fossae (e.g. MNHN MAA 5, 13, 53, 90, and 172: P. D. Mannion, pers. observ., 2011), as is also the case in the anterior-most dorsal vertebra preserved (MNHN MAA 201: P. D. Mannion, pers. observ., 2011). One note of caution is that *Lapparentosaurus* is known only from juvenile material (Ogier, 1975), and Upchurch (1995) mentioned the possibility that some of these plesiomorphic features might instead reflect ontogeny. However, a partial skeleton of an adult (MNHN MAJ 289) found at a locality close to that of *Lapparentosaurus*, also displays a number of plesiomorphic features suggesting a non-titanosauriform position (Läng & Goussard, 2007). As with the juvenile material, the anterior-most dorsal vertebrae of this adult specimen possess a lateral pneumatic fossa, with this feature absent from more posterior dorsal centra (MNHN MAJ 289: P. D. Mannion, pers. observ., 2011). This shared characteristic, coupled with a lack of clear anatomical differences, provides tentative evidence that MNHN MAJ 289 might be referable to *Lapparentosaurus* (although see Läng & Goussard, 2007), and suggests that this is probably not an ontogenetic feature in the juvenile material. In conclusion, a non-neosauropod position for *Lapparentosaurus* appears to be well supported, but its exact placement will have to await future analyses focused on the inter-relationships of basal eusauropods.

*Atlasaurus*, from the Bathonian–Callovian (Middle Jurassic) of Morocco, was initially described as 'brachiosaurid-like' (Monbaron, Russell & Taquet, 1999); if this identification is correct, this would represent the oldest known member of Neosauropoda. However, the taxon was recovered as a non-titanosauriform macronarian by Upchurch *et al*. (2004a), and as a non-neosauropod eusauropod in all other analyses (Table 7), including all of our trees. Although its brachiosaurid affinities seem unlikely (see also D'Emic, 2012), *Atlasaurus* has received only a very brief description (Monbaron *et al*., 1999), and a revision of this taxon will be vital in determining its precise phylogenetic affinities.

*Tendaguria*, from the Tithonian-aged Tendaguru Formation of Tanzania, was regarded as Sauropoda *incertae sedis* by Bonaparte *et al*. (2000) and Upchurch *et al*. (2004a), with the former study erecting the monospecific family Tendaguriidae. McIntosh (1990) merely noted that the material comprising *Tendaguria* was unique (at the time the two holotypic dorsal vertebrae were assigned to *Janenschia*), and Mannion & Calvo (2011) suggested possible titanosaurian affinities. The only previous analysis to include *Tendaguria* recovered it as either a non-neosauropod or as a non-titanosauriform macronarian (Carballido *et al*., 2011b). All of our analyses placed *Tendaguria* outside of Macronaria: in our LSDM and LCDM it was recovered as the sister taxon to Neosauropoda, whereas it was placed as a basal diplodocoid in our $LSDM_{iw}$ analysis. Clearly, *Tendaguria* appears to be positioned close to the base of Neosauropoda: revision of the material, and its inclusion in a phylogenetic analysis focused on basal eusauropod relationships, should help to determine its exact placement.

*Janenschia* has a complex taxonomic history (Bonaparte *et al*., 2000), but has generally been regarded as a basal titanosaur by most workers, even after the exclusion of the referred tail sequence (HMN MB.R.2091.1–30 – see above) from the genus (e.g. Janensch, 1929; Upchurch, 1995; Wilson & Sereno, 1998; Upchurch *et al*., 2004a; Curry Rogers, 2005; Mannion & Calvo, 2011). Consequently, *Janenschia* has been considered to represent the earliest body fossil evidence for Titanosauria (Upchurch, 1995; Upchurch *et al*., 2004a). However, Bonaparte *et al*. (2000) disagreed with a titanosaurian position for *Janenschia*, and instead suggested close affinities with the basal macronarian *Camarasaurus*. Royo-Torres & Cobos (2009) also suggested that at least some of the material included in *Janenschia* might be referable to the non-neosauropod group Turiasauria, although this is yet to be tested through phylogenetic analysis. Carballido *et al*. (2011b) recovered *Janenschia* in a non-titanosauriform macronarian position, and D'Emic (2012) noted a lack of evidence supporting somphospondylan affinities. Here, we support the placement in the analysis of Carballido *et al*. (2011b), with *Janenschia* positioned at or close to the base of Macronaria, forming a sister-taxon relationship with *Tehuelchesaurus* in our LSDM and $LSDM_{iw}$. *Tehuelchesaurus*, from the Late Jurassic of Argentina (Rich *et al*., 1999; Rauhut *et al*., 2005), was initially regarded as a cetiosaurid by Rich *et al*. (1999), and a non-neosauropod eusauropod position was supported by the analysis of Upchurch *et al*. (2004a). However, Rauhut *et al*. (2005) recovered it in a polytomy with other macronarians, and the analyses of Carballido *et al*. (2011a, b) and D'Emic (2012) agree with a non-titanosauriform macronarian placement.

*Aragosaurus*, from the Early Cretaceous of Spain (Sanz *et al*., 1987), was placed as a non-titanosauriform macronarian in all our analyses. Sanz *et al*. (1987) regarded it as a 'camarasaurid', and Upchurch *et al*. (2004a) referred it to Eusauropoda

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*incertae sedis*, whereas Barco, Canudo & Cuenca-Bescós (2006), Mannion & Calvo (2011), Canudo *et al*. (2012), and D'Emic (2012) all suggested that it represented a basal titanosauriform. However, its only previous inclusion in a phylogenetic analysis also placed it as a non-titanosauriform macronarian, albeit within 'Laurasiaformes' (Royo-Torres, 2009; see above).

In our LSDM analysis, the latest Jurassic–earliest Cretaceous taxon *Galveosaurus* is recovered as the sister taxon to Titanosauriformes, and as the sister taxon to *Dongbeititan* + (*Lusotitan* + Titanosauriformes) in our LCDM. *Galveosaurus* was originally described as a cetiosaurid (Sánchez-Hernández, 2005), and its position as a non-neosauropod eusauropod (in a turiasaur clade) was supported by Royo-Torres *et al*. (2006) and Royo-Torres & Upchurch (2012). D'Emic (2012) suggested a basal titanosauriform placement, whereas Barco *et al*. (2006) and Carballido *et al*. (2011a, b) recovered it in the same position as the current study.

## Implications for phylogenetic characters

### *Treatment of quantitative character data*

Quantitative characters comprise 27% of our data matrix and thus clearly play an important role in the elucidation of titanosauriform relationships. Our use of discretized and continuous characters for quantitative morphological data produced notable differences to tree topology in our two parallel sets of analyses (LSDM and LCDM). The positions of most taxa are only subtly affected, with the composition of Titanosauria the most disparate between the two analyses. In particular, Titanosauria is considerably more diverse in our LCDM than LSDM trees, with the latter largely resembling previous analyses, whereas numerous taxa almost universally regarded as basal somphospondylans or basal titanosauriforms (see Table 7 for a summary of previous assignments) have been included within Titanosauria in our LCDM. The latter might be largely caused by pushing *Andesaurus*, a clade specifier for Titanosauria, lower in the LCDM trees. Clearly, numerous placements of taxa in at least one of our agreement subtrees are incorrect.

By comparing the LSDM with the $LSDM_{iw}$ and LCDM, it is clear that the use of implied weights has a greater effect on the data set and resultant trees than the treatment of quantitative characters as continuous data. Although implied weighting, by itself (i.e. the $LSDM_{iw}$), produced MPTs that still lie in a set of trees that are not statistically significantly distinguishable from those produced by the LSDM, the treatment of continuous data as such pushes the resulting MPTs into the significant difference range (see 'Templeton's tests' above). The majority of the differences in the topology of the LCDM, in comparison to that of the LSDM, were also recovered in the $LSDM_{iw}$. As such, only a few alternative placements between the trees can be explained by the application of continuous rather than discrete data. These are: (1) the placement of *Dongbeititan* and *Lusotitan* outside of Titanosauriformes in the LCDM, rather than within Somphospondyli and Brachiosauridae, respectively, in the LSDM; (2) the basal position of *Venenosaurus* within Brachiosauridae in the LCDM, in contrast to its derived placement in the LSDM; and (3) the placement of the 'French *Bothriospondylus*' as a derived brachiosaurid in the LCDM, rather than a basal member of this clade as in the LSDM. All other differences in topology seem to result from the effect of character weighting, suggesting that the continuous data had only a relatively small impact on tree topology.

### *Distributions of well-known synapomorphies*

Numerous character states used in this analysis have previously been regarded as well-supported synapomorphies of certain titanosauriform clades, but have been shown here to be highly homoplastic and/or to characterize more inclusive clades. Here we discuss a small number of exemplar characters and detail their more complex distributions. Lists of synapomorphies for the main macronarian clades recovered from the LSDM and LCDM are provided in Appendices 4 and 5, respectively.

A lateral pneumatic foramen ('pleurocoel') situated within a fossa in dorsal vertebrae (C145) has been considered a characteristic of titanosaurs by previous authors (Bonaparte & Coria, 1993; Upchurch *et al*., 2004a). However, it is present in a number of non-titanosaurian somphospondylans based on the LSDM analysis, as well as being convergently present in the brachiosaurid *Cedarosaurus* (Tidwell *et al*., 1999: fig. 2; DMNH 39045: P. D. Mannion, pers. observ., 2008).

Procoely in anterior caudal vertebrae (C27) has traditionally been regarded as a derived titanosaur feature, with this convergently present in *Mamenchisaurus* and flagellicaudatans (McIntosh, 1990; Jacobs *et al*., 1993; Upchurch, 1995, 1998; Salgado *et al*., 1997; Wilson, 2002). However, mild procoely is present in the anterior caudal vertebrae of the basal titanosaur *Andesaurus* (Mannion & Calvo, 2011), as well as the somphospondylan *Tastavinsaurus* (Canudo *et al*., 2008), and the non-titanosaurian *Dongbeititan* possesses strongly procoelous anterior caudal vertebrae (Wang *et al*., 2007). Furthermore, a number of probable non-neosauropods also display strongly procoelous anterior caudal vertebrae [i.e. *Bellusaurus* (Dong, 1990), *Chuanjiesaurus* (Sekiya, 2011), HMN MB.R.2091.1–30 (Bonaparte *et al*., 2000;

this study), and *Losillasaurus* (Casanovas, Santafe & Sanz, 2001)]. Similarly, the extension of procoely into middle-posterior caudal vertebrae (C184) has been considered a feature of lithostrotian titanosaurs (Jacobs *et al*., 1993; Upchurch, 1995, 1998; Salgado *et al*., 1997; Wilson, 2002). Although its uninterrupted presence still remains a feature of derived titanosaurs (C177), the possession of some procoelous middle caudal vertebrae is much more widespread amongst titanosauriforms. Some middle caudal vertebrae referred to the Late Jurassic brachiosaurid *Giraffatitan* (Janensch, 1950: pl. 3, fig. 22; HMN MBR specimens: P. D. Mannion, pers. observ., 2011) display the procoelous condition (D'Emic, 2012, 2013), and a number of taxa of uncertain taxonomic affinities within Somphospondyli (this study) also display this morphology [e.g. *Brontomerus* (Taylor *et al*., 2011), *Gobititan* (You *et al*., 2003), *Malarguesaurus* (González Riga *et al*., 2009), *Astrophocaudia* (D'Emic, 2013), and *Tastavinsaurus* (Royo-Torres, 2009)].

Salgado *et al*. (1997) noted that titanosaurian pubes are markedly longer than their ischia, whereas in other sauropods these two elements are subequal. However, a number of taxa recovered as non-titanosaurian somphospondylans in our LSDM trees have very low (< 0.8) ischium to pubis length ratios (C60) [e.g. *Qiaowanlong* (You & Li, 2009) and *Tastavinsaurus* (Canudo *et al*., 2008)], suggesting that this feature characterizes a more inclusive clade.

The presence of a lateral bulge and medially deflected proximal femur (C255) has long been regarded as a synapomorphy of Titanosauriformes (McIntosh, 1990; Calvo & Salgado, 1995; Salgado *et al*., 1997); however, this feature has previously been poorly defined and in its current state categorizes most eusauropods to some extent (see Salgado *et al*., 1997: fig. 10). Here we have modified the character so that it describes whether the proximolateral margin, above the lateral bulge, is level with/lateral (plesiomorphic state), or medial (derived state) to the lateral margin of the distal half of the shaft, based on Royo-Torres (2009) and Royo-Torres *et al*. (2012). As such, the derived feature characterizes macronarians, other than *Camarasaurus*, and is lost in some derived titanosaurs (e.g. *Opisthocoelicaudia*, *Rapetosaurus*, *Saltasaurus*, and *Xianshanosaurus*), as well as the more basal somphospondylan *Tastavinsaurus*.

*Evolution of postcranial pneumaticity*

The presence of camellae in presacral vertebrae has generally been regarded as either a titanosauriform synapomorphy, or convergently acquired by brachiosaurids and derived titanosaurs (Wedel, 2003), along with the Chinese non-neosauropod *Mamenchisaurus* (Young & Zhao, 1972; Russell & Zheng, 1993; Ouyang & Ye, 2002). However, presacral camellate vertebrae are now recognized as characterizing most somphospondylans, rather than just derived titanosaurs (e.g. Carballido *et al*., 2011b; D'Emic, 2012). The non-titanosauriform macronarian *Galveosaurus* also possesses camellate cervical (Barco *et al*., 2006; Barco, 2009) and anterior-most dorsal vertebrae (C115) [note that the 'posterior cervical' in Barco *et al*. (2006: fig. 2) is much more likely to represent an anterior dorsal vertebra]. Along with the absence of camellae in more posterior dorsal vertebrae and thoracic ribs of *Galveosaurus* (Barco *et al*., 2006; Barco, 2009), this suggests that a camellate internal tissue structure within the anterior portion of the presacral series is synapomorphic of *Galveosaurus* + Titanosauriformes (or a slightly more inclusive clade), with its extension into the full dorsal series (C141) [including thoracic ribs (C170)] characterizing Titanosauriformes (see also discussion in Carballido *et al*., 2011b). Moreover, this interpretation is supported by the position of *Tehuelchesaurus* as a non-titanosauriform macronarian (see also Carballido *et al*., 2011b; D'Emic, 2012), because its dorsal vertebrae lack camellae, although no cervical vertebrae are preserved (Carballido *et al*., 2011b). Interestingly, a similar 'front-to-back' pattern is also observed in the evolution of theropod dinosaur pneumaticity (Benson *et al*., 2012).

Extension of camellae into the sacrum (C172) is restricted to Somphospondyli and its continuation into the ilium (C249) characterizes a more exclusive grouping within this clade. Caudal pneumaticity, in the form of camellae (C176), has generally been thought to be restricted to a small clade of latest Cretaceous South American titanosaurs, the Saltasaurinae (Wilson, 2002; Powell, 2003; Wedel, 2003). However, this internal tissue structure is also present in the caudal neural arches of the latest Cretaceous North American saltasaurid *Alamosaurus* (Fronimos, 2011), the early Late Cretaceous Chinese derived titanosaur *Xianshanosaurus* (Henan Geological Museum specimen KLR-07–62-6: P. D. Mannion & P. Upchurch, pers. observ., 2012), and the Aptian-aged African basal lithostrotian *Malawisaurus*, based on referred (Wedel, 2009) and holotypic material (SAM 7405: P. D. Mannion, pers. observ., 2008). It is also present in the probable Aptian-aged Chinese specimen PMU R263 (Wiman, 1929; Whitlock *et al*., 2011), which was described as a diplodocid by Upchurch & Mannion (2009), but reinterpreted as a titanosauriform by Whitlock *et al*. (2011). As our data sets do not include many 'traditional' derived titanosaurs, it is difficult to determine whether the possession of camellate caudal vertebrae truly optimizes as a lithostrotian (or slightly more inclusive titanosaurian clade) character, or if this feature is convergently acquired by these taxa and Saltasaurinae; nevertheless, it clearly has a more widespread distribution

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amongst Titanosauria than previously realised. Currently, saltasaurines represent the only known taxa in which camellae invade the distal portions of the tail, as well as the pectoral girdle (Cerda, Salgado & Powell, 2012b).

## Spatiotemporal distribution of titanosauriforms

### *Jurassic titanosaurs?*

The presence of titanosaurs in the Jurassic was originally founded upon a titanosaurian interpretation of remains attributed to the Tithonian-aged Tendaguru genus *Janenschia* (e.g. Janensch, 1929; Jacobs *et al*., 1993; Upchurch, 1995; Salgado & Calvo, 1997; Wilson & Sereno, 1998). Day *et al*. (2002, 2004) presented evidence for earlier occurrences of titanosaurs in the form of Middle Jurassic 'wide-gauge' trackways. However, *Janenschia* and all previously referred remains, have been shown to lie outside of Titanosauria by a number of authors (Bonaparte *et al*., 2000; Carballido *et al*., 2011b; this study), and a number of studies have expressed doubt as to whether wide-gauge trackways are produced solely by titanosaurs (e.g. Henderson, 2006; Santos, Moratalla & Royo-Torres, 2009). As such, here we review additional specimens and discuss further lines of evidence for the presence of Jurassic titanosaurs.

A poorly preserved and incomplete middle caudal centrum was originally misidentified as a left metatarsal V by Lapparent & Zbyszewski (1957: 38 and pl. 25, fig. 89) (Fig. 30). These authors referred this isolated element from the Late Jurassic of Castanheira, Portugal, to *Lourinhasaurus* ('*Apatosaurus*') *alenquerensis*, despite the lack of overlapping material with that taxon. The element (MG 4799) preserves only the right half of a strongly procoelous centrum (figured in lateral view in Lapparent & Zbyszewski, 1957: pl. 25, fig. 89). Its lateral surface is dorsoventrally convex and anteroposteriorly concave, and the condylar convexity merges smoothly into the lateral surface of the main body of the centrum, lacking a distinct rim (Fig. 30). In lateral view the dorsal and ventral margins are concave, and the internal tissue structure appears to be solid. The anterior end is dorsoventrally taller than the posterior end. It is clear that the neural arch was restricted to the anterior half of the centrum (excluding the condylar ball). Although it is not possible to accurately determine the elongation index (EI) value, it is less than 1.5. Procoely in middle caudal centra has traditionally been regarded as a feature restricted to derived titanosaurs (Jacobs *et al*., 1993; Upchurch, 1995, 1998; Wilson, 2002), i.e. lithostrotians (Upchurch *et al*., 2004a). As such, this caudal vertebra would represent the earliest occurrence of a lithostrotian titanosaur, extending this lineage from the earliest known example in the Barremian (Early Cretaceous) of the UK ['*Titanosaurus* (*Iuticosaurus*) *valdensis*': Wilson & Upchurch, 2003; Mannion *et al*., 2011b] back into the Kimmeridgian–Tithonian (Late Jurassic). However, as noted above, procoelous middle caudal centra are now known to be more widespread amongst Titanosauriformes, casting doubt on the lithostrotian, or even titanosaurian, affinities of MG 4799 and '*Titanosaurus valdensis*'. This leaves three possible conclusions regarding the taxonomic affinities of MG 4799 (and '*Titanosaurus valdensis*'): (1) it represents an early lithostrotian titanosaur; (2) it represents an individual of the temporally contemporaneous *Giraffatitan brancai* (or, less likely, one of the Cretaceous taxa mentioned above with procoelous middle caudal centra); or (3) it represents an indeterminate titanosauriform. Based on our current understanding of titanosauriforms, as well as subtle morphological differences with *Giraffatitan*, we consider it preferable to follow the third option.

Although *Janenschia*, *Tendaguria*, and HMN MB.R.2091.1–30 are all excluded from Titanosauria in the current study (see also Carballido *et al*., 2011b), our recovery of *Australodocus* as a basal titanosaur maintains the presence of pre-Cretaceous body fossil evidence for this clade of sauropods. This pre-Cretaceous origin is also partially supported by trackways from the middle Bathonian (late Middle Jurassic) Ardley tracksite in England (Day *et al*., 2002, 2004). At this site, 'narrow' and 'wide' gauge sauropod trackways are found on the same bedding plane, with the former preserving manual claw impressions, whereas these are absent in the wide-gauge tracks. Wide-gauge tracks have been attributed to titanosaurs based on a number of anatomical specializations (Wilson & Carrano, 1999; Mannion & Upchurch, 2010a), although there is some evidence to suggest that other sauropods might also have produced such tracks (Henderson, 2006; Santos *et al*., 2009). Although it remains possible that non-titanosaurs, including some basal titanosauriforms (Wilson & Carrano, 1999; Mannion & Upchurch, 2010a), might also have produced wide-gauge trackways, only derived titanosaurs (based on this analysis) entirely lack manual claws (Salgado *et al*., 1997; Wilson & Sereno, 1998; Day *et al*., 2002). As such, the absence of claw impressions in the wide-gauge tracks at the Ardley tracksite, when combined with their presence in the spatiotemporally contemporaneous narrow-gauge tracks, suggests that this absence is unlikely to merely represent a taphonomic artefact, and instead supports the view that these wide-gauge tracks were produced by titanosaurs (Day *et al*., 2002). One final note of caution reflects the dearth of preserved titanosauriform manüs: only five members of this clade (in our analysis) preserve the relevant

manual material. Thus, currently, we do not know how reduced the manual claws were in most titanosauriform taxa, although it should be noted that the claw of the somphospondylan *Diamantinasaurus* is fairly prominent (Hocknull *et al*., 2009).

*Affinities of other putative basal titanosauriforms*

A number of putative basal titanosauriform taxa were not included in our analyses as a result of their fragmentary nature. In light of our revised understanding of titanosauriforms, we discuss the taxonomic affinities of these body fossils and ichnofossils (in approximate stratigraphical order), including indeterminate material that would potentially extend stratigraphical or geographical ranges of clades if correctly identified.

Early–Middle Jurassic

Fragmentary pelvic material (NHMUK R9472: P. D. Mannion & P. Upchurch, pers. observ., 2012) used for histological work (Reid, 1981) from the Aalenian of the UK (Naish & Martill, 2007) has been suggested to represent an indeterminate brachiosaurid (Hunt *et al*., 1994; Weishampel *et al*., 2004). If correctly identified, this would not only represent the earliest known brachiosaurid and titanosauriform, but also the earliest known neosauropod (Naish & Martill, 2007). However, the material is highly incomplete and fragmentary (Reid, 1981), and an identification beyond Sauropoda indet. is not possible.

Hulke (1887) named '*Ornithopsis*' *leedsi* for a dorsal vertebra, thoracic rib, and pelvic material (NHMUK R1985-1988) from the Callovian Kellways Formation of the UK (Naish & Martill, 2007). Four caudal vertebrae (NHMUK R1984) from the overlying Lower Oxford Clay Formation were mistakenly included within the '*Ornithopsis*' *leedsi* type by Upchurch & Martin (2003) [Noé, Liston & Chapman (2010)], with these authors suggesting that all of this material represented an indeterminate brachiosaurid. However, re-examination of this material (P. D. Mannion & P. Upchurch, pers. observ., 2012) demonstrates no evidence for titanosauriform or even macronarian affinities (e.g. the anterior articular surface of the dorsal centrum is flat to very mildly convex) and, instead, we regard both individuals as indeterminate non-neosauropod eusauropods.

Early–Middle Jurassic sub-wide-gauge tracks from Tibet have been tentatively suggested to represent a titanosauriform (Xing, Harris & Currie, 2011), although these authors noted that the morphology of the manus impressions differed greatly from those of other tracks usually attributed to titanosauriforms (i.e. *Brontopodus*). Based on this difference, along with the possibility that other eusauropods might also have produced wide-gauge tracks (see above), we consider it safest to regard these Tibetan tracks as belonging to an eusauropod of uncertain affinities. Additional tracks from the Middle Jurassic of Pakistan were named as a new ichnogenus, *Malasaurus mianwali*, by Malkani (2007). This author described the tracks as narrow-gauge prints of a sauropod of uncertain taxonomic affinities. Subsequently, Malkani (2008) provided a new name for this ichnogenus, *Malakhelisaurus* (as *Malasaurus* was preoccupied), and re-interpreted the tracks as wide-gauge and thus representing a titanosaur. However, it is not clear from the figures in Malkani (2007, 2008) that these prints represent the left and right prints of a single trackway, and so it cannot be determined whether they were formed by a narrow-gauge or wide-gauge individual. Furthermore, the absence of manus claw impressions might merely reflect the poor preservation of the prints, and the shallow nature of the prints might indicate that they are undertracks, in which case claw impressions might not have formed in these deeper layers (see Falkingham *et al*., 2011: fig. 7). Lastly, based on the photograph in Malkani (2008: fig. 7b), even ascertaining a sauropod affinity for the prints with any degree of confidence is difficult (P. L. Falkingham pers. comm., 2012), and the pes morphology is somewhat more reminiscent of the three-toed foot of an ornithopod (e.g. Lockley, 1991: fig. 3.2). As such we regard these tracks as belonging to an indeterminate dinosaur pending re-study.

Dong (1990) named a new Chinese sauropod taxon, *Bellusaurus sui*, for a late Middle Jurassic bonebed of juvenile sauropods. He erected a new subfamily to accommodate this taxon, Bellusaurinae, which he included within Brachiosauridae. Subsequently, Ye, Gao & Jiang (2005) referred a second taxon to this subfamily – *Daanosaurus zhangi* – from the Late Jurassic of China, which was also based on juvenile remains. Jacobs *et al*. (1993) suggested that *Bellusaurus* might represent a titanosaur as a result of its procoelous anterior caudal vertebrae, although this feature is now known to be much more widespread amongst Eusauropoda. The phylogenetic analysis of Upchurch *et al*. (2004a) was the first to include *Bellusaurus*, recovering it as a non-titanosauriform macronarian. However, reanalysis of this matrix, following revised scoring of *Euhelopus*, positioned *Bellusaurus* as a non-neosauropod eusauropod (Wilson & Upchurch, 2009). *Daanosaurus* has never been included in a phylogenetic analysis, and the description by Ye *et al*. (2005) is very brief. D'Emic (2012) suggested macronarian affinities based on the presence of opisthocoelous posterior dorsal centra, although this morphology is also present in some basal taxa, including the contemporaneous non-neosauropod eusauropod *Mamenchisaurus* (e.g. Ouyang & Ye, 2002). Both *Bellusaurus* and *Daano-*

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*saurus* are in need of revision, but seem to lack any clear titanosauriform synapomorphies. Based on its placement in the most recent analyses to include *Bellusaurus* (e.g. Wilson & Upchurch, 2009; Royo-Torres & Upchurch, 2012), as well as the non-neosauropod affinities of all other well-studied Middle–Late Jurassic Chinese sauropods (Upchurch *et al*., 2004a), we tentatively consider both taxa to represent non-neosauropod eusauropods.

McIntosh (1990) suggested brachiosauid affinities for the Middle Jurassic Argentinean taxon *Volkheimeria chubutensis*, although all other treatments have regarded it as a non-neosauropod (Bonaparte, 1986, 1999a; Wilson, 2002; Upchurch *et al*., 2004a; Rauhut, 2006), a position agreed upon here pending a much-needed redescription of this genus.

Late Jurassic

Rauhut (2006) described sauropod remains representing three individuals from the Kimmeridgian–Tithonian (Late Jurassic) of Argentina as brachiosaurids. One individual was not excavated and only briefly described, and so its taxonomic affinities cannot be fully evaluated. Rauhut (2006) regarded the presence of a posterior dorsal centrum that is much wider than tall as a titanosauriform synapomorphy, although this is variable amongst members of this clade, and this morphology is also present (albeit to a lesser extent) in the non-titanosauriform *Galveosaurus*. The long and slender radius was also suggested to indicate possible brachiosaurid affinities, but this morphology is again more widespread amongst eusauropods (see present analysis). We regard this individual as an indeterminate macronarian pending its excavation and full description. The most complete individual is represented by caudal vertebrae, chevrons, and a pubis. The presence of anteriorly placed neural arches in middle caudal vertebrae is also found in the non-titanosauriform *Galveosaurus*, and so can no longer be used to support titanosauriform affinities. Rauhut (2006) noted that the possession of a V-shaped first chevron was a feature previously seen only in *Giraffatitan*, but urged caution in that this element was known in few sauropods; subsequently, a similar morphology has been described in *Andesaurus* and some other titanosaurs (Mannion & Calvo, 2011). As such, we regard this individual as pertaining to an indeterminate titanosauriform pending further study. Finally, an isolated humerus was described as providing the most convincing evidence for brachiosaurids in the Late Jurassic of Argentina. Based on Rauhut (2006), this element has a rounded proximolateral corner, a medially deflected deltopectoral crest, a straight lateral margin along the diaphysis, a midshaft width to humeral length ratio of 0.14, and a moderately deep anconeal fossa. This combination of features indicates titanosauriform affinities, but there are no clear brachiosaurid synapomorphies. As such we regard it as an indeterminate titanosauriform, which removes any unambiguous record of South American brachiosaurids.

*Duriatitan humerocristatus* is based on an isolated humerus from the early Kimmeridgian of the UK (Barrett, Benson & Upchurch, 2010). Some authors have suggested brachiosaurid affinities for the specimen based on its slenderness (e.g. McIntosh, 1990; Upchurch & Martin, 2003; Upchurch *et al*., 2004a), but Barrett *et al*. (2010) more cautiously regarded it as a basal titanosauriform. It is difficult to be certain of the affinities of this specimen: slender humeri are also known in non-titanosauriforms [e.g. *Lapparentosaurus* (MNHN MAA 160: P. D. Mannion, pers. observ., 2011)]. However, there is some indication that the deltopectoral crest extends medially across the anterior face of the humerus (Hulke, 1874: pl. 2), a feature that would support titanosauriform affinities, although this region is badly damaged (Barrett *et al*., 2010). We tentatively retain it within Titanosauriformes, but a more precise assignment is currently not possible.

Malkani (2003) erected *Brohisaurus kirthari* for fragmentary remains from the Kimmerdigian of Pakistan, regarding this new taxon as a titanosaur. The material is too poorly preserved and incomplete to be diagnostic and, based on the brief description and images, there is no evidence to suggest that this material represents a titanosaur. However, the apparent presence of pneumaticity in thoracic ribs and a strongly anteroposteriorly compressed femoral midshaft (Malkani, 2003) suggests that *Brohisaurus* should be provisionally regarded as an indeterminate titanosauriform.

Mook (1917b) named a new species of *Apatosaurus* – *Apatosaurus minimus* – based on a sacrum and pelvis from the Late Jurassic Morrison Formation of North America. McIntosh (1990) argued against this assignment to *Apatosaurus*, and regarded it as Sauropoda *incertae sedis*, with Upchurch *et al*. (2004a) suggesting possible macronarian affinities. The sacrum of '*Apatosaurus*' *minimus* possesses six centra, a feature otherwise known only in somphospondylans (Upchurch, 1998; Wilson & Sereno, 1998), and some old individuals of *Camarasaurus* (Tidwell, Stadtman & Shaw, 2005). Otherwise, it lacks any other clear titanosauriform synapomorphies and we follow Upchurch *et al*. (2004a) in regarding it as a basal macronarian pending restudy.

Dong (2001) described a partial manus from the latest Jurassic (or possibly earliest Cretaceous; see Sullivan *et al*., 2009) of north-eastern China as a brachiosaurid, although he provided no clear evidence for this assignment. The distal ends of the metacar-

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pals extend prominently onto the dorsal surface, and the distal end of metacarpal I is also strongly bevelled, contrasting with the condition seen in most titanosauriforms (Wilson, 2002; D'Emic, 2012; this study). Furthermore, the presence of two carpals indicates that the specimen probably represents a non-neosauropod (Upchurch, 1995, 1998; Wilson, 2002). The arrangement of the articulated manus into a vertically orientated, 'horseshoe'-shaped structure in proximal view (Dong, 2001) suggests that this specimen represents an eusauropod (Upchurch, 1995, 1998; Wilson & Sereno, 1998; Wilson, 2002, 2005b), and thus we regard it as an indeterminate non-neosauropod eusauropod.

Early Cretaceous

A poorly preserved partial skeleton from the Valanginian–Barremian of Japan (the 'Toba dinosaur') was described as an indeterminate titanosaur (Tomida & Tsumura, 2006). The ventral surfaces of the anterior caudal centra are transversely concave, with this concavity bounded by ventrolateral ridges, which indicates somphospondylan affinities for this specimen. A titanosaurian identification cannot currently be supported (see also Wilson & Upchurch, 2009).

In addition to suggestions of a brachiosaurid identification for *Phuwiangosaurus* (Royo-Torres, 2009), *Qiaowanlong* (You & Li, 2009), and the Chinese manus described by Dong (2001) (see above), the presence of brachiosaurids in Asia has previously been based on a tooth from the Barremian–Aptian of South Korea (Lim, Martin & Baek, 2001). However, Barrett *et al*. (2002) demonstrated the lack of evidence for identifying the former as a brachiosaurid, regarding the tooth as an indeterminate titanosauriform. Here we regard this tooth as an indeterminate macronarian, because features previously considered as characteristic of Titanosauriformes are also present in the tooth of the non-titanosauriform macronarian *Aragosaurus* (see above). Consequently, there is currently no evidence for Asian brachiosaurids (see also Ksepka & Norell, 2010).

Two teeth from the Early Cretaceous ('Neocomian') of Lebanon were described as brachiosaurids (Buffetaut *et al*., 2006), and used as support for this clade's presence in Asia (You & Li, 2009). However, present-day Lebanon was part of the Afro-Arabian plate in the Early Cretaceous and thus part of Gondwana, not Asia (Buffetaut *et al*., 2006; Ksepka & Norell, 2010). The better-preserved tooth crown displays some degree of twisting (Buffetaut *et al*., 2006), which might suggest that its referral to Brachiosauridae is correct based on the presence of this feature in the upper teeth of *Abydosaurus* and *Giraffatitan* (Chure *et al*., 2010), as well as *Europasaurus* (D'Emic, 2012).

Sauropods from the Early Cretaceous Wealden Supergroup of the UK have recently received a thorough revision (Upchurch *et al*., 2011b). In particular, the taxonomic affinities of the titanosauriforms *Eucamerotus foxi*, *Ornithopsis hulkei*, '*Ornithopsis eucamerotus*', and *Pelorosaurus conybeari* are largely unaffected by our results and are not discussed further here.

Taylor & Naish (2007) erected *Xenoposeidon proneneukos* for an incomplete dorsal vertebra from the Berriasian–Valanginian of the UK Wealden. Uncertain of its taxonomic affinities, these authors referred it to Neosauropoda *incertae sedis*, and further suggested that it might represent a new sauropod family. Subsequent authors have proposed titanosaurian (Mannion & Calvo, 2011), basal somphospondylan (Upchurch *et al*., 2011b), titanosauriform (D'Emic, 2012), or 'laurasiaform' (Royo-Torres *et al*., 2012) affinities. One of the features argued to support a titanosaurian placement is that the lateral foramen is set within a fossa (Taylor & Naish, 2007; Mannion & Calvo, 2011); however, this feature is also known in several non-titanosaurs (see above). A purportedly more contradictory feature of *Xenoposeidon* is the camerate internal tissue structure (Taylor & Naish, 2007), which contrasts with the camellae seen in the dorsal vertebrae of titanosauriforms. However, this camerate structure is present in the dorsal vertebrae of the non-titanosauriform macronarians *Galveosaurus* (Barco, 2009) and *Tehuelchesaurus* (Carballido *et al*., 2011b) (see 'Evolution of postcranial pneumaticity' above). The fragmentary nature of the *Xenoposeidon* holotype means that an unambiguous taxonomic assignment will always be difficult, but here we tentatively suggest that it represents an indeterminate basal macronarian.

MIWG 7306 is an incomplete cervical vertebra from the Wealden of the Isle of Wight, UK. It was originally described as an indeterminate brachiosaurid, with closest affinities to *Sauroposeidon* (Naish *et al*., 2004). The new placement of the latter taxon as a somphospondylan (D'Emic, 2012, 2013; this study) suggests that MIWG 7306 might be more accurately identified as an indeterminate somphospondylan. This is further supported by a higher aEI value for MIWG 7306 (4.2) than in known brachiosaurids, as well as a lateral pneumatic fossa that extends almost to the posterior end of the centrum (Naish *et al*., 2004), a feature shared only with *Sauroposeidon* and the synonymous or closely related *Paluxysaurus* (Wedel *et al*., 2000a; D'Emic, 2013). With the above reassessment of MIWG 7306, there is no longer any unambiguous evidence for brachiosaurids in the Wealden, although revision of *Eucamerotus* (P. Upchurch *et al*., unpubl. data) and description of the 'Barnes High sauropod' might alter this conclusion.

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NHMUK R5333 comprises two caudal vertebrae and the posterior condyle of a third caudal vertebra from the Wealden of the Isle of Wight (Blows, 1998; Upchurch *et al*., 2011b). This articulated series is from the posterior section of the anterior caudal region, based on the presence of reduced caudal ribs. All three vertebrae are strongly procoelous, with a distinct rim separating the posterior condyle from the lateral surface of the main body of the centrum. Prominent ventrolateral ridges extend along the full length of the centrum (excluding the condylar 'ball'), and the ventral surface in between is transversely concave. These features indicate that NHMUK R5333 represents a titanosaur and possibly a lithostrotian, which would make it the earliest known (Barremian) member of Lithostrotia (see also D'Emic, 2012).

Dong, Paik & Kim (2001) described *Pukongosaurus millenniumi* from the Hauterivian–Barremian of South Korea, regarding it as closely related to *Euhelopus*. Upchurch *et al*. (2004a) listed it as a *nomen dubium*, without further comment, and it was listed as a titanosauriform by Wilson (2005a) and Wilson & Upchurch (2009), and as a somphospondylan by D'Emic (2012). We here regard it as an indeterminate titanosauriform based on a lack of diagnostic features and the presence of camellate internal tissue structure in the presacral vertebrae.

*Amargatitanis macni*, from the Barremian of Argentina, is known from fragmentary and poorly preserved caudal vertebrae and appendicular elements, and was originally described as a titanosaur, mainly on the basis of its scapular morphology (Apesteguía, 2007). The anterior-most caudal centra are mildly procoelous, which might be considered to indicate basal titanosaurian affinities (Salgado *et al*., 1997; Mannion & Calvo, 2011), although it is now clear that procoely in caudal vertebrae is more widespread (see 'Implications for phylogenetic characters' above). The distal blade of the scapula shows no dorsal or ventral expansion, a feature only seen in the titanosaur *Jiangshanosaurus* in our analysis, but known also in several other derived titanosaurs (Apesteguía, 2007). However, the dorsal and ventral margins of the scapular blade are incomplete (MACN PV N34: R. N. Barnes. pers. observ., 2009), and thus it cannot be confirmed whether this unexpanded blade is a genuine feature. Other features pertaining to the scapula support titanosauriform affinities, e.g. the medial deflection of the glenoid (Apesteguía, 2007). Within titanosauriforms, only somphospondylans possess procoelous caudal vertebrae. As such, we consider *Amargatitanis* to represent a somphospondylan, but recognize no diagnostic features: the proposed autapomorphies in Apesteguía (2007) are all more widespread or based on incompletely preserved elements, and thus we regard it as a *nomen dubium*. Furthermore, the material was not found closely associated (D'Emic, 2012), and so is likely to represent a chimera.

Santafé-Llopis *et al*. (1981) described and figured associated postcranial remains of an individual from the early Aptian of Spain that they regarded as an indeterminate brachiosaurid (listed as 'Brachiosaurinae'). The humerus has a rounded proximolateral margin, anteriorly projecting deltopectoral crest, and is extremely gracile (midshaft mediolateral width to humerus length ratio = 0.12). There also appears to be a moderately deep supracondylar fossa. The femur displays a lateral bulge, and the proximal chevron is unbridged dorsally. This combination of character states supports placement within Titanosauriformes, and we regard it as an indeterminate member of that clade.

The taxonomy of *Astrodon* and *Pleurocoelus* from the early Aptian Arundel Formation of the eastern USA is extremely complex and has been reviewed recently by Carpenter & Tidwell (2005) and D'Emic (2013). Whereas the former authors regarded *Astrodon* as valid, with *Pleurocoelus* a junior synonym, D'Emic (2013) demonstrated that neither holotype is diagnostic, with the referred remains from the same geological formation lacking documented association (see also Upchurch *et al*., 2004a, and note that most previously referred material from elsewhere is now referred to other taxa; Rose, 2007; D'Emic, 2013). We follow D'Emic (2013) in regarding both taxa as *nomina dubia*, and note that the material clearly seems to represent a macronarian, with at least some elements from the Arundel fauna indicating titanosauriform affinities (e.g. the anteromedial arm of the proximal ulna is almost twice the length of the anterolateral arm, similar to the condition in the 'Cloverly titanosauriform' (YPM 5449: P. D. Mannion, pers. observ., 2008) and *Venenosaurus* (Tidwell *et al*., 2001)].

A well-preserved partial skeleton, including a complete skull, from the Aptian of Brazil was described as a new taxon, *Tapuiasaurus macedoi* (Zaher *et al*., 2011). Based on the description of the skull, and brief information on the postcrania, a titanosaurian placement seems secure (Zaher *et al*., 2011). Zaher *et al*. (2011) also incorporated *Tapuiasaurus* into a phylogenetic analysis (based on an updated version of the Wilson, 2002, matrix), recovering it within Lithostrotia, as the sister taxon to *Rapetosaurus* and forming a clade with *Nemegtosaurus*. Its lithostrotian affinities thus appear well supported (Zaher *et al*., 2011), although we register a note of caution in its grouping with *Rapetosaurus* and especially *Nemegtosaurus* (known only from cranial material; Wilson, 2005a), in that these are the only three lithostrotian taxa in the analysis based on substantial cranial remains. Con-

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sequently, there is a risk that these taxa are drawn to one another on the basis of cranial characters, to the exclusion of other taxa. This concern is supported by the observation that all unambiguous synapomorphies supporting the relationships of these three taxa pertain to cranial characters (Zaher *et al*., 2011: supporting information).

Woodruff (2012) erected *Rugocaudia cooneyi* on the basis of a partial tail sequence, tooth, and associated fragmentary appendicular remains from the Aptian–Albian of the USA. The presence of a procoelous middle–posterior caudal vertebra supports Woodruff's (2012) assignment of the material to Titanosauriformes. However, all of the characters used to diagnose *Rugocaudia* are more widespread amongst titanosauriforms and do not form an unusual character combination (see this analysis), or are of dubious diagnostic value (see also D'Emic & Foreman, 2012), including the rugose texture on the caudal vertebrae, which is present in other sauropods such as *Gobititan* (IVPP 12579: P. D. Mannion & P. Upchurch, pers. observ., 2012); as such, we follow D'Emic & Foreman (2012) in considering *Rugocaudia* a *nomen dubium*.

*Agustinia ligabuei*, from the Aptian–Albian of Argentina, was described by Bonaparte (1999b) on the basis of a fragmentary partial skeleton. Unsure of its position within Sauropoda, Bonaparte (1999b) erected the new monogeneric family Agustinidae, on the basis of the unusual 'dermal ossifications' present in *Agustinia*, and suggested possible affinities with Rebbachisauridae. Upchurch *et al*. (2004a) noted features that supported a lithostrotian or diplodocoid identification and, based on the presence of six sacral vertebrae and osteoderms, as described by Bonaparte (1999b), regarded it as Titanosauria *incertae sedis*. However, as noted by D'Emic, Wilson & Chatterjee (2009), the fragmentary nature of the material means that accurate identification of six sacral vertebrae is not possible. We agree with D'Emic *et al*. (2009) that the 'dermal ossifications' of Bonaparte (1999b) are not osteoderms: the 'type 1' and 'type 3' 'osteoderms' appear to be partial thoracic ribs (MCF-PVPH 110: P. D. Mannion, pers. observ., 2009) or possibly hypertrophied ossifications (D'Emic *et al*., 2009), whereas the 'type 2' element possibly represents a pair of fused, distorted, and partially incomplete ischia (S. Poropat, pers. comm., 2012). The fibula appears to possess an anteromedially directed proximal crest (Bonaparte, 1999b: fig. 6), a feature of several somphospondylans (Wilson & Upchurch, 2009; D'Emic, 2012; this study), which would correspond with the animal potentially possessing six sacral vertebrae. The absence of diagnostic features leads us to tentatively regard *Agustinia* as an indeterminate somphospondylan.

'*Dinodocus mackesoni*' is known from poorly preserved appendicular material (NMHUK 14695: P. D. Mannion & P. Upchurch pers. observ., 2012) from the Aptian–Albian Lower Greensand of England (Owen, 1884; Woodward, 1908; Naish & Martill, 2007). Both McIntosh (1990) and Upchurch (1995) considered it to be a brachiosaurid, with the former author regarding it as a diagnostic taxon, but referring it to a new species of *Pelorosaurus*. Upchurch *et al*. (2004a) listed it as a *nomen dubium* without further discussion, and Naish & Martill (2007) considered it an indeterminate titanosauriform. Only the humerus, incomplete radius, and ulna provide useful anatomical information. The humerus has a rounded proximolateral margin [Woodward, 1908: fig. 1 (note that this region is now largely reconstructed with plaster)], and the deltopectoral crest projects anteriorly; both of these represent the plesiomorphic condition in sauropods, but are variable amongst titanosauriforms (e.g. Upchurch, 1999; Wilson, 2002; this study). Although incomplete along the midshaft, it clearly had a very mediolaterally narrow midshaft in relation to the humeral length (a ratio of approximately 0.11), comparable to several brachiosaurids, but also the basal macronarian *Aragosaurus* and somphospondylan *Ligabuesaurus*. Based on a lack of titanosauriform synapomorphies in the radius and ulna, we regard '*Dinodocus*' as an indeterminate macronarian.

'*Macrurosaurus semnus*' is known from numerous caudal vertebrae from at least two localities in the late Albian Cambridge Greensand of England (Seeley, 1876; Le Loeuff, 1993), and has been regarded as an indeterminate titanosaur by most authors (e.g. Le Loeuff, 1993; Upchurch, 1995; Naish & Martill, 2007; Mannion & Calvo, 2011). The majority of remains preserve middle caudal centra, along with their neural arch pedicels. Most are amphicoelous, although some are strongly procoelous. As noted above, the presence of caudal procoely by itself can no longer be used to infer titanosaurian affinities for these specimens. Furthermore, none of the centra possess ventral longitudinal hollows or ventrolateral ridges (CAMSM B55630–55654: P. D. Mannion, pers. observ., 2010), in contrast to many somphospondylans. Several of the specimens show an anterior bias of the neural arch, but this is not the case in all of the vertebrae. It seems probable that most of the material represents an indeterminate titanosauriform, but its precise affinities cannot currently be ascertained. Also known from the Cambridge Greensand is '*Acanthopolis platypus*' (Seeley, 1871), a partial left pes (preserving all five metatarsals) that was subsequently referred to *Macrurosaurus* (Seeley, 1876). Other material originally included in this species has since been shown to represent an indeterminate ankylosaur (Pereda-Suberbiola & Barrett, 1999). The pedal material (CAMSM B55449–55453: P. D. Mannion, pers. observ., 2010) displays one unambigu-

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ous titanosauriform feature: the medial surface of the proximal portion of metatarsal IV is concave (C270). As such, we regard this individual as an indeterminate titanosauriform.

*Austrosaurus mckillopi* is known from the late Albian of Australia (Longman, 1933; Hocknull *et al*., 2009) and is represented by a series of eight poorly preserved dorsal vertebrae (Longman, 1933; Molnar & Salisbury, 2005). Material subsequently tentatively referred to *Austrosaurus* (Coombs & Molnar, 1981) has since been shown to be distinct and now forms the type of *Wintonotitan* (Hocknull *et al*., 2009). *Austrosaurus* has been regarded as a titanosaur by most recent authors [Upchurch *et al*., 2004a (although coding for this OTU included some of the material now comprising *Wintonotitan*); Molnar & Salisbury, 2005], but Hocknull *et al*. (2009) expressed doubt as to this assignment and regarded it as a *nomen dubium*. Based on the presence of camellae throughout the dorsal series (Hocknull *et al*., 2009), we regard *Austrosaurus* as a titanosauriform and follow Hocknull *et al*. (2009) in considering it a *nomen dubium* pending its restudy. A full revision of the remaining unnamed Australasian middle Cretaceous sauropod material is beyond the scope of this study, but nearly all other specimens have been described as either titanosaurs or basal titanosauriforms; thus, these additional remains (Molnar & Salisbury, 2005; Salisbury, Molnar & Lamanna, 2006; Molnar & Wiffen, 2007) do not contradict or augment our current understanding of this fauna based on '*Austrosaurus*', *Diamantinasaurus*, and *Wintonotitan*. The sole exception is an incomplete cervical vertebra that Molnar & Salisbury (2005: 460–461, fig. 20.6) suggested might represent a brachiosaurid. However, there are no brachiosaurid synapomorphies observable in this element; for example, although all brachiosaurids preserving cervical vertebrae possess a dividing lamina within the lateral foramen, this is plesiomorphic for neosauropods and is also retained in many basal somphospondylans. Pending restudy, we regard this Australian cervical as a probable titanosauriform of indeterminate nature.

*Jiutaisaurus xidiensis* was named on the basis of an articulated series of 18 anterior to middle amphicoelous caudal vertebrae from the Aptian–Cenomanian Cretaceous of China (Wu *et al*., 2006). Originally described as Sauropoda *incertae sedis* (Wu *et al*., 2006), it was listed as a *nomen dubium* by Wilson & Upchurch (2009) and Mannion & Calvo (2011), with the latter authors suggesting non-titanosaurian titanosauriform affinities for the material (see also D'Emic, 2012). The haemal canal depth is approximately 50% of the total height in the proximal chevron (Wu *et al*., 2006), a feature restricted to titanosauriforms. Lü *et al*. (2007) also noted the presence of a longitudinal hollow along the ventral surface of each caudal centrum, which would support its titanosauriform affinities. All of the features listed as diagnostic by Wu *et al*. (2006) are more widespread amongst sauropods and, as such, we follow previous authors (Wilson & Upchurch, 2009; Mannion & Calvo, 2011) in regarding *Jiutaisaurus* as an indeterminate titanosauriform.

A fragmentary partial sauropod skeleton from pre-Cenomanian 'Continental Intercalaire' deposits in Mali was described as an indeterminate titanosaur (O'Leary *et al*., 2004). The possession of procoelous caudal vertebrae throughout the tail sequence and the presence of osteoderms indicate that this specimen represents a derived titanosaur (O'Leary *et al*., 2004). Currently, osteoderms associated with sauropod postcrania are rare (D'Emic *et al*., 2009), and are restricted to lithostrotian titanosaurs (e.g. González Riga, 2003; Gomani, 2005). Along with *Malawisaurus*, the Malian sauropod represents the earliest known occurrence of sauropod osteoderms in the fossil record (D'Emic *et al*., 2009), and is regarded as an indeterminate lithostrotian.

Late Cretaceous

Vullo, Neraudeau & Lenglet (2007) referred teeth from three early Cenomanian French localities to Brachiosauridae. However, brachiosaurid teeth can only be distinguished from other basal macronarian teeth by the strong degree of twisting present along the axis (Chure *et al*., 2010; D'Emic, 2012), a feature absent in the French teeth. Consequently, we regard these teeth as pertaining to indeterminate macronarians.

A poorly preserved caudal vertebra from the late Cenomanian of Spain was briefly described and figured by Vullo, Bernárdez & Buscalioni (2009) as an indeterminate titanosaur. Based on its general morphology and the apparent presence of a reduced caudal rib (Vullo *et al*., 2009: fig. 3L), the element appears to be one of the last vertebrae from the anterior region of the tail. The centrum is strongly procoelous and the neural arch is restricted to the anterior half of the centrum (Vullo *et al*., 2009). Interestingly, the upper half of the lateral surface of the centrum is pierced by a large, sharp-lipped lateral pneumatic foramen (Vullo *et al*., 2009). This combination of features leads us to suggest lithostrotian affinities for this specimen, and we note the uncommon occurrence of lateral pneumatic foramina amongst somphospondylans [reported in *Alamosaurus* (Wilson, 2002) and *Xianshanosaurus* (Lü *et al*., 2009a)].

*Arkharavia heterocoelica* was named for an incomplete anterior caudal centrum and base of neural arch from the Maastrichtian of eastern Russia, with additional caudal vertebrae referred from the same local-

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ity, as well as a tooth from a different locality (Alifanov & Bolotsky, 2010). Alifanov & Bolotsky (2010) regarded it as a basal titanosauriform. The holotype specimen lacks any diagnostic features (all are more widespread – see the current analysis) and, furthermore, at least some of the referred material probably belongs to a hadrosaurid (Godefroit, Bolotsky & Bolotsky, 2012), which is the dominant vertebrate group in the fauna. In particular, the referred caudal vertebra with an extremely elongate neural spine (Alifanov & Bolotsky, 2010: fig. 2b–d) does not resemble any known sauropod, as the spine lacks lateral laminae, and is comparably longer than in any sauropod (even including diplodocoid taxa with long caudal neural spines). We tentatively retain the holotype specimen within Sauropoda, regarding it as an indeterminate somphospondylan based on its mildly procoelous, anteroposteriorly short centrum, and assign the referred material from this locality to Hadrosauridae indet. (see also Godefroit *et al*., 2012). The referred tooth is from a different locality and, as there is no overlapping material, cannot be referred to *Arkharavia* regardless of its taxonomic affinities. The tooth is poorly preserved, but appears to be approximately cylindrical (Alifanov & Bolotsky, 2010); as such, it should be regarded as an indeterminate titanosaur.

Rauhut & Werner (1997) described an isolated femur from the Maastrichtian of Egypt as a probable brachiosaurid, which, if correctly identified, would make it the only unambiguous Late Cretaceous occurrence of this clade. However, as noted by Barrett [2001 (pers. comm. in Naish & Martill, 2001)], the features used to refer it to Brachiosauridae are more widespread amongst Titanosauriformes, or even Macronaria (this study). Furthermore, the shaft eccentricity (mediolateral width to anteroposterior width ratio at midshaft) is much lower (1.57) than in *Brachiosaurus* and *Giraffatitan* [both > 2.0 (see the LCDM data set)]. However, one feature suggests possible somphospondylan affinities, in that the distal end appears to be dorsomedially bevelled with respect to the long axis of the femoral shaft. As such, we provisionally consider this femur to represent an indeterminate somphospondylan.

*Macroevolutionary history of Titanosauriformes*

We created phylogenetic diversity estimates (PDEs) for titanosauriforms from our LSDM agreement subtree and LCDM strict consensus tree using time-calibrated phylogenies (Figs 22, 27), with ghost ranges or lineages reflecting gaps in the fossil record (see Mannion *et al*., 2011b, and references therein). In general the two PDEs match one another closely, although diversity is always higher for the LCDM PDE as a result of no taxa being pruned from this tree. Both PDEs indicate that late Oxfordian titanosauriform diversity is notably higher than any assessment based only on observed diversity (i.e. a single taxon, the 'French *Bothriospondylus*'). This suggests that the Oxfordian was not as depauperate a time interval as indicated by previous analyses (e.g. Upchurch & Barrett, 2005; Mannion *et al*., 2011b), suggesting that this stage is especially poorly sampled and/or that some Late Jurassic outcrops might be inaccurately dated (Mannion *et al*., 2011b). The stratigraphical age and phylogenetic placement of the 'French *Bothriospondylus*' results in the extension of numerous brachiosaurid lineages back into the late Oxfordian, as well as the somphospondylan lineage. Currently there are no body fossil occurrences that suggest an earlier origin for titanosauriforms, but the trackway record suggests that the clade had already originated and diversified in the late Middle Jurassic [the middle Bathonian Ardley tracksite (Day *et al*., 2002); see above]. Unambiguous examples of titanosauriforms are known from the Late Jurassic of Africa, Europe, North America, and probably South America and Pakistan (see above). Their absence in Jurassic rocks in Antarctica and Australasia most likely reflects a sampling bias, although their Asian absence might be a genuine feature (see below). Thus, this near-global pattern, coupled with putative Middle Jurassic titanosauriform occurrences from Europe, suggests that Titanosauriformes most likely originated no later than the Middle Jurassic, i.e. prior to the initiation of Pangaean fragmentation (Day *et al*., 2002; Upchurch *et al*., 2002).

Whereas the LSDM PDE maintains an approximately constant diversity throughout the Late Jurassic (Fig. 22), there is a Tithonian peak in the LCDM PDE (Fig. 27). This is mainly a result of the placement of *Australodocus* as a titanosaur, which extends three additional titanosaur lineages back into the Tithonian in the LCDM PDE (note that *Australodocus* was pruned a posteriori from the LSDM agreement subtree, although was recovered as a member of Titanosauria). The near absence of titanosaurs from the Jurassic body fossil record most likely indicates that they were a rare component of Middle–Late Jurassic terrestrial faunas, but it is also possible that they displayed a different environmental preference (inland terrestrial) to other sauropods (Mannion & Upchurch, 2010a; see also Falkingham, Bates & Mannion, 2012). The newly recovered position of the coastal taxon *Janenschia* outside of Titanosauria strengthens the results of Mannion & Upchurch's (2010a) environmental analyses, although other modifications in terms of the composition of Titanosauria might result in additional changes. It is interesting to observe that rebbachisaurid diplodocoids

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also show a comparable and contemporaneous ghost lineage (Upchurch & Barrett, 2005; Sereno *et al*., 2007) to that of titanosaurs, and Mannion & Upchurch (2010a) noted that rebbachisaurids display some evidence for the same inland terrestrial environmental association as that recovered for titanosaurs. Thus, it is plausible that some combination of low diversity and abundance, coupled with a rarity in preservation of suitable environments, might account for the paucity of titanosaurs and absence of rebbachisaurids in the Jurassic, and their consequent parallel ghost lineages.

There is no decline in titanosauriform diversity across the J/K boundary (Figs 22, 27), which supports the view that the sauropod 'diversity crash' at this boundary was mainly restricted to diplodocids and non-neosauropods (Upchurch & Barrett, 2005; Barrett, McGowan & Page, 2009; Mannion *et al*., 2011b; Upchurch *et al*., 2011a; Upchurch & Mannion, 2012). In fact, diversity is roughly constant (LCDM) or even increased (LSDM) across the boundary, although the latter is largely an artefact of the exclusion of *Australodocus*, whose omission prevents the extension of several somphospondylan lineages into the Tithonian, thereby creating a time lag for this initial diversity peak. Although overall titanosauriform diversity does not decrease over the J/K boundary, brachiosaurid diversity outside of North America appears to have declined sharply or even reduced to zero in the Early Cretaceous. However, this might merely reflect the absence of suitably aged terrestrial outcrops for much of this interval, a view that is supported by putative brachiosaurid occurrences in the Early Cretaceous of Lebanon (Buffetaut *et al*., 2006). The absence of brachiosaurids in the Cretaceous of East Asia, once reconnected to Europe (see below), provides weak support that the clade did genuinely go extinct in Europe and thus never had the opportunity to disperse into East Asia (Ksepka & Norell, 2010), but it is also possible that ecological barriers prevented their dispersal.

Ghost ranges indicate the existence of several unsampled somphospondylan lineages in the earliest Cretaceous (Berriasian–Hauterivian); however, '*Pelorosaurus*' *becklesii* is the only body fossil evidence from this interval, again indicative of the lack of terrestrial outcrops at this time. A prominent increase in titanosauriform diversity can be detected in the Barremian, reflecting the radiation of somphospondylans and marking the earliest known putative lithostrotian (NHMUK R5333; see also D'Emic, 2012). The Aptian–Albian represents a peak in titanosauriform diversity (Figs 22, 27), with derived titanosaurs (lithostrotians, or taxa closely related to this radiation) known from north-western (O'Leary *et al*., 2004) and south-eastern Africa (*Malawisaurus*: Jacobs *et al*., 1993; Gomani, 2005), northern (*Mongolosaurus*: Mannion, 2011) and south-eastern Asia (*Jiangshanosaurus*: Tang *et al*., 2001b), and South America (*Tapuisaurus*: Zaher *et al*., 2011). This wide distribution of derived forms suggests an earlier origin and dispersal for titanosaurs, and supports the view that poor sampling of the earliest Cretaceous (and possible environmental biases in the Late Jurassic) obscures their early evolution (see also D'Emic, 2012).

Titanosauriform diversity suffered a severe drop in species numbers at, or around, the Albian/Cenomanian boundary in the LCDM PDE (40% decrease; Fig. 27), although this is less pronounced in the LSDM PDE (23% decrease; Fig. 22). However, in both cases, this is followed by a further gradual decline, representing a faunal turnover whereby basal titanosauriforms (comprising brachiosaurids, basal somphospondylans, and andesauroids) were replaced by derived 'titanosauroids' (N.B. the low diversity throughout the remainder of the Late Cretaceous is an artefact generated by the exclusion of most 'definite' titanosaurs from our study). This transition to a sauropod fauna dominated by 'titanosauroids' (especially lithostrotians) is consistent with previous work that has noted a middle Cretaceous faunal turnover in dinosaurs (e.g. Coria & Salgado, 2005), squamates (e.g. Evans, 2003), crocodylomorphs (e.g. Martin & Delfino, 2010), and other groups, and it seems that this transition occurred in a spatiotemporally staggered fashion (Benson *et al*., 2013). Brachiosaurids appear to have become extinct at, or close to this boundary (see the stratigraphical range uncertainty of the putative brachiosaurid *Sonorasaurus*: Table 4), and there are no unambiguous occurrences of this clade in post-Cenomanian outcrops. A few late surviving basal titanosauriforms are known from the early Late Cretaceous of Asia (e.g. '*Huanghetitan*' *ruyangensis* and *Ruyangosaurus*), South America (*Malarguesaurus*), and Africa (*Angolatitan*). Post-Cenomanian, sauropods are absent from Europe and North America until the latest Cretaceous [with the exception of a late Turonian–early Coniacian Croatian tracksite (Mezga *et al*., 2006)], although whether this 'hiatus' reflects regional extinctions, poor sampling, or a combination of the two remains controversial (Lucas & Hunt, 1989; Le Loeuff, 1993; Williamson & Weil, 2008; D'Emic, Wilson & Thompson, 2010; Mannion & Upchurch, 2011; D'Emic & Foreman, 2012; see below).

Although a poor fossil record might partly account for low somphospondylan diversity prior to the 'middle' Cretaceous, in comparison to the relatively high, early burst in Late Jurassic diversity of its sister clade Brachiosauridae, there is a clearer imbalance in tree shape when comparing the overall topology of Titanosauriformes: whereas the total number

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of known brachiosaurid species is fewer than ten, the Somphospondyli clade diverged into approximately 80 known species (including derived titanosaurs not included in this study). This asymmetry in tree shape and in the timing of diversification indicates variation in speciation and/or extinction rates in the two titanosauriform clades (see Mooers & Heard, 1997, for a discussion of tree shape). Although the causes of this difference are not yet understood and it is beyond the scope of this study to fully explore this issue, ecological differences and geographical factors are usually proposed as the most likely explanations (Schluter, 2000; Pigot *et al*., 2010). Pigot *et al*. (2010) showed through simulations that diversification rates slowed under scenarios of stable geographical ranges, and increased under conditions of faster rates of range expansion. It is therefore possible that the eventual global distribution of somphospondylans accounts for their disproportionately higher diversity, with brachiosaurids apparently never reaching Asia (see also Ksepka & Norell, 2010; Mannion, 2011), Australasia (this study), or (probably) South America (this study), and unambiguous Cretaceous occurrences restricted to North America (D'Emic, 2012, 2013; this study).

*East Asian Cretaceous sauropods*

The Cretaceous of East Asia has played an important role in discussions of sauropod evolutionary history and biogeography. Prior to the Cretaceous, there is currently no unambiguous evidence for the presence of neosauropods in East Asia (Upchurch *et al*., 2004a; Wilson, 2005a; this study), whereas a diverse array of Late Jurassic representatives of this clade is known from all other continents preserving appropriately aged terrestrial sediments (i.e. Africa, Europe, and the Americas; Upchurch *et al*., 2004a; Weishampel *et al*., 2004; Mannion & Calvo, 2011; Whitlock, 2011b; D'Emic, 2012; Mannion *et al*., 2012). Although it is possible that their absence might be a sampling bias (Barrett *et al*., 2002; Wilson & Upchurch, 2009; for example, they might have been low in diversity and abundance, or lived in different, unpreserved/undersampled environments), Middle–Late Jurassic East Asian non-neosauropods are extremely diverse and abundant (Upchurch *et al*., 2004a), leading to the view that the absence of pre-Cretaceous neosauropods might be a genuine pattern, resulting from the isolation of East Asia from the rest of Pangaea during the Middle Jurassic (Russell, 1993; Upchurch, 1995; see discussions in Barrett *et al*., 2002, Upchurch *et al*., 2002, and Wilson & Upchurch, 2009). Poor dating obfuscates the exact end of this isolation (or earliest evidence of East Asian neosauropods, should a sampling bias explanation turn out to be correct), but the East Asian basal titanosauriforms *Dongbeititan* and *Fukuititan* are known from Barremian deposits (Wang *et al*., 2007; Azuma & Shibata, 2010), and earlier macronarian occurrences are known from the ?Berriasian–?Valanginian of Japan (Barrett *et al*., 2002; Saegusa & Tomida, 2011).

A Middle Jurassic–Early Cretaceous East Asian isolation has also been used to support a monophyletic and endemic basal eusauropod clade (Euhelopodidae), comprising the Jurassic taxa *Shunosaurus*, *Omeisaurus*, and *Mamenchisaurus*, and Early Cretaceous *Euhelopus* (Upchurch, 1995, 1998). Whereas the monophyly of this group of taxa has broken down, with *Euhelopus* now regarded as a somphospondylan (e.g. Wilson & Sereno, 1998; Wilson, 2002; Wilson & Upchurch, 2009; D'Emic, 2012; this study), the idea of an euhelopodid clade of titanosauriforms closely related to *Euhelopus* has remained (Canudo *et al*., 2002; Wilson & Upchurch, 2009; see also Ksepka & Norell, 2010), and has recently been formally defined (D'Emic, 2012; see Table 6 for phylogenetic definition). Six Early–middle Cretaceous East Asian species (*Daxiatitan*, *Erketu*, *Euhelopus*, *Phuwiangosaurus*, *Qiaowanlong*, and *Tangvayosaurus*) were recovered as a monophyletic Euhelopodidae by D'Emic (2012), with a number of contemporaneous or slightly stratigraphically younger taxa (*Baotianmansaurus*, *Dongyangosaurus*, *Huabeisaurus*, and *Mongolosaurus*) tentatively assigned to this group based on recovered synapomorphies (D'Emic, 2012: table 9). The affinities of several other East Asian taxa (*Dongbeititan*, *Fukuititan*, *Fusuisaurus*, *Gobititan*, *Huanghetitan*, '*Huanghetitan*' *ruyangensis*, *Jiutaisaurus*, *Pukyongosaurus*, and *Ruyangosaurus*) remained ambiguous within Macronaria, whereas a number of primarily Late Cretaceous taxa (*Jiangshanosaurus*, *Nemegtosaurus*, *Opisthocoelicaudia*, *Qingxiusaurus*, *Sonidosaurus*, and *Xianshanosaurus*) were regarded as derived titanosaurs (D'Emic, 2012).

Here, we found support for an euhelopodid clade in our LSDM analysis, comprising five of the six taxa recovered by D'Emic (2012), as well as two additional taxa (*Gobititan* and *Liubangosaurus*; see Fig. 22). Our Euhelopodidae composition primarily differs in that *Daxiatitan* is recovered as a derived titanosaur. Although the cervical vertebrae of *Daxiatitan* share the presence of ventrolaterally deflected parapophyses, a posteriorly extensive intrapostzygapophyseal lamina, and prong-like epipophyses with euhelopodids, *Daxiatitan* appears to differ from this clade in a number of ways: its cervical neural spines are unbifurcated, its middle-posterior dorsal neural spines are gently bifid, and its anterior caudal vertebrae are strongly procoelous (You *et al*., 2008). However, in our $LSDM_{iw}$ and LCDM analyses (Figs 26, 27), Euhelopodidae is composed only of *Euhelopus* and *Daxiatitan*. Currently, regardless of its composition, euhelopodid taxa are known only from East Asia and thus might

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represent an endemic clade; however, at least one putative occurrence has been described from outside this region. Canudo *et al*. (2002) described spatulate teeth from the Barremian of Spain that possess a lingual boss, a feature currently known only in *Euhelopus* and isolated teeth from the Early Cretaceous of China and Thailand (Buffetaut *et al*., 2002; Barrett & Wang, 2007; Wilson & Upchurch, 2009). Although extension of a clade from East Asia to western Europe based solely on teeth means that this referral must remain tentative, the Early–middle Cretaceous European sauropod fossil record is dominated by fragmentary and poorly preserved specimens (e.g. Upchurch *et al*., 2011b), and so any absence of unambiguous euhelopodid remains might purely reflect a sampling bias.

In addition to a clade of euhelopodids, all other Cretaceous East Asian taxa also represent titanosauriforms (and probably are members of Somphospondyli; although see the non-titanosauriform position of *Dongbeititan* in our LCDM), but appear to correspond to an array of lineages. Some cluster with other East Asian taxa in all analyses, although the membership of these clades often varies. Several taxa are extremely fragmentary and it is difficult to fully reconcile their phylogenetic positions, but there is evidence for derived titanosaurs in the Aptian–Albian, with *Mongolosaurus* recovered as a lithostrotian (or placed just outside that clade), and the caudal vertebra PMU R263 (Upchurch & Mannion, 2009) also displays evidence for belonging to this clade (Whitlock *et al*., 2011; this study). A lithostrotian identification of a contemporaneous embryo from Mongolia (Grellet-Tinner *et al*., 2011) has been refuted and we follow D'Emic (2012) in regarding it as an indeterminate member of Macronaria. The Albian-aged *Jiangshanosaurus* is placed as a saltasaurid (see also Tang *et al*., 2001b; D'Emic, 2012), and as the sister taxon to the latest Cretaceous North American sauropod *Alamosaurus* in all our analyses (Figs 22, 26, 27). This potentially has interesting implications for our understanding of the 'sauropod hiatus' (see above) in that it would support an Asian, rather than South American, origin for the *Alamosaurus* lineage. Whereas an Asian origin has been proposed by other authors (e.g. Wilson & Sereno, 1998), and can be inferred from previous titanosaurian phylogenetic analyses (see discussion in Mannion & Upchurch, 2011), this has always been based on the nesting of *Alamosaurus* with the latest Cretaceous Mongolian taxon *Opisthocoelicaudia*. Thus, the placement of *Jiangshanosaurus* is novel and would imply an approximately 30 million year ghost range for the *Alamosaurus* lineage. Although we cannot determine when the lineage leading to *Alamosaurus* dispersed to North America, dinosaur dispersal between Asia and North America appeared to be possible throughout the middle–Late Cretaceous (D'Emic *et al*., 2010, and references therein), and this ghost range is coeval with the duration of the North American 'sauropod hiatus'. As such, the *Alamosaurus* lineage might be: (1) unsampled purely in East Asia, followed by a latest Cretaceous dispersal to North America, or (2) dispersal might have occurred earlier and the lineage is unsampled in North America until the latest Cretaceous. Teasing these two scenarios apart will have to await increased sampling of Late Cretaceous sediments from both regions. Finally, one important caveat to this is our taxon sampling: the focus of our analysis was on basal titanosauriforms. Although all North American titanosauriform taxa are included, and most East Asian taxa (including *Opisthocoelicaudia*), the vast majority of South American titanosaurs were not incorporated into this study (32 valid, or potentially valid genera omitted; Mannion & Otero, 2012: table 8). As such, a sister-taxon relationship between a South American taxon and *Alamosaurus* or *Jiangshanosaurus* would contradict, or at least complicate, an Asian origin. Increased taxonomic sampling of titanosaurs will be crucial to resolving this issue, as well as determining the ancestry of latest Cretaceous European titanosaurs (see Pereda-Suberbiola, 2009; Garcia *et al*., 2010; Mannion & Upchurch, 2011; Grellet-Tinner *et al*., 2012).

The Late Cretaceous sauropod faunas of China seem to be comprised mainly of titanosaurs, or derived somphospondylans (LSDM), with *Erketu* (and possibly *Huabeisaurus*; D'Emic, 2012) potentially representing a late-surviving euhelopodid (LSDM only). *Dongyangosaurus* [and possibly *Baotianmansaurus* (LSDM) and *Liubangosaurus* ($LSDM_{iw}$ and LCDM)] appears to represent a titanosaur with close affinities to the latest Cretaceous Mongolian taxon *Opisthocoelicaudia*, suggesting a clade of East Asian opisthocoelicaudine saltasaurids, and *Xianshanosaurus* is placed just outside of Lithostrotia (Figs 22, 27). Derived titanosaurian affinities for four further Late Cretaceous Asian taxa that were not included in this analysis (*Nemegtosaurus*, *Qingxiusaurus*, *Quaesitosaurus*, and *Sonidosaurus*) seem well supported (Curry Rogers, 2005; Wilson, 2005a; Xu *et al*., 2006; Mo *et al*., 2008; Wilson & Upchurch, 2009; Ksepka & Norell, 2010; Mannion & Calvo, 2011; D'Emic, 2012), although their relationships to other titanosaurs from East Asia and elsewhere will have to await their incorporation into new phylogenetic analyses.

Lastly, it has been proposed that titanosaurs (You *et al*., 2003), or a more inclusive clade of titanosauriforms (Xu *et al*., 2006), might have originated in East Asia. *Dongbeititan* is recovered as the most basal somphospondylan in our LSDM (and $LSDM_{iw}$) and lies just outside Titanosauriformes in our LCDM

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(Figs 22, 26, 27), which might give some support to this hypothesis. However, the presence of a titanosaur in the Tithonian (Late Jurassic) of Tanzania, the extension of the somphospondylan lineage back to at least the late Oxfordian (as a consequence of the age of the earliest known brachiosaurid), and the existence of possible titanosaurian tracks from the late Middle Jurassic, all indicate that titanosaur (or somphospondylan) origins remain enigmatic, with poor sampling of key time intervals/geographical regions shrouding their early evolutionary history.

## CONCLUSIONS

We have presented a new phylogenetic analysis, focused on elucidating the relationships of basal titanosauriforms, in which we treated quantitative characters as discrete and continuous data in two parallel analyses. Our two analyses agree on the approximate positions of most taxa, but several genera are placed in different parts of the tree depending on the coding/character weighting strategy, and Titanosauria is considerably more diverse when we apply implied weights.

Redescription of the Late Jurassic Portuguese sauropod dinosaur *Lusotitan atalaiensis* demonstrates its validity on the basis of six autapomorphies. Incorporation of *Lusotitan* into a phylogenetic analysis for the first time demonstrates its macronarian affinities, and a brachiosaurid position is partly supported. Our analyses also support the generic separation of *Brachiosaurus altithorax*, *Giraffatitan brancai*, and *Lusotitan atalaiensis*, following recent proposals (Antunes & Mateus, 2003; Upchurch *et al*., 2004a; Taylor, 2009; D'Emic, 2012). '*Brachiosaurus nougaredi*' cannot be referred to *Brachiosaurus* and is a *nomen dubium*, with the various materials included within the species by Lapparent (1960) regarded here as belonging to indeterminate sauropods or titanosauriforms.

The earliest unambiguous body fossil evidence for titanosauriform sauropods is the late Oxfordian (Late Jurassic) brachiosaurid known as the 'French *Bothriospondylus*'. Titanosauriforms are known from Africa, Europe, and the Americas, as well as Pakistan, by the Late Jurassic. Their Late Jurassic absence from Antarctica and Australasia probably reflects a lack of suitably aged outcrops, but their Asian absence might represent a genuine biogeographical pattern. A pre-Cretaceous origin for titanosaurs is supported by the recovery of the Tithonian Tendaguru taxon *Australodocus* as a member of this clade. An earlier origin for titanosaurs (or at least derived somphospondylans), and thus brachiosaurids and Titanosauriformes as a whole, is supported by the late Middle Jurassic Ardley (UK) tracksite (Day *et al*., 2002). Titanosauriform diversity was largely unaffected at the Jurassic/Cretaceous boundary, with somphospondylans becoming the dominant clade of sauropods in the Cretaceous. By the Early Cretaceous, titanosauriforms are known from all continents except Antarctica, for which terrestrial deposits are not yet known from this time interval. There is no evidence for brachiosaurids surviving into the Late Cretaceous, and most basal somphospondylans disappeared in the middle Cretaceous, although this transition to a global fauna dominated by derived titanosaurs appears to have been spatiotemporally staggered.

## ACKNOWLEDGEMENTS

We wish to express our gratitude to all those who allowed us to study sauropod material in their care or helped us with access, in particular: Ronan Allain, Sebastián Apesteguía, Ricardo Araújo, Paul Barrett, Brent Breithaupt, Michael Brett-Surman, Daniel Brinkman, Jorge Calvo, Gao Chunling, Rodolfo Coria, Gao Diansong, David Elliott, Zhang Fengjiao, You Hailu, Oliver Hampe, Pu Hanyong, Amy Henrici, Scott Hocknull, Logan Ivy, Rubén Juárez, Lü Junchang, Sheena Kaal, Tyler Keillor, Nicole Klein, Nils Knötschke, Alejandro Kramarz, Xu Li, Susannah Maidment, Bob Masek, Neffra Matthews, Carl Mehling, John Peel, Juan Porfiri, Stephen Poropat, Matt Riley, Rafael Royo-Torres, Rainer Schoch, Daniela Schwarz-Wings, William Simpson, Trish Sloan, Roger Smith, Solweig Steunes, Corwin Sullivan, Virginia Tidwell, Yuan Wang, Oliver Wings, and Xu Xing. Roger Benson and Michael D'Emic also helped with data collection in China. We are also grateful to M. D'Emic (*Phuwiangosaurus* and *Sonorasaurus*), D. Schwarz-Wings (*Australodocus* and *Tendaguria*), and Matthew Wedel (*Sauroposeidon*) for providing unpublished data; to R. Allain (*Tangvayosaurus*), P. Barrett (*Fusuisaurus* and *Liubangosaurus*), M. D'Emic (*Tendaguria*), R. Royo-Torres (*Aragosaurus* and *Janenschia*), You Hailu (*Qiaowanlong*), and Mo Jin-You (*Fusuisaurus*) for additional photographs of specimens; to Jerry Harris, Liguo Li, and Marina Suarez for help with information on the stratigraphical age of the Hekou Group; and to Matthew Carrano for discussion on the taxonomy of *Lapparentosaurus*. Frequent discussions with M. D'Emic regarding titanosauriform evolution also greatly improved this work, as did comments from two anonymous reviewers. We gratefully acknowledge the Willi Hennig Society, which has sponsored the development and free distribution of TNT, as well as our use of The Paleobiology Database (http://www.paleodb.org), an excellent resource for searching for taxonomic opinions and fossil occurrences. English translations of many of the foreign-language papers used in this study are available at The Polyglot Pale-

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ontologist website (http://www.paleoglot.org). P. D. Mannion's research was funded by the University College London Department of Earth Sciences, an Alexander von Humboldt Research Fellowship at the Museum für Naturkunde (Berlin), and a Junior Research Fellowship at Imperial College London. Additional research visits were supported by grants from the Centre for Ecology and Evolution (London) and the Jurassic Foundation that enabled study of sauropod specimens in China and South America, respectively. P. Upchurch is supported by Leverhulme Trust research grant RPG-129, and received funding from The Palaeontological Association and the Abbey International Collaboration scheme, enabling study of sauropod specimens in Portugal and Spain. R. N. Barnes is supported by NERC studentship NE/F012764/1.

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## APPENDIX 1

### CHARACTER LIST

Characters 1–74 were treated as continuous and discrete characters, respectively, in the two separate analyses; characters 75–279 were treated only as discrete characters. The following characters were treated as ordered: 11, 14, 15, 27, 104, 122, 147, 148, 177, 205, and 259.

Cervical characters always pertain to postaxial cervical vertebrae, unless stated otherwise. The division of cervical and dorsal vertebrae into anterior, middle, and posterior regions was based on splitting each sequence into three equally numbered sets of vertebrae. Serial variation in caudal vertebrae is demarcated here using the following criteria: (1) anterior caudal vertebrae possess ribs, even reduced ones; (2) middle caudal vertebrae lack ribs, but have distinct

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neural spines and postzygapophyses; (3) posterior caudal vertebrae lack ribs, as well as distinct neural spines and postzygapophyses; (4) distal caudal vertebrae lack ribs and neural arches. Nomenclature for vertebral laminae and fossae follow Wilson (1999) and Wilson *et al*. (2011). Neural arch height was measured from the dorsal surface of the centrum up to the base of the articular surfaces of the postzygapophyses, and neural spine height from this point upwards, unless stated otherwise. The scapulocoracoid was treated as if the long axis of the scapular blade was orientated horizontally, whereas in life it would have sloped posterodorsally.

*Quantitative characters*

Cranial characters

C1. *Premaxillary anterior margin, shape*: without step or with anteroposteriorly short 'muzzle', less than 0.25 of skull length (measured up to the anterior point of the ascending process of premaxilla) (0); elongate, boot-shaped snout, equal to or greater than 0.25 of skull length (1) (new character: based on Wilson, 2002).

C2. *External naris, greatest diameter to greatest diameter of orbit ratio:* greater than 1.0 (0); 1.0 or less (1) (McIntosh, 1990; Upchurch, 1995; Upchurch *et al*., 2004a; quantified and polarity reversed here).

C3. *Parietal occipital process, dorsoventral height to greatest diameter of foramen magnum ratio:* greater than 1.0 (0); 1.0 or less (1) (Wilson, 2002; modified and polarity reversed here).

C4. *Parietal, distance separating supratemporal fenestrae to long axis of supratemporal fenestra ratio:* 1.0 or greater (0); less than 1.0 (1) (Wilson, 2002; modified and polarity reversed here).

C5. *Quadratojugal, anterior process to dorsal process length ratio:* 1.3 or less (0); greater than 1.3 (1) (Upchurch, 1998; Wilson & Sereno, 1998; modified here).

C6. *Supraoccipital, dorsoventral height to foramen magnum dorsoventral height ratio:* 1.0 or greater (0); less than 1.0 (1) (Wilson, 2002; modified here).

C7. *Occipital condyle, dorsoventral height to combined occipital condyle + basal tubera dorsoventral height ratio:* less than 0.6 (0); 0.6 or greater (1) (new character: based on Mannion, 2011).

C8. *Basal tubera, mediolateral width to occipital condyle mediolateral width:* less than 1.5 (0); 1.5 or greater (1) (Wilson, 2002; modified here based on Mannion, 2011).

C9. *Basipterygoid processes, length to basal diameter ratio:* less than 3.0 (0); 3.0 or greater (1) (Wilson, 2002; Upchurch *et al*., 2004a; modified here; length is measured up to the base of the basal tubera).

C10. *Surangular, dorsoventral height to maximum dorsoventral height of angular ratio:* 2.0 or greater (0); less than 2.0 (1) (Wilson & Sereno, 1998; Upchurch *et al*., 2004a; polarity reversed here).

C11. *Tooth crowns, slenderness index values (apicobasal length of the tooth crown divided by its maximum mesiodistal width):* less than 2.0 (0); 2.0 to < 4.0 (1); 4.0 or greater (2) (Upchurch, 1998; Upchurch *et al*., 2004a; modified here) [ordered].

C12. *Maxillary teeth, number:* 17 or more (0); fewer than 17 (1) (new character).

C13. *Dentary teeth, number:* greater than 15 (0); 15 or fewer (1) (Wilson & Sereno, 1998; modified here).

Axial characters

C14. *Cervical vertebrae, number:* 13 or fewer (0); 14–15 (1); more than 15 (2) (Upchurch, 1995, 1998; Wilson & Sereno, 1998; modified here) [ordered].

C15. *Cervical centra, highest average elongation index value [aEI; centrum anteroposterior length (excluding articular ball) divided by the mean average value of the posterior articular surface mediolateral width and dorsoventral height] of:* less than 3.0 (0); between 3.0 and < 4.0 (1); greater than 4.0 (2) (Upchurch, 1995, 1998; Upchurch *et al*., 2004a; Chure *et al*., 2010) [ordered].

C16. *Anterior cervical centra, posterior articular face dorsoventral height to mediolateral width ratio:* greater than 1.0 (0); less than 1.0 (1) (Upchurch, 1998; Upchurch *et al*., 2004a; modified and polarity reversed here).

C17. *Middle-posterior cervical centra, posterior articular face dorsoventral height to mediolateral width ratio:* 1.0 or less (0); greater than 1.0 (1) (Curry Rogers, 2005; quantified and polarity reversed here).

C18. *Posterior cervical neural arch to centrum dorsoventral height ratio, measured on anterior face of vertebra (arch height measured from dorsal surface of centrum to base of prezygapophyses):* 0.5 or greater (0); less than 0.5 (1) (new character: based on Bonaparte *et al*., 2006).

C19. *Posterior-most cervical and anterior-most dorsal neural spines, dorsoventral height divided by posterior centrum height:* 1.0 or greater (0); less than 1.0 (1) (D'Emic, 2012; quantified here).

C20. *Dorsal vertebrae, number:* 13 or more (0); 12 or fewer (1) (McIntosh, 1990; Upchurch, 1998; Wilson & Sereno, 1998; Upchurch *et al*., 2004a).

C21. *Anterior dorsal centra, posterior articular face mediolateral width to dorsoventral height ratio:* less than 1.3 (0); 1.3 or greater (1) (new character).

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C22. *Middle-posterior dorsal centra, posterior articular face mediolateral width to dorsoventral height ratio:* less than 1.0 (0); 1.0 or greater (1) (Upchurch, 1998; Upchurch *et al*., 2004a; quantified here).

C23. *Posterior dorsal neural spines, dorsoventral height divided by posterior centrum dorsoventral height:* 1.0 or greater (0); less than 1.0 (1) (McIntosh, 1990; Upchurch, 1995, 1998; modified and polarity reversed here).

C24. *Sacral vertebrae, number:* five or fewer (0); six or more (1) (McIntosh, 1990; Upchurch, 1995, 1998; Wilson & Sereno, 1998).

C25. *Anterior caudal centra, mediolateral width to dorsoventral height (excluding chevron facets) of anterior surface ratio:* less than 1.0 (0); 1.0 or greater (1) (Upchurch *et al*., 2004a; modified and quantified here).

C26. *Anterior caudal centra, lowest aEI [centrum anteroposterior length (excluding articular ball) divided by the mean average value of the anterior surface mediolateral width and dorsoventral height] value of*: less than 0.6 (0); 0.6 or greater (1) (Gauthier, 1986; Upchurch, 1995, 1998; Upchurch *et al*., 2004a; modified and polarity reversed here).

C27. *Anterior caudal centra, anteroposterior length of posterior condylar ball to mean average radius [(mediolateral width + dorsoventral height) divided by 4] of anterior articular surface of centrum ratio:* zero (posterior articular surface of centrum is flat or concave) (0); less than or equal to 0.3 (posterior articular surface of centrum is mildly convex) (1); greater than 0.3 (posterior articular surface of centrum is strongly convex) (2) (McIntosh, 1990; Upchurch, 1995, 1998; Salgado *et al*., 1997; Wilson, 2002; quantified and modified here based on Whitlock *et al*., 2011; note that the highest value for a taxon is always used) [ordered].

C28. *Middle caudal centra, mediolateral width to dorsoventral height (excluding chevron facets) of anterior surface ratio:* less than 1.0 (0); 1.0 or greater (1) (Upchurch *et al*., 2004a; modified and quantified here).

C29. *Middle caudal centra, aEI [centrum anteroposterior length (excluding articular ball) divided by the mean average value of the anterior surface mediolateral width and dorsoventral height (excluding chevron facets)] value:* less than 1.4 (0); 1.4 or higher (1) (Upchurch & Martin, 2003; Upchurch *et al*., 2004a; Whitlock, 2011b; modified here).

C30. *Posterior caudal centra, mediolateral width to dorsoventral height (excluding chevron facets) of anterior surface ratio:* less than 1.2 (0); 1.2 or greater (1) (Upchurch *et al*., 2004a; modified and quantified here).

C31. *Posterior caudal centra, aEI [centrum anteroposterior length (excluding articular ball) divided by the mean average value of the anterior surface mediolateral width and dorsoventral height (excluding chevron facets)] value:* less than 1.7 (0); 1.7 or higher (1) (Upchurch & Martin, 2003; Upchurch *et al*., 2004a; Whitlock, 2011b; modified here).

C32. *Anterior-most caudal neural spines, dorsoventral height divided by centrum height:* 1.2 or greater (0); less than 1.2 (1) (McIntosh, 1990; Calvo & Salgado, 1995; Upchurch, 1995, 1998; modified and polarity reversed here).

C33. *Anterior caudal neural spines, maximum mediolateral width to anteroposterior length ratio:* less than 1.0 (0); 1.0 or greater (1) (Upchurch, 1998; modified and quantified here).

C34. *Anterior caudal neural spines, maximum mediolateral width to minimum mediolateral width ratio:* less than 2.0 (0); 2.0 or greater (spines expand dorsally, forming 'club'- or 'mace'-shaped spinous processes) (1) (Canudo *et al*., 2008; Taylor, 2009; modified and quantified here).

C35. *Anterior chevrons (excluding first chevron), dorsoventral height of haemal canal divided by total chevron height:* less than 0.40 (0); 0.40 or greater (1) (Curry Rogers & Forster, 2001; Wilson, 2002; modified here; note that dorsoventral height of the haemal canal is measured from the proximal tip of the chevron down to the distal tip of the haemal canal, regardless of whether the chevron is dorsally bridged).

### Appendicular characters

C36. *Scapular acromion process, dorsoventral height to minimum dorsoventral height of scapular blade ratio:* less than 3.0 (0); 3.0 or greater (1) (Wilson & Sereno, 1998; modified here; dorsoventral height is measured perpendicular to long axis of scapular blade).

C37. *Scapular blade, maximum (measured at or close to distal end) to minimum dorsoventral height ratio:* 2.0 or greater (0); less than 2.0 (1) (Wilson, 2002; Rose, 2007; modified and quantified here).

C38. *Coracoid, anteroposterior length to dorsoventral height of scapular articulation ratio:* 1.0 or greater (0); less than 1.0 (1) (Wilson, 2002; modified and polarity reversed here).

C39. *Sternal plate, maximum length divided by humerus proximodistal length:* less than 0.65 (0); 0.65 or greater (1) (McIntosh, 1990; Upchurch, 1998; modified here).

C40. *Humerus to femur proximodistal length ratio:* 0.9 or less (0); greater than 0.9 (1) (Wilson, 2002; Upchurch *et al*., 2004a).

C41. *Humerus, maximum mediolateral width of proximal end divided by proximodistal length:* 0.4 or greater (0); less than 0.4 (1) (new character).

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C42. *Humerus, minimum mediolateral width divided by proximodistal length:* 0.15 or greater (0); less than 0.15 (1) (Curry Rogers, 2005; modified and polarity reversed here).

C43. *Humerus shaft eccentricity, mediolateral to anteroposterior width ratio at midshaft:* greater than 1.5 (usually close to 1.8) (0); 1.5 or lower (usually close to 1.3) (1) (Wilson, 2002; Mannion *et al*., 2012; polarity reversed here).

C44. *Radius to humerus proximodistal length ratio:* 0.65 or greater (0); less than 0.65 (1) (Yates & Kitching, 2003; modified here).

C45. *Radius, maximum diameter of the proximal end divided by proximodistal length:* less than 0.3 (0); 0.3 or greater (1) (McIntosh, 1990; Upchurch, 1995, 1998; Upchurch *et al*., 2004a).

C46. *Radius, mediolateral width of proximal to distal end ratio:* 1.0 or greater (0); less than 1.0 (1) (Curry Rogers, 2005; modified, quantified, and polarity reversed here; note that in taxa with a twisted radius, the dimension of the long axis of the distal end is used).

C47. *Radius, distal end mediolateral width to midshaft mediolateral width ratio:* less than 2.0 (0); 2.0 or greater (1) (Wilson, 2002; Rose, 2007; modified here; note that in taxa with a twisted radius, the dimension of the long axis of the distal end is used).

C48. *Radius, distal end mediolateral to anteroposterior width ratio:* 1.5 or greater (0); less than 1.5 (1) (Wilson & Sereno, 1998; quantified and polarity reversed here).

C49. *Radius, distal condyle orientation:* perpendicular or bevelled less than 20° to long axis of shaft (0); bevelled at least 20° to long axis of shaft (1) (Curry Rogers & Forster, 2001; Wilson, 2002; modified here; note that in most taxa only the lateral half of the distal end is bevelled, but this is used as the measurement in those instances).

C50. *Ulna, ratio of maximum mediolateral width of proximal end to ulna length:* gracile, ratio is less than 0.4 (0); stout, ratio is 0.4 or greater (1) (Wilson, 2002; Curry Rogers, 2005; modified here).

C51. *Ulna, ratio of maximum mediolateral width of proximal end (equivalent to anteromedial arm) to maximum anteroposterior width of proximal end (equivalent to anterolateral arm):* less than 2.0 (0); 2.0 or greater (1) (Wilson, 2002; modified and quantified here).

C52. *Metacarpals, longest metacarpal to radius proximodistal length ratio:* less than 0.40 (0); 0.40 or greater (1) (McIntosh, 1990; Calvo & Salgado, 1995; Upchurch, 1998; Wilson & Sereno, 1998; Upchurch *et al*., 2004a).

C53. *Metacarpals, metacarpal I proximal end dorsoventral height to mediolateral width ratio:* less than 1.8 (0); 1.8 or greater (1) (new character: based on Apesteguía, 2005b, and Mannion & Calvo, 2011; note that the metacarpal is measured with the flat surface of the 'D' shape facing laterally, such that the long axis is dorsoventrally aligned).

C54. *Metacarpals, metacarpal I to metacarpal II or III proximodistal length ratio:* less than 1.0 (0); 1.0 or greater (1) (Upchurch, 1998; note that an average is taken when both metacarpals II and III are preserved).

C55. *Metacarpals, metacarpal I to metacarpal IV proximodistal length ratio:* less than 1.0 (0); 1.0 or greater (1) (Wilson & Sereno, 1998).

C56. *Manual ungual on digit I to metacarpal I proximodistal length ratio:* 0.5 or greater (0); less than 0.5 (1) (Upchurch *et al*., 2004a; modified here).

C57. *Ilium, pubic peduncle (measured at the articular surface), anteroposterior to mediolateral width ratio:* greater than 0.5 (0); 0.5 or less (1) (new character: based on Taylor, 2009).

C58. *Pubis, iliac articular surface, anteroposterior to mediolateral width ratio:* less than 2.0 (0); 2.0 or greater (1) (new character: based on Mannion & Calvo, 2011).

C59. *Pubis, dorsoventral height of ischial articulation of the pubis divided by pubis proximodistal length is:* 0.4 or greater (0); less than 0.4 (1) (Salgado *et al*., 1997; Wilson & Sereno, 1998; Upchurch *et al*., 2004a; modified and polarity reversed here).

C60. *Ischium to pubis proximodistal length ratio:* greater than 0.8 (0); 0.80 or less (1) (Calvo & Salgado, 1995; Salgado *et al*., 1997; Upchurch, 1998; modified here).

C61. *Ischium, ratio of anteroposterior length of proximal plate to ischium proximodistal length:* greater than 0.25 (0); 0.25 or less (1) (new character).

C62. *Ischium, ratio of anteroposterior length of iliac peduncle to anteroposterior length of proximal plate:* less than 0.7 (large ischial contribution to acetabulum) (0); 0.7 or greater (small ischial contribution to acetabulum) (1) (Wilson, 2002; D'Emic, 2012; modified and quantified here).

C63. *Ischium, ratio of dorsoventral width across the distal shaft (mediolateral in taxa with fully coplanar shafts) to ischium proximodistal length:* 0.2 or greater (0); less than 0.2 (1) (Jacobs *et al*., 1993; Upchurch, 1998; Upchurch *et al*., 2004a; modified and polarity reversed here).

C64. *Ischium, ratio of dorsoventral width of distal end of shaft to minimum shaft dorsoventral width (both dimensions are mediolateral in taxa with fully coplanar shafts):* 1.5 or greater (0); less than 1.5 (1) (Berman & McIntosh, 1978; McIntosh, 1990; Upchurch, 1995, 1998; modified, quantified, and polarity reversed here).

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C65. *Femur shaft eccentricity, mediolateral width to anteroposterior width ratio at midshaft:* less than 1.85 (0); 1.85 or greater (1) (Wilson, 2002; modified here).

C66. *Femoral distal condyles, tibial to fibular condylar anteroposterior length ratio:* less than 1.2 (0); 1.2 or greater (1) (Upchurch *et al*., 2004a; modified here).

C67. *Tibia, distal end mediolateral width to long axis of a cross-section horizontally through the midshaft ratio:* 2.0 or greater (0); less than 2.0 (1) (Wilson, 2002; modified and polarity reversed here; midshaft dimension modified to reflect that the shafts of many sauropod tibiae are twisted, such that a transverse width at midshaft would not always relate to the same dimension between taxa).

C68. *Tibia, distal end, mediolateral to anteroposterior width ratio:* 1.5 or greater (0); less than 1.5 (1) (Salgado *et al*., 1997; Upchurch *et al*., 2004a; modified here).

C69. *Fibula, mediolateral width of distal end to mediolateral width at midshaft ratio:* 2.0 or greater (0); less than 2.0 (1) (Wilson, 2002; polarity reversed here).

C70. *Astragalus, mediolateral width to maximum proximodistal height ratio:* 1.8 or greater (0); less than 1.8 (1) (Wilson, 2002; modified here).

C71. *Astragalus, mediolateral width to maximum anteroposterior length ratio:* 1.5 or greater (0); less than 1.5 (1) (D'Emic, 2012; modified here).

C72. *Metatarsals, metatarsal I to metatarsal V proximodistal length ratio:* less than 1.0 (0); 1.0 or greater (1) (new character).

C73. *Metatarsals, metatarsal III to tibia proximodistal length ratio:* less than 0.25 (0); 0.25 or greater (1) (Wilson & Sereno, 1998; Upchurch *et al*., 2004a; modified and polarity reversed here).

C74. *Metatarsals, metatarsal V proximal end to distal end maximum mediolateral width ratio:* 1.6 or greater (0); less than 1.6 (1) (new character).

*Discrete characters*

Cranial characters

C75. *Premaxilla, posterolateral processes and lateral processes of maxilla:* without midline contact (0); with midline contact forming marked narial depression, subnarial foramen not visible laterally (1) (Upchurch, 1998; Wilson & Sereno, 1998).

C76. *Premaxillary anterior margin, shape:* with step (0); without step (1) (Upchurch, 1995, 1998; Wilson & Sereno, 1998; polarity reversed here).

C77. *Premaxilla–maxilla sutural contact, shape in lateral view:* straight (0); sinuous (1) (Chure *et al*., 2010).

C78. *Maxillary ascending process, medial plate-like projections:* do not contact each other on the midline (0); contact each other on the midline (1) (Upchurch, 1998).

C79. *Maxilla, preantorbital fenestra:* absent (0); present (1) (Berman & McIntosh, 1978; Upchurch, 1995, 1998; Wilson & Sereno, 1998).

C80. *Lacrimal, anterior process:* absent (0); present (1) (Wilson, 2002; polarity reversed here).

C81. *Jugal–quadratojugal contact:* articulation point includes the posterior margin of jugal (0); posterior margin of jugal excluded from articulation and only the ventral margin of the jugal contributes to articulation (1) (Curry Rogers, 2005; modified here).

C82. *Prefrontal, shape of posterior end in dorsal view:* acute, with a subtriangular outline (0); broadly rounded or 'square' (1) (Berman & McIntosh, 1978; Upchurch, 1998; polarity reversed here).

C83. *Frontal, medial convexity in dorsal view:* absent (0); present (1) (Curry Rogers, 2005).

C84. *Parietal, elongate posterolateral process:* present (0); absent (1) (Curry Rogers, 2005; polarity reversed here).

C85. *Parietal, contribution to post-temporal fenestra:* present (0); absent (1) (Wilson, 2002).

C86. *Supratemporal fenestra, lateral exposure:* visible laterally, temporal bar shifted ventrally (0); not visible laterally, obscured by temporal bar (1) (Wilson & Sereno, 1998; polarity reversed here).

C87. *Postorbital, ventral process:* anteroposterior and mediolateral diameters equal, or mediolaterally compressed (0); anteroposteriorly compressed (1) (Wilson & Sereno, 1998; Upchurch *et al*., 2004a).

C88. *Infratemporal (or laterotemporal) fenestra, anterior extension:* reaching midpoint of orbit (0); reaching or surpassing anterior margin of orbit (1) (Upchurch, 1995, 1998; Ksepka & Norell, 2010; modified here).

C89. *Squamosal–quadratojugal contact:* present (0); absent (1) (Gauthier, 1986; Upchurch, 1995, 1998; Wilson & Sereno, 1998).

C90. *Quadratojugal, anterior ramus, ventral triangular projection (close to the anterior tip):* absent (0); present (1) (D'Emic, 2012).

C91. *Quadrate, excavation in the posterior surface:* absent or shallow (0); deep (1) (Wilson & Sereno, 1998; Upchurch *et al*., 2004a).

C92. *Quadrate fossa, orientation:* posterior (0); posterolateral (1) (Wilson, 2002).

C93. *Palatobasal contact for basipterygoid articulation has a dorsomedially orientated 'hook'- or 'finger'-like projection, which curves round to clasp the end of the basipterygoid process:* present (0); absent (1) (Madsen *et al*., 1995; Upchurch, 1998; Wilson & Sereno, 1998; Wilson, 2002; modified and polarity reversed here).

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C94. *Palatine, dorsomedial blade (that articulates with maxilla), lateral margin:* curved (0); straight (1) (new character: based on Wilson & Upchurch, 2009).
C95. *Vomer, anterior articulation with:* maxilla (0); premaxilla (1) (Wilson, 2002).
C96. *Paroccipital process, ventral non-articular process:* absent (0); present (1) (Wilson, 2002).
C97. *Basal tubera, degree of divergence:* no divergence, or restricted to ventral half of basal tubera (0); extends into dorsal half of basal tubera, usually fully divergent (1) (Curry Rogers, 2005; modified here based on Mannion, 2011).
C98. *Basioccipital, fossa/fossae on the posterior surface of the basal tubera:* absent (0); present (1) [Wilson, 2002; modified here (see also Mannion, 2011)].
C99. *Basioccipital, foramen/foramina between basal tubera and basipterygoid processes:* present (0); absent (1) [Wilson, 2002; modified here (see also Mannion, 2011)].
C100. *Basisphenoid–quadrate contact:* absent (0); present (posterior surface of basal tubera bordered laterally and ventrally by a raised lip) (1) (Wilson, 2002, 2005a).
C101. *Basipterygoid processes, shape in cross-section:* elliptical or subtriangular (0); subcircular (1) (Upchurch *et al*., 2004a).
C102. *External mandibular fenestra:* present (0); absent (1) (McIntosh, 1990; Upchurch, 1995).
C103. *Dentary, posteroventral process, shape:* single (0); forked (1) (Chure *et al*., 2010).
C104. *Tooth rows:* restricted anterior to orbit (0); restricted anterior to antorbital fenestra (1); restricted anterior to external naris (2); restricted anterior to subnarial foramen (3) (Gauthier, 1986; Upchurch, 1998; Wilson, 2002; modified by Chure *et al*., 2010 and here) [ordered].
C105. *Teeth, occlusal (wear) pattern:* interlocking, V-shaped facets (0); high-angled planar facets (1); low-angled planar facets (2) (Wilson & Sereno, 1998).
C106. *Tooth crowns, orientation:* aligned anterolingually, tooth crowns overlap (0); aligned along jaw axis, crowns do not overlap (1) (Wilson, 2002; polarity reversed here).
C107. *Tooth crowns in upper and lower tooth rows, relative diameters:* subequal (0); lower crowns smaller than upper crowns (1) (Chure *et al*., 2010).
C108. *Tooth crowns, shape in labial view:* spatulate or 'spoon'-like (i.e. constricted at the base relative to midheight of the crown) (0); parallel-sided (i.e. little expansion above the root) (1) (Calvo, 1994; Upchurch, 1998).
C109. *Tooth crowns, cross-sectional shape at mid-crown:* 'D'-shaped (0); cylindrical (1) (Wilson & Sereno, 1998; modified here).
C110. *Tooth crowns, lingual surface:* concave or flat (0); convex (1) (Upchurch, 1998; Upchurch *et al*., 2004a; polarity reversed here).
C111. *Tooth crowns, apicobasally orientated lingual ridge:* present (0); absent (1) (new character: based on Barrett *et al*., 2002).
C112. *Tooth crowns, distinct mesial and distal carinae (labiolingually thinner than the rest of the tooth crown) along the full crown length:* absent (0); present (1) (new character: based on Mannion, 2011).
C113. *Tooth serrations/denticles:* present (0); absent (1) (Wilson, 2002; Upchurch *et al*., 2004a; modified here).
C114. *Maxillary teeth, shape:* straight along axis (0); twisted axially through an arc of 30–45° (1) (Chure *et al*., 2010; D'Emic, 2012).

## Axial characters

C115. *Cervical and anterior-most dorsal vertebrae, internal tissue structure:* solid (0); camerate (1); camellate (2) (Wilson & Sereno, 1998; Carballido *et al*., 2011b; modified here to separate the anterior portion of the presacral series and middle-posterior dorsal vertebrae).
C116. *Atlantal intercentrum, occipital facet shape:* rectangular in lateral view, length of dorsal aspect subequal to that of ventral aspect (0); expanded anteroventrally in lateral view, anteroposterior length of dorsal aspect shorter than that of ventral aspect, producing an anteroventral lip (1) (Wilson, 2002).
C117. *Cervical axis, midline ventral keel:* absent (0); present (1) (new character: based on Mannion, 2011).
C118. *Postaxial cervical centra, anterior half of ventral surfaces are:* flat or mildly convex mediolaterally (0); concave mediolaterally (1) (Upchurch, 1998; modified here to distinguish between anterior and posterior concavities).
C119. *Postaxial cervical centra, posterior half of ventral surfaces are:* flat or mildly convex mediolaterally (0); concave mediolaterally (1) (Upchurch, 1998; modified here to distinguish between anterior and posterior concavities).
C120. *Postaxial cervical centra, ventral midline keel:* present (0); absent (1) (Upchurch, 1998; modified here).
C121. *Postaxial cervical centra, parapophyses dorsally excavated:* absent (0); present (1) (Upchurch, 1998; modified here).
C122. *Postaxial cervical centra, lateral surfaces:* lack an excavation or have a shallow fossa (0); possess a deep foramen that is not divided into portions by accessory laminae (1); have a deep foramen that is divided into separate portions by one prominent and occasionally several

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smaller accessory laminae (2) (McIntosh, 1990; Russell & Zheng, 1993; Upchurch, 1995, 1998) [ordered].

C123. *Middle cervical centra, lateral pneumatic fossa/foramen extends almost to the posterior end of the centrum, leaving only a thin strip of bone:* absent (0); present (1) (new character: based on Wedel *et al*., 2000a; D'Emic, 2013).

C124. *Middle-posterior cervical centra, parapophyses, dorsal surfaces:* face dorsally or slightly dorsolaterally (0); deflected to face strongly dorsolaterally, such that the cervical ribs are displaced ventrally at least the same height as the centrum (1) (Wilson & Upchurch, 2009; D'Emic, 2012; modified here).

C125. *Middle-posterior cervical centra, parapophyses:* restricted to anterior half of centrum (excluding condylar ball) (0); elongate, extending more than half of the centrum length (excluding condylar ball) (D'Emic, 2012; modified here).

C126. *Cervical neural arches, 'pre-epipophyses' present on prezygapophyses:* absent (0); present (1) (new character: based on Wilson & Upchurch, 2009).

C127. *Cervical neural arches, epipophyses present on postzygapophyses:* absent (0); present (1) (Yates, 2007).

C128. *Cervical neural arches (post-Cv3), epipophyses:* do not extend beyond the posterior margin of the postzygapophyses (0); extend beyond the posterior margin of the postzygapophyses (usually as prongs) (1) (Sereno *et al*., 1993; Yates, 2007; D'Emic, 2012; modified here).

C129. *Cervical neural arches, epipophyseal–prezygapophyseal lamina (EPRL):* absent (0); present (1) (Sereno *et al*., 2007; Wilson & Upchurch, 2009) [D'Emic (2012: C25; p. 661) included two character states to describe different morphologies for an EPRL – his plesiomorphic state is the same as our derived state here (i.e. the presence of an EPRL), whereas his derived state pertained to an EPRL that comprises a 'thick, subvertically oriented strut that joins the spinopostzygapophyseal lamina at the neural spine'. However, this is vague and problematic in that it is not clear that this strut contacts either the epipophysis or the prezygapophysis. Furthermore, with the exception of *Erketu*, in which there is an additional lamina (see Wilson *et al*., 2011: fig. 6d–e) that might be best described as a spinodiapophyseal lamina, it is difficult to see how this ridge is anything other than a postzygodiapophyseal lamina (PODL), a feature present in all sauropods].

C130. *Middle-posterior cervical neural arches, centroprezygapophyseal lamina:* single (0); bifurcates into medial and lateral branches that both contact the prezygapophysis (1) (Upchurch, 1995, 1998; Wilson, 2002; modified here based on Whitlock, 2011a: 337).

C131. *Middle-posterior cervical neural arches, intrapostzygapophyseal lamina projects beyond the posterior margin of the neural arch [including the centropostzygapophyseal laminae (CPOL)], forming a prominent subrectangular projection in lateral view:* absent (0); present (1) (D'Emic, 2012; modified here).

C132. P*ostaxial cervical and anterior dorsal neural spines:* unbifurcated (0); bifurcated (1) (Gauthier, 1986; McIntosh, 1990; Upchurch, 1995, 1998; Wilson & Sereno, 1998).

C133. *Cervical bifurcated neural spines (excluding the posterior-most cervical vertebrae), median process at base of 'notch':* absent (0); present (1) (Gauthier, 1986; McIntosh, 1990; Upchurch, 1995, 1998; Wilson & Sereno, 1998; modified here).

C134. *Middle cervical neural spines, abrupt increase in height (height approximately doubled), following low anterior cervical neural spines (occurs around Cv6–8):* absent (0); present (1) (new character: based on Wedel *et al*., 2000a; Rose, 2007).

C135. *Middle cervical neural spines, dorsal surface with mediolaterally orientated midline ridge flanked by small fossae at its anterior and posterior ends:* absent (0); present (1) (new character: based on D'Emic, 2013).

C136. *Posterior-most cervical and anterior dorsal neural arches, spinodiapophyseal lamina (SPDL):* single structure (0); divided into anterior and posterior spinodiapophyseal laminae (1) (Salgado *et al*., 1997; Salgado & Powell, 2010; D'Emic, 2012).

C137. *Posterior-most cervical and anterior dorsal unbifurcated neural spines, prespinal lamina:* absent (0); present (1) (Salgado *et al*., 1997; D'Emic, 2012).

C138. *Posterior-most cervical and anterior dorsal bifurcated neural spines, 'trifid' with median tubercle at least as tall as metapophyses:* absent (0); present (1) (Wilson & Upchurch, 2009; D'Emic, 2012; modified here).

C139. *Cervical ribs, longest shafts are:* short and do not project far beyond the end of the centrum to which they attach (0); elongate and form overlapping bundles (1) (McIntosh, 1990; Upchurch, 1995, 1998; polarity reversed here).

C140. *Cervical ribs, longest shafts extend beneath:* fewer than three vertebrae (0); three vertebrae or more (1) (new character: based on Wedel *et al*., 2000a).

C141. *Middle-posterior dorsal vertebrae, internal tissue texture:* solid (0); camerate (1); camellate (2) (Wilson & Sereno, 1998; Carballido *et al*., 2011b; modified here to separate the anterior portion of

the presacral series and middle-posterior dorsal vertebrae).

C142. *Dorsal centra, ventral keel:* absent (0); present (1) (Mannion *et al*., 2012; modified here).

C143. *Dorsal centra, lateral pneumatic foramen:* absent (0); present (1) (Upchurch, 1998).

C144. *Dorsal centra, lateral pneumatic foramina are:* shallow fossae or excavations that do not ramify throughout the centrum (0); deep excavations that ramify throughout the centrum and into the base of the neural arch, often leaving only a thin septum on the midline of the centrum (1) (Upchurch, 1998; modified here).

C145. *Dorsal centra, lateral pneumatic foramina:* have margins that are flush with the lateral surface of the centrum (0); are set within a lateral fossa on the lateral surface of the centrum (1) (Bonaparte & Coria, 1993; Upchurch *et al*., 2004a).

C146. *Anterior dorsal centra, lateral pneumatic foramina have:* rounded posterior margins (0); acute posterior margins (1) (Upchurch, 1998).

C147. *Middle-posterior dorsal centra, anterior articular face shape:* flat or concave (0); mildly convex, with degree of convexity notably reducing along the dorsal sequence (1); strongly convex, with degree of convexity approximately consistent along the dorsal sequence (2) (Salgado *et al*., 1997; Wilson & Sereno, 1998; modified here) [ordered].

C148. *Middle-posterior dorsal neural arches, posterior centroparapophyseal lamina:* absent (0); present as a single lamina (1); two parallel laminae (2) (Upchurch, 1998; Wilson, 2002; D'Emic, 2012; modified here) [ordered].

C149. *Middle-posterior dorsal neural arches, hyposphene–hypantrum system:* present (0); absent (1) (Salgado *et al*., 1997; Upchurch, 1998).

C150. *Middle-posterior dorsal neural arches, hyposphene shape:* narrow, ventral end subequal to or only slightly wider than dorsal tip (0); wide, triangular shape, with ventral end at least twice width of dorsal tip (1) (new character: based on Apesteguía, 2005a).

C151. *Middle-posterior dorsal neural arches, posterior centrodiapophyseal lamina (PCDL):* has an unexpanded ventral tip (0); expands and bifurcates towards its ventral tip (1) (Salgado *et al*., 1997).

C152. *Middle-posterior dorsal neural arches, PODL:* present (0); absent (1) (Salgado *et al*., 1997; Sanz *et al*., 1999; polarity reversed here).

C153. *Anterior dorsal diapophyses are:* directed laterally or slightly upwards (0); directed strongly dorsolaterally at approximately 45° to the horizontal (1) (Upchurch, 1998; modified here to separate anterior and middle-posterior dorsal vertebrae).

C154. *Anterior-middle dorsal diapophyses:* short and dorsoventrally tall (0); elongate and dorsoventrally narrow (1) (Janensch, 1950; Taylor, 2009; D'Emic, 2012).

C155. *Middle-posterior dorsal diapophyses are:* directed strongly dorsolaterally at approximately 45° to the horizontal (0); directed laterally or slightly upwards (1) (Upchurch, 1998; polarity reversed here; modified here to separate anterior and middle-posterior dorsal vertebrae).

C156. *Middle-posterior dorsal diapophyses, distal end:* curves smoothly into the remaining dorsal surface of the process (0); is set off from the remaining dorsal surface by a lip, forming a distinct area (1) (Sanz *et al*., 1999; Upchurch *et al*., 2004a; D'Emic, 2012).

C157. *Posterior-most dorsal diapophyses lie:* posterior or posterodorsal to the parapophysis (0); vertically above the parapophysis (1) (Upchurch, 1998).

C158. *Dorsal neural spines, height:* anterior dorsal neural spines subequal to or dorsoventrally shorter than posterior dorsal neural spines (0); anterior dorsal neural spines dorsoventrally taller than posterior dorsal neural spines (1) (new character: based on Wilson, 2002; Taylor, 2009).

C159. *Dorsal neural spines, anteroposterior width:* approximately constant along the height of the spine, with subparallel anterior and posterior margins (0); narrows dorsally to form a triangular shape in lateral view, with the base approximately twice the width of the dorsal tip (1) (new character: based on Taylor, 2009).

C160. *Anterior dorsal neural spines, orientation:* project dorsally or slightly anterodorsally (0); project posterodorsally (1) (Upchurch *et al*., 2004a; modified here).

C161. *Middle dorsal neural spines:* unbifurcated (0); bifurcated (dorsal surface excavated transversely) (1) (new character).

C162. *Middle-posterior dorsal neural spines:* tapering or not flaring distally (0); flared distally with triangular aliform processes projecting laterally from the top [formed primarily from the expansion of the spinopostzygapophyseal laminae (SPOLs)] (1) (Upchurch, 1998; Wilson & Sereno, 1998; Wilson, 2002; Upchurch *et al*., 2004a).

C163. *Middle-posterior dorsal neural spines:* tapering or not flaring distally, or with absent or weakly developed triangular aliform processes (0); strongly developed triangular aliform processes so that the lateral tips of these processes extend further laterally than the postzygapophyses (1) (Upchurch, 1998; Wilson & Sereno, 1998; Wilson, 2002; Upchurch *et al*., 2004a).

C164. *Middle-posterior dorsal neural spines, orientation:* vertical or slightly posterodorsal (0); strongly posterodorsal, neural spine summit

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approaches level of diapophyses (1) (Wilson, 2002; modified here).

C165. *Middle-posterior dorsal neural spines, SPOL shape:* single (0); divided into medial and lateral branches (1) (Wilson, 1999, 2002).

C166. *Middle-posterior dorsal neural spines, SPDL:* absent or restricted to posterior dorsals (0); present on middle and posterior dorsals (1) (Wilson, 2002; Upchurch *et al*., 2004a).

C167. *Middle-posterior dorsal neural spines, prespinal and postspinal laminae:* form mediolaterally wide surfaces, with little anterior relief, 'infilling' the prespinal and postspinal fossae (0); form distinct, mediolaterally narrow ridges or laminae along the midline of the prespinal and postspinal fossae (1) (new character).

C168. *Middle-posterior dorsal neural spines, midline prespinal lamina (forming distinct ridge) along proximal (lower) half of neural spine:* present (0); absent (1) (Salgado *et al*., 1997; Curry Rogers, 2005; modified and polarity reversed here; note that taxa coded as '0' for C167 are scored as a '?' here).

C169. *Middle-posterior dorsal neural spines, postspinal lamina (forming distinct ridge) along proximal (lower) half of neural spine:* present (0); absent (1) (Bonaparte, 1986; Upchurch, 1995, 1998; Curry Rogers, 2005; modified and polarity reversed here; note that taxa coded as '0' for C167 are scored as a '?' here).

C170. *Thoracic (dorsal) ribs, pneumatized (with proximal pneumatocoels):* absent (0); present (1) (Wilson & Sereno, 1998).

C171. *Anterior thoracic ribs, cross-sectional shape:* subcircular (0); plank-like, anteroposterior breadth more than three times mediolateral breadth (1) (Wilson, 2002).

C172. *Sacral vertebrae, camellate internal tissue structure:* absent (0); present (1) (new character).

C173. *Sacral centra, lateral pneumatic foramina or very deep depressions:* absent (0); present (1) (Upchurch, 1998).

C174. *Sacral neural spines, dorsal portions of at least sacral vertebrae 1–4 fused, forming a dorsal 'platform':* absent (0); present (1) (new character: based on Lü *et al*., 2007).

C175. *Caudal vertebrae, number:* more than 35 (0); 35 or fewer (1) (Wilson, 2002; modified here).

C176. *Anterior-most caudal vertebrae, camellate internal tissue structure:* absent (0); present (1) (Powell, 1986; Wilson, 2002).

C177. *Anterior caudal centra, posterior articular surface:* flat or concave throughout series (0); convex in anterior-most caudal vertebrae, changing to flat or concave in more distal anterior caudal vertebrae (1); convex throughout all anterior caudal vertebrae with ribs (2) (new character) [ordered].

C178. *Anterior caudal centra, lateral pneumatic fossae or foramina:* absent (0); present, (McIntosh, 1990; Upchurch, 1995).

C179. *Anterior caudal centra, lateral pneumatic fossae or foramina:* without sharply defined margins (0); with sharply defined margins (1) (new character based on Tidwell *et al*., 2001; Whitlock *et al*., 2011).

C180. *Anterior–middle caudal centra, small, shallow vascular foramina pierce the lateral and/or ventral surfaces:* absent (0); present (1) (new character: based on Mannion & Calvo, 2011).

C181. *Anterior–middle caudal centra (excluding the anterior-most caudal vertebrae), ventral longitudinal hollow:* absent (0); present (1) (McIntosh, 1990; Upchurch, 1995, 1998; Wilson, 2002).

C182. *Anterior–middle caudal centra (excluding the anterior-most caudal vertebrae), distinct ventrolateral ridges, extending the full length of the centrum:* absent (0); present (1) (McIntosh, 1990; Upchurch, 1995, 1998; Upchurch *et al*., 2004a; modified here).

C183. *Middle caudal centra, anteroposteriorly elongate ridge situated at approximately two-thirds of the way up the lateral surface:* absent (0); present (1) (new character: based on Upchurch & Martin, 2003).

C184. *Middle-posterior caudal centra (at least some), posterior articular surface:* flat or concave (0); convex (1) (Jacobs *et al*., 1993; Upchurch, 1995, 1998; Salgado *et al*., 1997; Wilson, 2002).

C185. *Middle-posterior caudal centra with convex posterior articular surface:* condylar convexity merges smoothly into the lateral surface of the main body of the centrum (0); distinct rim rings the condyle, separating it from the lateral surface of the main body of the centrum (1) (new character).

C186. *Distal caudal centra, biconvex:* absent (0); present (1) (Wilson & Sereno, 1998).

C187. *Anterior caudal neural arches, hyposphenal ridge:* present (0); absent (1) (Upchurch, 1998; polarity reversed here; usually only present in the anterior-most region of the tail).

C188. *Anterior caudal neural arches, hyposphenal ridge shape:* slender ridge (0); block-like hyposphene (1) (new character: based on Taylor, 2009).

C189. *Anterior caudal neural arches, distinct prezygodiapophyseal lamina:* absent (0); present (1) (Chure *et al*., 2010; usually only present in the anterior-most region of the tail).

C190. *Anterior caudal neural arches, sharp-lipped lateral coel (postzygapophyseal centrodiapophyseal fossa of Wilson et al., 2011) bounded by PCDL (or caudal rib itself), CPOL, and PODL:* absent (0); present (1) (new character: based on Lü *et al*., 2008; Whitlock *et al*., 2011).

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C191. *Anterior–middle caudal neural arches, prezygapophyses switch from projecting anterodorsally, anteriorly, and back to anterodorsally along the sequence:* absent (0); present (1) (new character: based on Mannion & Calvo, 2011).

C192. *Middle caudal neural arches:* situated over the midpoint of the centrum with approximately subequal amounts of the centrum exposed at either end (0); located on the anterior half of the centrum (1) (Calvo & Salgado, 1995; Upchurch, 1995, 1998; Salgado *et al*., 1997).

C193. *Middle-posterior caudal neural arches, distance that prezygapophyses extend beyond the anterior margin of the centrum:* less than 20% of centrum length (excluding ball), short prezygapophyses (0); 20% or greater of centrum length (excluding ball), elongate prezygapophyses (1) (González Riga, 2003; modified here; note that in taxa without anteriorly biased neural arches this prezygapophyseal extension is extrapolated as if the arch was anteriorly positioned on the centrum).

C194. *Anterior-most caudal neural spines, sharp-lipped lateral coel [spinodiapophyseal fossa (SDF) of Wilson et al. 2011] bounded by spinoprezygapophyseal lamina (SPRL), SPOL, and PODL:* absent (0); present (1) (Wilson, 2002; modified here based on Whitlock *et al*., 2011, and Wilson *et al*., 2011).

C195. *Anterior caudal neural spines, project:* posterodorsally (0); dorsally (sometimes with a subtle anterior deflection) (1) (González Riga *et al*., 2009; modified and polarity reversed here).

C196. *Anterior caudal neural spines, anterodorsal margin of neural spine:* level with or posterior to posterior margin of postzygapophyses (0); situated anterior to posterior margin of postzygapophyses (usually does not even approach postzygapophyses) (1) (Salgado *et al*., 1997; modified here).

C197. *Anterior caudal neural spines, prespinal and postspinal laminae:* absent or form mediolaterally wide surfaces, with little anterior relief, 'infilling' the prespinal and postspinal fossae (0); form distinct, mediolaterally narrow ridges or laminae along the midline of the prespinal and postspinal fossae (1) (new character).

C198. *Anterior caudal neural spines, SPRL–SPOL contact:* absent (0); present, forming a prominent lateral lamina on the neural spine (1) (Wilson, 1999, 2002).

C199. *Middle caudal neural spines, in lateral view, widen anteroposteriorly (approximately doubling) from their base to their summit:* absent (0); present (1) (new character).

C200. *Middle caudal neural spines, extend posteriorly to the midpoint (or beyond) of the proceeding caudal centrum:* present (0); absent (usually do not extend beyond the posterior margin of the centrum) (1) (Remes *et al*., 2009; modified here; note that in taxa with anteriorly biased neural arches this posterior extension is extrapolated as if the arch was centrally positioned on the centrum).

C201. *Caudal ribs:* present beyond approximately Cd10 (usually at least up to approximately Cd15) (0); only present through to approximately Cd10 (1) (Upchurch, 1998; Wilson, 2002).

C202. *First caudal rib (transverse process), with prominent ventral bulge:* absent (0); present (1) (Wilson, 2002; Chure *et al*., 2010; modified here; note that this feature is sometimes present in subsequent caudal vertebrae too: consequently, this character is coded as the derived state if present in any anterior caudal vertebrae, but coded as a '?' if the first caudal vertebra is not preserved and the feature is absent in other anterior caudal vertebrae).

C203. *First caudal rib, expands anteroposteriorly towards its distal end, forming an 'anchor' shape in dorsal view:* absent (0); present (1) (new character: based on Suteethorn *et al*., 2010).

C204. *Anterior caudal ribs, shape in anterior view:* triangular, tapering distally (0); wing-like, with a dorsolaterally orientated dorsal margin (1) (Berman & McIntosh, 1978; McIntosh, 1990; Upchurch, 1995, 1998; Whitlock *et al*., 2011).

C205. *Anterior caudal ribs:* curve strongly anterolaterally (0); mainly laterally (1); curve strongly posterolaterally (2) (new character: based on Mannion & Calvo, 2011) [ordered].

C206. *Anterior caudal ribs:* do not extend beyond posterior end of centrum (excluding posterior ball) (0); extend beyond posterior end of centrum (excluding posterior ball) (1) (new character: based on Mannion & Calvo, 2011).

C207. *First chevron, morphology:* Y-shaped and does not differ notably from subsequent chevrons (0); anteroposteriorly flattened and V-shaped, with dorsoventrally reduced distal blade (1) (new character: based on Gomani, 2005; Rauhut, 2006; Mannion & Calvo, 2011).

C208. *Anterior chevrons, proximal ends:* open dorsally (0); bridged dorsally by a bar of bone (1) (Powell, 1992; Calvo & Salgado, 1995; Upchurch, 1995, 1998; polarity reversed here).

C209. *Anterior–middle chevrons, lateral bulges close to distal ends of chevron blades:* absent (0); present (1) (new character).

C210. *Middle-posterior chevrons, with anterior expansion of distal blade:* present (0); absent (1) [Berman & McIntosh, 1978; Upchurch, 1995, 1998; Wilson & Sereno, 1998; modified (and polarity reversed) here to separate development of anterior and posterior projections].

C211. *Middle-posterior chevrons, with posterior expansion of distal blade (excluding the natural pos-*

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*teroventral curvature of many chevrons):* present (0); absent (1) [Berman & McIntosh, 1978; Upchurch, 1995, 1998; Wilson & Sereno, 1998; modified (and polarity reversed) here to separate development of anterior and posterior projections].

Appendicular (and miscellaneous) characters

C212. *Scapular acromion (proximal plate), area situated posterior to the acromial ridge:* flat or convex (0); forms a separate excavated area (1) (Upchurch *et al*., 2004a).

C213. *Scapular glenoid surface, orientation:* faces anteroventrally and/or slightly laterally (0); deflected to face anteroventrally and medially (1) (Wilson & Sereno, 1998; Upchurch *et al*., 2004a).

C214. *Scapula, posterior margin of the dorsal part of the acromion:* straight and orientated vertically, or sloping to face posterodorsally (0); concave, posterodorsal corner of *acromion* overhangs the dorsal surface of the scapular blade (1) (Rauhut *et al*., 2005; modified here based on Mannion, 2009).

C215. *Scapular acromion, subtriangular process at posteroventral corner:* absent (0); present (1) [Smith *et al*., 2001; Bonaparte *et al*., 2006; Carballido *et al*., 2011b; modified here to distinguish between a process on the acromial plate and a process on the blade (see D'Emic *et al*., 2011)].

C216. *Scapular blade, subtriangular process at anteroventral corner:* absent (0); present (1) [Carballido *et al*., 2011b; modified here to distinguish between a process on the acromial plate and a process on the blade (see D'Emic *et al*., 2011)].

C217. *Scapular blade, cross-sectional shape at base:* rectangular (0); D-shaped (lateral surface is strongly convex dorsoventrally and medial surface flat) (1) (Wilson, 2002).

C218. *Coracoid, anterior and dorsal margins in lateral view:* merge smoothly into each other, giving a rounded profile (0); meet each other at an abrupt angle, making the coracoid quadrangular in outline (1) (Upchurch, 1998).

C219. *Coracoid, dorsal margin in lateral view:* lies below the level of the scapular acromion plate (separated from the latter by a V-shaped notch) (0); reaches or surpasses the level of the dorsal margin of the scapular acromion plate (1) (Upchurch, 1995, 1998; Upchurch *et al*., 2004a; polarity reversed here).

C220. *Coracoid, ventral margin in lateral view forms a notch anterior to the glenoid, resulting in an 'infraglenoid lip' anterior to the notch:* absent (0); present (1) (Wilson, 2002; modified here).

C221. *Sternal plate, shape in dorsal view:* subcircular or oval (0); triangular (created by an acute anterolateral projection) (1); elliptical with a mildly or strongly concave lateral margin (2) (Calvo & Salgado, 1995; Upchurch, 1998; Wilson, 2002; Upchurch *et al*., 2004a).

C222. *Sternal plate, prominent posterolateral expansion produces a 'kidney'-shaped profile in dorsal view:* absent (0); present (1) (McIntosh, 1990; Upchurch, 1998).

C223. *Humeral proximolateral corner, shape:* rounded, surfaces merge smoothly into each other to produce a transversely rounded proximal end, with the proximal-most point of the lateral margin at a lower level than the remaining lateral half of the proximal surface (0); square, surfaces meet each other at an abrupt angle to produce a 'squared' proximal end in anterior view, with the proximal-most point of the lateral margin level with the remaining lateral half of the proximal surface (1) [Upchurch, 1999; Wilson, 2002; Upchurch *et al*., 2004a; modified here (see also Harris, 2006)].

C224. *Humerus, shape of lateral margin of diaphysis (approximately the middle third of the humerus) in anterior view:* concave (0); straight (1) (Curry Rogers, 2005; modified and polarity reversed here).

C225. *Humeral deltopectoral crest:* restricted to lateral edge of humerus and projects anteriorly or anterolaterally (0); extends medially across the anterior face of the humerus (1) (Wilson, 2002; Upchurch *et al*., 2004a; modified here).

C226. *Humerus, strong bulge or tuberosity (site for M. latissimus dorsi) close to the lateral margin of the posterior surface, at approximately the level of the distal tip of the deltopectoral crest:* absent (0); present (1) (Borsuk-Bialynicka, 1977; Otero, 2010; D'Emic, 2012).

C227. *Humerus, anterior surface of distal lateral condyle:* divided by a notch, forming two ridges (0); undivided (1) (D'Emic, 2012).

C228. *Humerus, distal-most part of the posterior surface (supracondylar fossa) is:* flat or shallowly concave (0); deeply concave between prominent lateral and medial vertical condylar ridges (1) (Upchurch *et al*., 2004a).

C229. *Humeral distal condyles, articular surface:* flat anteroposteriorly and restricted to distal portion of humerus (0); anteroposteriorly convex so that it curves up onto the anterior and posterior faces of the humerus (1) (Wilson, 2002; Upchurch *et al*., 2004a).

C230. *Humeral distal articular surface, condyles:* undivided (0); divided (1) (Wilson, 2002; modified and polarity reversed here).

C231. *Radius, strong twist in axis, such that the long axes of the proximal and distal ends are not*

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*orientated in the same plane:* absent (0); present (1) (new character).

C232. *Radius, well-developed interosseous ridge that extends along most of the radius length (at least along the distal two-thirds):* absent (0); present (1) (Curry Rogers, 2005; modified here).

C233. *Ulnar olecranon process, development:* absent or only rudimentary, i.e. projecting just above the proximal articulation (0); prominent, projecting well above proximal articulation (1) (McIntosh, 1990; Wilson & Sereno, 1998; polarity reversed here).

C234. *Ulna, articular surface of anteromedial process is:* flat (0); concave along its length (1) (Upchurch, 1995, 1998).

C235. *Ulna, orientation of anteromedial process:* flat or sloping downwards less than 40° (0); sloping downwards at an angle of at least 40° to the horizontal (1) (new character).

C236. *Ulna, distal end:* prominently expanded posteriorly (0); unexpanded (1) (D'Emic, 2012).

C237. *Carpal bones, number:* three or more (0); fewer than three (1) (Upchurch, 1995, 1998).

C238. *Carpal bones:* at least one carpal present (0); absent (1) (Upchurch, 1995, 1998).

C239. *Metacarpals, distal articular surfaces:* extend onto dorsal/anterior surface of metacarpal (0); restricted to distal surface (except sometimes in metacarpal IV) (1) (D'Emic, 2012).

C240. *Metacarpals, metacarpal I distal end mediolateral axis orientation:* approximately perpendicular (or only gently bevelled) to long axis of shaft (0); bevelled approximately 20° proximodistally with respect to axis of shaft (1) (Wilson, 2002; polarity reversed here).

C241. *Metacarpals, metacarpal IV has a prominent proximolateral projection that wraps around the dorsal (anterior) face of metacarpal V (metacarpal IV often forms a chevron shape in proximal end view):* absent (0); present (1) (D'Emic, 2012; modified here).

C242. *Manual digits:* possess at least some phalanges (0); have lost the phalanges (1) (Wilson, 2002; Upchurch *et al*., 2004a).

C243. *Manual phalanx I.1, shape in dorsal view:* rectangular (0); wedge-shaped (1) (Wilson, 2002).

C244. *Ilium, preacetabular process in dorsal view:* projects anteriorly (0); projects anterolaterally (1) (Upchurch *et al*., 2004a).

C245. *Ilium, preacetabular process orientation:* lies in an approximately vertical plane (0); turns laterally towards its ventral tip to form a horizontal portion (1) (McIntosh, 1990; Powell, 1992; Upchurch, 1995, 1998).

C246. *Ilium, preacetabular process shape:* dorsoventrally tapers anteriorly to a point (0); semicircular, or rounded outline, such that it does not continue to taper along its anterior-most portion (1) (Calvo & Salgado, 1995; Upchurch, 1998; Wilson & Sereno, 1998; modified here).

C247. *Ilium, preacetabular process, bulge or 'kink' on ventral margin:* absent (0); present (1) (D'Emic, 2012).

C248. *Ilium, highest point on the dorsal margin:* occurs level with or posterior to the anterior margin of the base of the pubic process (0); occurs anterior to the anterior margin of the base of the pubic process (1) (Upchurch, 1998; modified here).

C249. *Ilium, pneumatized:* absent (0); present (1) (new character: based on Wilson & Upchurch, 2009).

C250. *Pubis, obturator foramen, in lateral view is:* subcircular (0); oval or elliptical, with long axis orientated in same plane as long axis of pubis (1) (new character: based on Mannion & Calvo, 2011).

C251. *Pubis, anterior margin of distal end strongly concave in lateral view, such that the distal end forms a prominent, anteriorly expanded boot:* absent (0); present (1) (new character: based on Naish & Martill, 2001).

C252. *Ischium, acetabular margin, in lateral view:* flat or mildly concave (0); strongly concave, such that the pubic articular surface forms an anterodorsal projection (1) (D'Emic, 2012; modified here).

C253. *Ischium, symphysis between the ischia:* terminates at the base of the proximal plates (emarginate distal to pubic articulation) (0); extends along the ventral edges of the proximal plates as well as the distal shafts, so that there is no V-shaped gap between the anterior ends of the ischia in dorsal view (no emargination distal to pubic articulation) (1) (McIntosh, 1990; Upchurch, 1998; Wilson, 2002).

C254. *Ischium, long axis of shaft, if projected upwards:* passes through the lower part of the acetabular margin or the upper part of the pubic articular surface (i.e. it is approximately 60° to the horizontal in lateral view) (0); passes through the upper part of the acetabular margin or even approaches the rim of the iliac articulation (i.e. the shaft is at approximately 80° to the horizontal) (1) (Upchurch, 1995, 1998).

C255. *Femur, proximolateral margin, above the lateral bulge:* level with or lateral to the lateral margin of the distal half of the shaft (0); medial to the lateral margin of the distal half of the shaft (1) [McIntosh, 1990; Calvo & Salgado, 1995; Salgado *et al*., 1997; modified here based on Royo-Torres (2009) and Royo-Torres *et al*. (2012) to take into account that nearly all sauropod femora have a lateral bulge of varying prominence (Salgado *et al*., 1997), and that there is substantial variation in morphology amongst taxa with a medially deflected proximolateral margin].

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C256. *Femur, anteroposterior thickness of lateral margin of proximal third:* relatively constant with main body of femur (0); narrows to form a flange-like trochanteric shelf, forming a medially bounding vertical ridge along the posterior surface (1) (new character).

C257. *Femur, proximodistally elongate midline ridge (linea intermuscularis cranialis) on anterior face, extending along most of shaft length:* absent (0); present (1) (Otero, 2010; D'Emic, 2012).

C258. *Femur, fourth trochanter:* not visible in anterior view (0); visible in anterior view (1) (Gallina & Apesteguía, 2005; Whitlock, 2011b).

C259. *Femoral distal condyles, orientation relative to long axis of femoral shaft:* bevelled dorsolaterally approximately 10° (tibial condyle extends further distally than fibular condyle) (0); perpendicular (tibial and fibular condyles extend approximately the same distance distally) (1); bevelled dorsomedially approximately 10° (fibular condyle extends further distally than tibial condyle) (2) (Wilson, 2002; modified here) [ordered].

C260. *Tibia, cnemial crest projects:* laterally (0); anteriorly or anterolaterally (1) (Wilson & Sereno, 1998; polarity reversed here; note that the tibia is orientated so that the flat, mediolaterally wide triangular surface of the distal end faces anteriorly).

C261. *Tibia, lateral edge of proximal end forms a pinched out projection, posterior to cnemial crest (the 'second cnemial crest' of Bonaparte et al., 2000):* present (0); absent (1) (new character: based on Bonaparte *et al*., 2000).

C262. *Fibula, proximal end with anteromedially directed crest extending into a notch behind the cnemial crest of the tibia:* absent (0); present (1) (Wilson & Upchurch, 2009; D'Emic, 2012; modified here).

C263. *Fibula, lateral muscle scar is:* oval in outline (0); formed from two vertically elongate, parallel ridges (1) (Powell, 1992; Upchurch, 1998).

C264. *Fibula, shaft in lateral view:* straight (0); sigmoidal (1) (Canudo *et al*., 2008; Royo-Torres, 2009).

C265. *Astragalus, in dorsal (or proximal) view:* rectangular, with anteroposterior lengths of medial and lateral margins subequal (or medial margin greater) (0); wedge-shaped, narrowing anteroposteriorly towards its medial end, such that it has a reduced anteromedial corner (1) (Cooper, 1981; Upchurch, 1995, 1998; Wilson & Sereno, 1998).

C266. *Astragalus, ascending process:* does not extend to the posterior margin of the astragalus (usually limited to anterior two-thirds of astragalus) (0); extends to the posterior margin of the astragalus (1) (Wilson & Sereno, 1998; Wilson, 2002).

C267. *Astragalus, laterally directed ventral shelf underlies the distal end of the fibula:* present (0); absent (1) (new character: based on Wilson & Upchurch, 2009).

C268. *Astragalus:* caps most, or all, of the distal end of the tibia (0); reduced so that medial edge of tibia is uncapped (1) (Wilson & Upchurch, 2009; Ksepka & Norell, 2010).

C269. *Astragalus, posterior margin bears a tongue-like projection posteromedial to the ascending process, which is separated from the latter by a groove:* present (0); absent (1) (D'Emic, 2012; modified here).

C270. *Calcaneum:* present (0); absent (1) (McIntosh, 1990; Upchurch, 1995, 1998).

C271. *Calcaneum, shape in proximal view:* subcircular (0); subrectangular (1) (new character: based on Wilson & Upchurch, 2009).

C272. *Metatarsals, metatarsal I with a prominent ventrolateral expansion along its distal half, such that the distal end expands further laterally than the proximal end:* absent (0); present (1) (Berman & McIntosh, 1978; McIntosh, 1990; Upchurch, 1995, 1998; D'Emic *et al*., 2011; modified and polarity reversed here).

C273. *Metatarsals, lateral margin of metatarsal II in proximal view:* concave (0); straight (1) (new character).

C274. *Metatarsals, metatarsal II distal articular surface extends up on to the dorsal surface (extending proximally approximately 25% of metatarsal length and most prominently along medial half):* absent (0); present (1) (new character: based on D'Emic *et al*., 2011).

C275. *Metatarsals, medial surface of the proximal portion of metatarsal IV concave (for reception of metatarsal III):* absent (0); present (1) (D'Emic *et al*., 2011; D'Emic, 2012).

C276. *Metatarsals, distal end orientation of metatarsal IV:* perpendicular to long axis of bone (0); bevelled to face medially (1) (D'Emic, 2012).

C277. *Pedal digit IV:* has at least three phalanges (0); has two phalanges or fewer (1) (Upchurch, 1995, 1998; Upchurch *et al*., 2004a).

C278. *Pedal unguals, tuberosity on the ventral margin, along distal half:* absent (0); present (1) (new character: based on Canudo *et al*., 2008).

C279. *Osteoderms:* absent (0); present (1) (Wilson, 2002; note that taxa are only coded as the plesiomorphic state when osteoderms are not found associated with a relatively complete postcranial skeleton or a specimen preserving numerous axial elements).

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## APPENDIX 2

### DATA MATRIX: DISCRETE DATA

Polymorphic character codings are represented by an A ({0,1}) or a B ({1,2}).

| | C1–10 | C11–20 | C21–30 | C31–40 |
|---|---|---|---|---|
| ***Shunosaurus*** | 0 0 ? 0 0 0 0 0 0 0 | 1 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 |
| ***Omeisaurus*** | 0 1 0 1 1 ? ? ? 0 1 | 0 0 0 2 2 0 1 1 0 1 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 1 1 0 0 |
| ***Mamenchisaurus*** | 0 0 0 1 0 0 ? 0 0 1 | 1 0 0 2 1 0 0 0 1 1 | 0 0 0 0 0 1 2 0 0 0 | 0 0 0 0 0 0 1 0 0 0 0 |
| ***Camarasaurus*** | 0 0 0 0 1 0 0 1 0 0 | 1 1 1 0 0 1 0 0 0 1 | 0 1 1 0 1 0 0 0 0 0 | 0 0 1 1 0 1 0 0 0 0 |
| ***Nigersaurus*** | 0 0 ? ? ? ? 0 0 1 1 | 2 0 0 0 0 1 1 0 0 1 | 0 0 ? ? ? ? ? 0 0 0 | 1 0 0 0 0 0 0 ? ? ? |
| ***Apatosaurus*** | 0 1 1 0 1 0 0 0 1 ? | 2 1 ? 1 1 1 0 0 0 1 | 1 1 0 0 1 0 1 1 0 0 | 1 0 1 0 0 1 1 0 0 0 |
| ***Diplodocus*** | 0 1 0 0 1 0 1 0 1 1 | 2 1 1 1 1 1 0 0 0 1 | 0 1 0 0 1 0 1 0 1 ? | 1 0 1 1 0 1 1 ? ? 0 |
| ***Abydosaurus*** | 1 1 1 1 1 ? ? ? ? 1 | 1 1 1 ? 1 1 ? ? ? ? | ? ? ? ? ? ? 0 ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Alamosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 0 ? 0 1 ? ? | ? ? ? 1 0 1 2 0 0 1 | 1 1 0 0 1 1 1 0 1 ? |
| ***Andesaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? 0 0 ? 0 1 1 0 1 0 | 1 ? 0 0 1 ? ? ? ? ? |
| ***Angolatitan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? 1 ? ? ? ? |
| ***Aragosaurus*** | ? ? ? ? ? ? ? ? ? ? | 1 ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 0 0 0 0 0 | 0 1 0 1 1 1 ? ? ? ? |
| ***Astrophocaudia*** | ? ? ? ? ? ? ? ? ? ? | 1 ? ? ? 0 ? 0 ? ? ? | ? ? ? ? 1 1 0 0 0 0 | 1 ? 0 0 0 ? 0 ? ? ? |
| ***Atlasaurus*** | ? ? 0 1 ? 0 1 0 1 ? | 1 1 1 ? ? ? ? ? ? ? | ? 0 0 0 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 1 |
| ***Australodocus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 ? 0 ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Baotianmansaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | 0 ? 0 ? 0 0 0 ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Brachiosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? 1 0 0 1 0 0 ? ? ? | ? 1 0 1 ? ? ? 0 ? 1 |
| ***Brontomerus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 0 | 1 ? ? ? ? ? 1 ? ? ? |
| ***Cedarosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? 1 ? ? 1 1 0 1 0 ? | ? 1 0 0 1 1 ? 0 0 1 |
| ***Chubutisaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | 0 1 ? ? 1 0 0 1 0 0 | 0 ? ? ? 0 ? 1 ? ? 0 |
| **Cloverly titanosauriform** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 ? | 1 0 0 ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Daxiatitan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 ? 1 ? 1 ? | ? ? ? ? ? ? 2 ? ? ? | ? ? 1 ? 0 1 0 1 ? ? |
| ***Diamantinasaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? 1 ? ? 0 |
| ***Dongbeititan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? 2 ? ? ? ? ? ? | 1 ? 0 ? 0 0 2 ? ? ? | ? ? 0 0 0 1 ? 0 ? ? |
| ***Dongyangosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? 1 ? 0 0 ? ? ? | ? 1 ? 0 ? ? ? ? ? ? |
| ***Erketu*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 2 0 1 ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Euhelopus*** | 1 ? ? ? 1 ? ? ? ? ? | 1 1 1 2 2 0 1 0 1 0 | 0 0 1 1 ? ? ? ? ? ? | ? ? ? ? ? 1 0 0 ? ? |
| ***Europasaurus*** | 0 ? 1 1 1 0 1 0 1 0 | 1 ? 1 ? 0 1 0 0 ? ? | 0 1 0 0 1 1 0 0 0 0 | 1 1 0 0 0 0 ? 0 ? ? |
| **French *Bothriospondylus*** | ? ? ? ? ? ? ? ? ? ? | 1 ? ? ? ? ? 1 ? ? ? | ? ? ? ? 1 ? 0 ? ? ? | ? ? ? ? ? ? ? ? ? 1 |
| ***Fukuititan*** | ? ? ? ? ? ? ? ? ? ? | 1 ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 0 | 1 ? ? ? ? ? ? ? ? ? |
| ***Fusuisaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 ? 0 ? ? ? | ? 1 0 0 ? ? ? ? ? ? |
| ***Galveosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 ? ? ? ? ? | 0 1 0 0 1 1 0 1 0 ? | ? ? ? ? ? 1 ? ? 0 ? |
| ***Giraffatitan*** | 1 0 0 1 1 0 1 0 1 0 | 1 1 1 1 1 1 0 0 ? 1 | 0 1 0 0 1 1 0 1 0 0 | 0 1 0 0 1 1 0 0 0 1 |
| ***Gobititan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? 1 0 1 | 0 ? ? ? 1 ? ? ? ? ? |
| **HMN MB.R.2091.1-30** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 0 1 2 0 0 0 | 1 0 0 1 ? ? ? ? ? ? |
| ***Huanghetitan liujiaxiaensis*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? 0 1 1 0 ? ? ? | ? ? 0 0 ? 1 0 0 ? ? |
| ***Huanghetitan ruyangensis*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? 1 1 1 0 ? ? ? | ? 1 0 0 1 ? ? ? ? ? |

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APPENDIX 2 *Continued*

| | C1–10 | C11–20 | C21–30 | C31–40 |
|---|---|---|---|---|
| ***Janenschia*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Jiangshanosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? 0 0 ? 0 0 ? 0 0 ? | ? 1 0 0 ? 1 1 0 ? ? |
| ***Lapparentosaurus*** | ? ? ? ? ? ? ? ? ? ? | 0 ? ? ? 0 1 0 ? ? ? | ? 1 ? ? 0 1 0 0 0 ? | ? ? 0 0 ? 1 0 0 ? ? |
| ***Ligabuesaurus*** | ? ? ? ? ? ? ? ? ? ? | 1 ? ? ? ? ? 0 1 0 ? | 1 1 ? ? ? ? ? ? ? ? | ? ? ? ? ? 1 1 1 ? 0 |
| ***Liubangosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? 0 1 ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Lusotitan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? 1 ? ? 1 1 0 1 0 ? | ? ? 0 ? 1 ? ? ? ? ? |
| ***Malarguesaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 1 0 1 0 0 | 1 1 0 0 ? ? ? ? ? ? |
| ***Malawisaurus*** | 0 ? ? 0 ? 1 0 1 1 ? | 2 ? 1 ? 2 1 0 1 1 ? | 1 1 0 1 1 0 2 0 1 1 | 1 1 1 0 1 ? ? 0 1 ? |
| ***Mongolosaurus*** | ? ? ? ? ? ? 1 1 ? ? | 2 ? ? ? ? 1 ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Opisthocoelicaudia*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 ? | 1 1 1 1 1 0 0 1 0 1 | 0 ? 1 0 1 0 1 0 1 0 |
| ***Paluxysaurus*** | ? ? ? ? ? ? ? ? ? ? | 1 ? ? ? 2 1 ? ? 0 ? | 0 1 0 0 1 0 0 1 0 0 | 1 1 1 0 0 1 1 1 ? 0 |
| ***Pelorosaurus becklesii*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Phuwiangosaurus*** | ? ? ? ? ? 0 1 0 1 ? | 2 ? ? ? 1 1 0 ? 1 ? | 1 1 1 1 1 0 0 1 0 ? | ? 1 0 0 1 1 ? ? ? 0 |
| ***Qiaowanlong*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 1 0 ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Rapetosaurus*** | 0 ? 1 0 ? 1 0 0 1 0 | 2 ? 1 2 2 1 0 1 1 1 | 1 1 0 1 1 1 2 1 1 ? | ? 1 0 0 1 0 1 0 1 0 |
| ***Ruyangosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? 1 ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Saltasaurus*** | ? ? ? ? ? 0 0 1 ? ? | ? ? ? ? 0 1 0 1 ? ? | ? 1 0 1 1 1 2 1 1 1 | 1 0 1 ? 0 0 1 ? ? ? |
| ***Sauroposeidon*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 2 ? 0 ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Sonorasaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 ? 0 ? ? ? | ? ? ? 0 ? ? ? ? ? ? |
| ***Tangvayosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | 0 0 0 ? 1 0 0 ? ? 1 | 1 1 1 0 1 ? ? ? ? ? |
| ***Tastavinsaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? 1 0 0 0 0 1 1 0 0 | 0 1 0 1 1 ? ? ? ? ? |
| ***Tehuelchesaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | 0 0 ? ? ? ? ? ? ? ? | ? ? ? ? ? 1 1 0 ? 0 |
| ***Tendaguria*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? 0 1 1 ? | 1 ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Venenosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 1 0 1 0 0 | 1 1 0 0 1 0 0 ? ? ? |
| ***Wintonotitan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 1 0 ? ? 0 | 1 ? ? ? 0 ? 1 ? ? ? |
| ***Xianshanosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 0 2 ? ? ? | ? 1 1 0 0 ? ? 0 ? ? |

| | C41–50 | C51–60 | C61–70 | C71–80 |
|---|---|---|---|---|
| ***Shunosaurus*** | 0 0 ? 0 0 0 0 0 0 0 | ? 0 0 0 0 0 ? ? 0 0 | 0 0 0 0 0 ? 0 ? 0 0 | 0 0 0 0 0 0 0 0 0 0 |
| ***Omeisaurus*** | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 1 0 | 0 0 1 0 0 0 1 ? ? 0 | 0 1 1 0 1 0 0 0 0 0 |
| ***Mamenchisaurus*** | 0 1 ? 0 0 1 0 0 0 0 | 0 1 ? 0 0 0 0 ? 1 0 | 0 0 0 0 ? 0 1 0 ? 0 | 0 ? ? 0 1 0 1 ? 0 0 |
| ***Camarasaurus*** | 0 0 1 0 0 0 1 1 0 0 | 0 1 0 0 1 0 0 0 0 0 | 0 0 1 0 0 0 0 1 1 0 | 0 1 0 0 1 0 0 1 1 0 |
| ***Nigersaurus*** | 0 1 1 0 0 0 0 1 0 0 | 0 ? 1 ? ? ? ? ? ? ? | ? 0 ? ? 0 ? 1 1 1 1 | ? ? ? 0 0 1 0 1 1 ? |
| ***Apatosaurus*** | 0 0 1 0 1 0 1 1 1 1 | 0 1 0 0 1 0 1 0 1 0 | 0 0 0 0 0 0 0 0 1 1 0 | 0 0 0 0 0 0 1 0 1 1 0 |
| ***Diplodocus*** | 1 0 1 0 0 0 0 1 0 0 | 0 0 1 0 0 0 0 ? 1 0 | 0 0 0 0 0 0 0 1 1 1 0 | 1 1 0 1 0 1 0 1 1 1 |
| ***Abydosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 0 1 ? 1 1 |
| ***Alamosaurus*** | ? 0 ? 1 1 1 1 0 1 0 | 0 1 0 1 1 1 ? ? 1 1 | 0 0 0 1 ? ? 1 0 0 ? | ? 0 ? 0 ? ? ? ? ? ? |
| ***Andesaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? 1 ? ? ? ? 1 ? 1 | 0 0 0 1 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Angolatitan*** | 1 0 0 1 0 1 0 0 1 0 | 0 1 0 0 1 ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |

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APPENDIX 2 *Continued*

| | C41–50 | C51–60 | C61–70 | C71–80 |
|---|---|---|---|---|
| ***Aragosaurus*** | ? 1 0 0 0 0 0 1 0 0 | 0 ? ? ? ? ? ? 0 1 0 | 0 0 1 0 1 ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Astrophocaudia*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Atlasaurus*** | ? ? ? 1 ? ? ? ? ? ? | ? 0 ? 0 0 ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? 1 ? 1 0 ? 1 ? ? |
| ***Australodocus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Baotianmansaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Brachiosaurus*** | 1 1 ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 0 ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Brontomerus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? 1 ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Cedarosaurus*** | 1 1 0 1 0 0 0 1 0 ? | 1 1 ? ? ? ? ? 0 0 ? | ? 1 ? ? 0 ? ? ? ? ? | ? 0 ? 1 ? ? ? ? ? ? |
| ***Chubutisaurus*** | 1 0 0 1 0 1 0 1 0 ? | ? 1 1 0 1 ? ? ? ? ? | ? ? 0 1 0 ? 1 1 ? ? | ? ? ? ? ? ? ? ? ? ? |
| **Cloverly titanosauriform** | ? ? ? ? ? ? ? 1 ? 1 | 1 ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Daxiatitan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 1 ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Diamantinasaurus*** | 0 0 1 ? ? ? ? ? ? 1 | 0 ? 0 0 1 1 1 0 0 1 | 0 0 0 0 1 1 0 1 0 1 | 1 ? ? ? ? ? ? ? ? ? |
| ***Dongbeititan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? 1 1 0 | 0 0 0 0 1 1 1 1 1 0 | 0 0 0 1 ? ? ? ? ? ? |
| ***Dongyangosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 0 | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Erketu*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? 1 ? 1 1 | ? ? ? ? ? ? ? ? ? ? |
| ***Euhelopus*** | 0 1 0 ? ? ? ? ? ? ? | ? ? ? ? ? ? 1 0 1 0 | 1 0 0 0 0 1 1 1 1 1 | 1 ? 0 ? 0 0 0 0 1 0 |
| ***Europasaurus*** | ? 0 1 ? 0 ? ? ? ? 0 | 0 ? ? ? ? ? ? ? 0 ? | 1 1 1 ? ? 0 1 1 ? ? | ? ? ? ? 1 0 0 1 1 ? |
| **French *Bothriospondylus*** | 1 1 ? 0 0 0 0 ? 0 0 | ? 1 ? ? ? ? ? ? ? ? | 1 1 1 0 ? ? 1 ? ? ? | 0 ? 1 ? ? ? ? ? ? ? |
| ***Fukuititan*** | ? ? 0 ? 0 1 0 ? 0 ? | ? 1 ? ? ? ? ? ? ? ? | ? ? ? ? 1 ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Fusuisaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Galveosaurus*** | 1 0 0 ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | 0 0 1 1 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Giraffatitan*** | 1 1 1 1 0 0 1 1 0 0 | 0 1 0 0 1 1 1 1 0 0 | 1 1 1 1 1 0 1 1 0 1 | 1 ? ? ? 1 0 1 1 1 1 |
| ***Gobititan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 0 0 1 1 1 0 | 1 0 0 1 ? ? ? ? ? ? |
| **HMN MB.R.2091.1-30** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Huanghetitan liujiaxiaensis*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Huanghetitan ruyangensis*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? 0 ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Janenschia*** | 0 0 1 0 0 1 1 0 1 1 | 0 ? ? ? ? 0 ? ? 0 ? | 0 0 0 1 0 0 1 1 1 0 | 0 1 0 0 ? ? ? ? ? ? |
| ***Jiangshanosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? 1 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Lapparentosaurus*** | 1 1 1 ? 0 0 0 1 1 0 | 0 ? 0 ? ? ? 0 0 0 ? | 0 0 1 1 0 0 1 1 ? 0 | 0 ? ? ? ? ? ? ? ? ? |
| ***Ligabuesaurus*** | 1 1 1 ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 ? 1 0 ? ? | ? 0 0 0 ? ? ? ? ? ? |
| ***Liubangosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Lusotitan*** | ? ? 0 ? 0 0 0 0 0 ? | ? ? ? ? ? ? ? ? ? ? | ? 1 ? ? ? ? 0 0 ? 0 | 0 ? ? ? ? ? ? ? ? ? |
| ***Malarguesaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Malawisaurus*** | 1 1 ? ? 0 0 1 1 1 0 | 0 ? 0 1 1 ? ? ? ? ? | 0 0 0 1 ? ? 0 1 ? ? | ? ? ? 1 1 0 0 ? ? ? |
| ***Mongolosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Opisthocoelicaudia*** | 0 0 0 1 1 0 1 0 1 1 | 0 1 0 1 1 1 0 1 1 1 | 0 0 0 0 1 1 0 0 0 1 | 1 1 1 ? ? ? ? ? ? ? |
| ***Paluxysaurus*** | 1 1 1 ? 0 0 1 0 0 0 | 0 1 ? 0 ? ? ? 0 1 1 | 0 0 1 0 1 0 1 1 1 ? | ? ? ? ? ? ? ? ? ? ? |
| ***Pelorosaurus becklesii*** | 0 0 1 0 0 1 0 1 1 1 | 0 ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Phuwiangosaurus*** | ? 1 ? ? 0 0 1 1 1 ? | ? ? ? ? ? ? ? 1 0 1 | 0 0 0 1 1 0 ? 0 0 ? | ? ? ? ? ? ? ? ? ? ? |
| ***Qiaowanlong*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 1 1 | 0 1 0 0 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |

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APPENDIX 2 *Continued*

| | C41–50 | C51–60 | C61–70 | C71–80 |
|---|---|---|---|---|
| ***Rapetosaurus*** | 1 0 1 0 0 1 0 0 1 0 | 0 1 1 0 0 1 ? ? 0 1 | 0 0 0 1 0 0 ? ? 1 ? | ? 1 ? 0 0 1 ? 0 1 1 |
| ***Ruyangosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? 1 1 ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Saltasaurus*** | 0 0 0 ? 1 0 0 0 1 1 | ? ? ? ? ? ? ? ? 0 ? | ? 1 ? ? 1 1 0 0 ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Sauroposeidon*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Sonorasaurus*** | ? ? ? ? 0 1 ? ? ? ? | ? 1 ? ? ? ? ? ? ? ? | ? ? ? ? 0 ? ? ? ? ? | ? 0 1 0 ? ? ? ? ? ? |
| ***Tangvayosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 1 | 0 0 0 1 1 ? 1 ? 1 0 | 1 ? 0 ? ? ? ? ? ? ? |
| ***Tastavinsaurus*** | ? ? ? ? 0 0 0 0 0 ? | ? ? ? ? ? ? 1 0 0 1 | 0 0 0 1 0 1 1 0 0 1 | 0 0 1 0 ? ? ? ? ? ? |
| ***Tehuelchesaurus*** | 0 0 1 0 1 1 1 0 1 0 | 0 ? ? ? ? ? ? ? 0 0 | 0 0 0 0 0 0 ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Tendaguria*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Venenosaurus*** | ? ? ? ? 0 0 0 1 0 0 | 1 1 1 ? ? ? ? ? 0 0 | 1 0 1 0 ? ? ? ? ? 0 | 1 ? ? ? ? ? ? ? ? ? |
| ***Wintonotitan*** | ? ? ? ? 0 1 1 0 1 0 | ? 1 0 ? ? ? ? ? ? ? | ? 0 ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Xianshanosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| | **C81–90** | **C91–100** | **C101–110** | **C111–120** |
| ***Shunosaurus*** | 0 0 0 0 ? 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 |
| ***Omeisaurus*** | ? 0 0 1 0 0 0 0 0 0 | 0 0 ? ? 1 0 ? 0 0 0 | 0 0 0 1 0 0 0 0 0 0 | 0 0 0 0 0 0 ? 0 0 0 |
| ***Mamenchisaurus*** | 1 0 ? 0 ? 0 ? 0 0 0 | 1 0 1 1 1 0 0 ? ? ? | 0 0 0 0 ? 0 0 0 0 0 | 0 0 1 0 2 0 1 0 0 0 |
| ***Camarasaurus*** | 0 1 0 1 0 0 1 0 0 0 | 1 0 0 1 1 0 A 0 1 0 | 0 1 0 0 0 0 0 1 0 0 | 0 0 1 0 1 A 0 0 0 1 |
| ***Nigersaurus*** | ? ? 0 ? ? ? 1 1 0 ? | 1 0 ? ? ? 0 0 1 1 0 | 0 0 0 3 B 1 1 1 1 1 | 1 1 1 0 1 ? ? 1 0 0 |
| ***Apatosaurus*** | 1 0 0 0 1 0 1 1 1 0 | 0 0 1 ? 0 0 1 0 0 0 | 1 ? ? 3 2 1 ? 1 1 1 | 1 0 1 0 1 1 0 1 1 0 |
| ***Diplodocus*** | 1 0 0 0 1 0 1 1 1 0 | 0 0 1 0 0 0 1 0 1 0 | 1 1 0 3 2 1 1 1 1 1 | 1 0 1 0 1 1 0 1 1 1 |
| ***Abydosaurus*** | 1 0 ? ? 0 0 1 0 0 1 | 1 0 1 ? ? 0 ? 1 0 0 | ? 1 1 2 1 1 1 1 0 1 | 1 0 1 1 2 0 ? ? ? ? |
| ***Alamosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 ? ? 1 1 1 | 1 0 1 ? 2 ? 0 1 1 1 |
| ***Andesaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Angolatitan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Aragosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 0 ? ? 1 0 0 | 1 0 1 ? ? ? ? ? ? ? |
| ***Astrophocaudia*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 0 ? ? 1 0 0 | 0 1 1 ? 2 ? ? 1 1 1 |
| ***Atlasaurus*** | ? ? ? ? ? 1 1 ? ? ? | 0 ? ? ? ? 0 ? ? ? ? | ? ? ? ? ? ? ? ? 1 0 ? | ? 0 0 ? ? ? ? ? ? ? |
| ***Australodocus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 2 ? ? 1 1 1 |
| ***Baotianmansaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Brachiosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Brontomerus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Cedarosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Chubutisaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| **Cloverly titanosauriform** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Daxiatitan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? 1 1 1 |
| ***Diamantinasaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Dongbeititan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 2 ? ? ? ? 1 |
| ***Dongyangosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |

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APPENDIX 2 *Continued*

| | C81–90 | C91–100 | C101–110 | C111–120 |
|---|---|---|---|---|
| ***Erketu*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? 2 0 1 1 0 0 |
| ***Euhelopus*** | ? ? ? ? ? ? 1 ? ? 0 | 1 0 ? 1 ? ? ? ? ? ? | ? 1 ? 0 0 0 1 1 0 0 | 0 1 1 0 2 ? 0 1 1 1 |
| ***Europasaurus*** | 1 1 0 1 ? 0 1 0 0 1 | 1 0 1 ? ? 0 1 1 1 0 | 0 1 0 0 0 1 0 1 0 0 | 0 0 0 1 ? 1 ? 1 0 1 |
| **French *Bothriospondylus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? 0 ? ? 1 0 0 | 0 0 0 ? ? 2 ? ? 1 0 1 |
| ***Fukuititan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? 1 ? ? 1 0 0 | 1 1 1 ? ? ? ? ? ? ? |
| ***Fusuisaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Galveosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? 2 ? ? 0 0 1 |
| ***Giraffatitan*** | 1 1 0 1 0 0 1 0 1 1 | 1 0 1 0 1 0 1 1 1 0 | 0 1 1 2 0 1 0 1 0 0 | 0 0 0 0 1 2 0 0 0 1 1 |
| ***Gobititan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| **HMN MB.R.2091.1-30** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Huanghetitan liujiaxiaensis*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Huanghetitan ruyangensis*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Janenschia*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Jiangshanosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Lapparentosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? 0 0 0 | 0 0 1 ? ? ? ? ? 1 0 0 |
| ***Ligabuesaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? 0 ? ? 1 0 0 | 1 ? 0 0 2 ? ? ? ? ? 1 |
| ***Liubangosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Lusotitan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? 1 1 1 1 |
| ***Malarguesaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Malawisaurus*** | ? ? ? ? 0 ? ? ? ? ? | 1 1 ? ? ? 1 0 ? ? 0 | 0 ? 0 0 1 1 ? ? 1 A | 1 1 1 1 0 2 ? ? 1 0 1 |
| ***Mongolosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? 0 1 0 | 0 ? ? ? ? 1 ? 1 1 A | 1 1 1 ? ? 1 1 1 0 0 |
| ***Opisthocoelicaudia*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Paluxysaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? 0 ? ? 1 0 0 | 0 0 1 ? ? 2 ? ? ? ? |
| ***Pelorosaurus becklesii*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Phuwiangosaurus*** | ? ? 1 ? ? ? ? ? 0 ? | 1 1 ? ? ? 0 0 1 0 0 | 0 ? ? ? 1 1 ? 1 0 1 | 1 1 1 ? ? ? ? ? 1 0 1 |
| ***Qiaowanlong*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 1 0 1 |
| ***Rapetosaurus*** | ? 1 1 0 1 1 ? 0 0 ? | 1 1 1 ? ? 1 0 0 0 1 | 0 1 0 0 1 1 ? 1 1 1 | 1 0 1 0 2 1 ? 0 0 0 0 |
| ***Ruyangosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Saltasaurus*** | ? 1 1 0 0 ? ? ? ? ? | ? ? ? ? ? ? 1 0 1 ? ? | 0 ? ? ? ? ? ? ? ? ? | ? ? ? ? ? 2 ? ? 0 1 1 1 |
| ***Sauroposeidon*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 1 1 1 |
| ***Sonorasaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Tangvayosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Tastavinsaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Tehuelchesaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Tendaguria*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? 1 ? ? 1 1 0 |
| ***Venenosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Wintonotitan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Xianshanosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |

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APPENDIX 2 *Continued*

| | C121–130 | C131–140 | C141–150 | C151–160 |
|---|---|---|---|---|
| ***Shunosaurus*** | 0 0 0 0 0 0 0 ? 0 0 | 0 0 ? 0 0 ? 0 ? 0 0 | 0 0 0 ? ? ? 0 0 0 ? | 0 0 A 0 0 0 0 0 0 0 |
| ***Omeisaurus*** | ? 2 0 0 0 0 1 0 0 0 | 0 0 ? 0 0 0 0 ? 1 ? | 0 0 1 0 0 0 1 0 0 A | 0 0 0 0 0 0 0 0 1 0 |
| ***Mamenchisaurus*** | 0 0 0 0 0 1 1 1 0 0 | 0 1 0 0 0 0 ? 0 1 1 | 2 0 1 0 0 0 2 0 0 0 | 0 0 0 0 1 0 0 0 1 0 |
| ***Camarasaurus*** | 1 2 0 0 0 1 1 0 1 0 | 0 1 1 0 0 0 ? 0 1 0 | 1 0 1 1 0 1 2 0 0 1 | 0 0 0 0 1 0 0 0 0 0 |
| ***Nigersaurus*** | 1 2 0 1 0 1 1 1 1 1 | 0 0 ? 0 0 0 1 ? 0 0 | 1 0 1 1 0 0 1 1 1 ? | 0 0 1 0 0 0 0 0 0 0 |
| ***Apatosaurus*** | 1 2 0 1 0 1 1 0 0 1 | 0 1 1 0 0 0 ? 0 0 0 | 1 0 1 1 0 0 0 1 0 1 | 0 0 0 0 1 0 0 0 0 0 |
| ***Diplodocus*** | 1 2 0 0 0 1 1 0 0 1 | 1 1 1 0 0 0 ? 0 0 0 | 1 1 1 1 0 0 0 2 0 1 | 0 0 0 0 1 0 0 0 0 0 |
| ***Abydosaurus*** | ? 2 ? ? ? 0 ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Alamosaurus*** | 0 0 0 0 1 1 0 ? 0 0 | 0 0 ? ? 0 ? 1 ? ? ? | 2 0 1 0 ? ? 2 0 0 0 | 0 1 0 0 0 1 1 0 1 0 |
| ***Andesaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | 2 0 1 0 1 ? 2 2 0 0 | 1 0 ? ? ? ? 0 ? 1 ? |
| ***Angolatitan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Aragosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Astrophocaudia*** | ? 2 0 ? 0 ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Atlasaurus*** | ? 1 ? 0 ? ? 1 0 0 ? | ? 0 ? ? ? ? ? ? 1 0 | ? ? 1 1 0 ? 1 ? 0 ? | 0 0 ? 0 0 0 0 ? 0 ? |
| ***Australodocus*** | 1 0 0 0 0 1 1 0 0 ? | ? 1 1 ? 0 ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Baotianmansaurus*** | ? ? ? ? ? ? ? ? ? ? | ? 1 ? ? ? ? ? 0 ? ? | 2 ? 1 1 1 1 2 1 1 ? | 0 0 ? ? 0 ? ? ? 1 0 |
| ***Brachiosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | 2 1 1 1 0 ? 2 2 0 1 | 0 0 ? 1 1 0 0 1 1 ? |
| ***Brontomerus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | 2 ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Cedarosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | 2 0 1 1 1 ? 2 2 ? ? | 0 0 ? ? 0 ? ? ? ? ? |
| ***Chubutisaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 1 ? | 2 0 1 1 1 1 2 ? 0 ? | 0 ? ? ? ? ? ? ? ? ? |
| **Cloverly titanosauriform** | ? ? ? ? ? ? ? ? ? ? | ? 0 ? ? ? 1 1 ? ? ? | 2 0 1 1 1 ? 2 2 0 1 | 1 0 0 0 0 ? 0 ? 1 0 |
| ***Daxiatitan*** | 0 0 0 1 0 ? 1 1 0 ? | 0 0 ? ? ? ? ? ? 1 1 | ? 0 1 0 1 1 2 1 0 ? | 0 ? 0 ? 1 ? 0 0 1 1 |
| ***Diamantinasaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | 2 ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Dongbeititan*** | ? ? 0 ? 0 ? ? ? ? ? | ? ? ? ? ? ? 1 ? ? ? | 2 0 1 0 0 ? 2 2 0 ? | 0 0 ? ? ? ? 0 ? 1 0 |
| ***Dongyangosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? 1 ? ? ? ? ? ? ? ? | 2 0 1 1 0 1 2 1 ? ? | 0 0 0 0 1 ? 0 ? 0 1 |
| ***Erketu*** | 1 2 0 1 0 1 1 1 0 0 | 1 1 0 1 0 ? ? ? 1 ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Euhelopus*** | 0 0 0 1 0 1 1 1 1 0 | 1 1 0 0 0 0 ? 1 1 0 | 2 1 1 0 1 1 2 1 0 ? | 1 0 1 0 0 1 0 0 0 0 |
| ***Europasaurus*** | 1 2 0 0 0 0 1 0 0 0 | 1 0 ? ? 0 0 0 ? 1 ? | ? 0 1 1 0 1 2 1 0 1 | 0 0 0 1 1 0 0 1 0 0 |
| **French *Bothriospondylus*** | 1 2 0 0 0 ? ? ? 0 ? | 0 0 ? ? ? ? ? ? ? ? | ? ? 1 1 0 ? 2 ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Fukuititan*** | ? ? ? ? ? ? 1 1 ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Fusuisaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Galveosaurus*** | ? 2 0 ? 0 ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | 1 0 1 1 0 1 ? 0 0 0 | 0 0 ? ? ? ? 0 ? 0 ? |
| ***Giraffatitan*** | 1 2 0 0 0 1 1 0 0 0 | 0 0 ? 1 0 0 0 ? 1 1 | 2 1 1 1 0 1 2 2 0 1 | 0 0 1 1 0 0 0 1 A 1 |
| ***Gobititan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| **HMN MB.R.2091.1-30** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Huanghetitan liujiaxiaensis*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Huanghetitan ruyangensis*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Janenschia*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Jiangshanosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? 0 1 0 0 ? 2 2 ? ? | 0 ? ? ? ? ? ? ? 0 ? |
| ***Lapparentosaurus*** | 0 1 0 0 0 ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? 0 A 0 0 0 0 ? 0 1 | 0 0 ? ? ? ? ? ? 0 ? |

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APPENDIX 2 *Continued*

| | C121–130 | C131–140 | C141–150 | C151–160 |
|---|---|---|---|---|
| ***Ligabuesaurus*** | 1 1 0 0 0 ? ? ? 0 0 | 0 0 ? ? 0 1 1 ? ? ? | 2 ? 1 0 0 ? 2 2 0 ? | 1 ? 0 0 1 ? ? ? 1 0 |
| ***Liubangosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? 0 1 1 0 ? 2 1 0 1 | 1 0 ? ? 0 ? 0 ? 1 ? |
| ***Lusotitan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? 0 1 1 0 1 1 ? ? ? | ? ? ? ? ? ? ? ? 0 ? |
| ***Malarguesaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Malawisaurus*** | 1 0 0 0 0 1 1 0 0 0 | 0 0 ? 0 ? 1 1 ? 1 0 | 2 ? 1 0 1 1 2 2 1 ? | 1 0 1 0 0 1 ? ? 1 1 |
| ***Mongolosaurus*** | 0 0 ? ? ? ? 0 1 ? 0 ? | ? 1 ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Opisthocoelicaudia*** | ? ? ? ? ? ? ? ? ? ? ? | ? 1 ? ? ? ? ? 1 0 ? ? | ? 1 1 ? 1 1 2 2 1 ? | 0 1 0 0 1 0 0 1 1 0 |
| ***Paluxysaurus*** | 1 2 1 0 0 1 1 0 0 0 | 0 0 ? 1 1 1 1 ? 1 ? | 2 0 1 1 1 1 2 1 0 1 | 1 0 0 0 0 0 0 ? 1 0 |
| ***Pelorosaurus becklesii*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Phuwiangosaurus*** | 1 2 0 0 0 0 1 1 1 0 0 | 1 1 0 0 0 0 0 ? 1 1 0 | ? 1 1 1 1 1 1 2 1 0 1 | 0 0 0 0 0 0 1 1 ? 0 1 |
| ***Qiaowanlong*** | 1 0 0 0 0 0 ? 1 1 0 0 | 1 1 0 0 0 0 ? ? ? 1 ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Rapetosaurus*** | 0 0 0 0 0 0 ? ? ? 0 0 | 0 0 ? ? 0 0 0 1 ? 1 1 | 2 0 1 1 0 1 2 1 1 ? | 1 0 0 0 0 1 1 1 1 1 1 |
| ***Ruyangosaurus*** | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? ? | 2 0 1 ? 0 ? 2 1 0 0 | 1 0 ? ? 0 1 ? 0 ? ? ? |
| ***Saltasaurus*** | 0 0 0 0 1 0 0 ? 0 ? | 0 0 ? ? ? 0 1 1 ? ? ? | 2 0 1 0 1 1 2 1 1 ? | 1 0 1 0 0 1 1 ? 1 1 |
| ***Sauroposeidon*** | 1 2 1 0 0 1 1 0 0 0 | 0 0 ? ? 1 1 ? ? ? 1 1 | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Sonorasaurus*** | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? ? | 2 ? ? 1 1 0 ? ? 2 ? | ? ? ? ? ? ? ? ? ? ? |
| ***Tangvayosaurus*** | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? 1 A 1 1 2 1 0 | ? 0 ? ? ? ? ? ? 0 ? |
| ***Tastavinsaurus*** | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? ? | 2 0 1 1 0 ? 2 0 0 ? | 0 0 ? ? 0 0 0 ? 1 ? |
| ***Tehuelchesaurus*** | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 ? ? | 1 0 1 1 0 1 2 0 0 ? | 1 0 0 ? 1 0 0 ? 1 ? |
| ***Tendaguria*** | 0 2 0 0 0 0 0 1 0 0 0 | 0 0 ? ? 0 ? 1 ? ? ? | ? 0 1 1 0 0 ? ? ? ? | ? ? 0 0 ? ? ? ? 0 0 |
| ***Venenosaurus*** | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Wintonotitan*** | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | 2 ? 1 1 0 ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 1 |
| ***Xianshanosaurus*** | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |

| | C161–170 | C171–180 | C181–190 | C191–200 |
|---|---|---|---|---|
| ***Shunosaurus*** | 0 0 0 0 0 0 ? ? 0 | 0 0 0 0 0 0 0 ? 0 | 0 0 0 ? 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 |
| ***Omeisaurus*** | 0 0 0 0 1 1 0 ? ? 0 | ? 0 0 0 0 0 0 ? 0 | 0 0 1 0 ? 0 0 1 0 0 | 0 0 0 0 0 0 1 0 0 0 |
| ***Mamenchisaurus*** | 0 1 1 0 0 0 0 ? ? 0 | ? 0 1 1 0 0 2 0 ? 0 | 0 0 0 A 0 0 0 0 1 0 | ? 0 0 0 0 0 0 0 1 0 |
| ***Camarasaurus*** | 1 1 1 0 1 1 0 ? ? 0 | ? 0 1 0 0 0 0 0 ? 0 | 0 0 1 0 ? 0 0 0 0 0 | 0 0 0 0 0 1 1 0 0 1 |
| ***Nigersaurus*** | 0 1 1 0 1 1 1 0 0 0 | ? ? ? ? 0 ? ? ? ? ? | 0 0 0 0 0 ? 1 1 ? 1 0 | 0 0 0 0 0 ? 1 1 1 0 1 |
| ***Apatosaurus*** | 1 0 0 0 1 1 1 1 0 0 1 | 0 0 1 0 0 0 0 1 A 1 1 | 1 1 1 0 ? 1 0 0 1 0 | 0 0 0 0 0 0 0 1 1 0 1 |
| ***Diplodocus*** | 1 0 0 0 1 1 1 1 0 0 0 | 0 0 0 1 0 0 0 0 1 1 0 | 1 1 1 1 0 ? 1 0 0 1 0 | 0 0 0 0 0 0 0 1 1 0 1 |
| ***Abydosaurus*** | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 1 0 ? | 0 ? ? ? ? ? ? ? 1 ? | ? ? ? ? ? ? ? ? ? ? |
| ***Alamosaurus*** | 0 1 0 0 0 0 1 1 0 0 1 | 1 1 1 ? ? 1 1 2 1 1 1 1 | 1 1 1 0 1 1 ? 1 ? 0 1 | 0 1 1 1 1 1 1 1 0 0 1 |
| ***Andesaurus*** | 0 ? 0 0 0 0 1 1 0 1 ? | 1 ? ? 0 ? 0 0 1 0 ? 1 | 1 1 1 1 0 ? ? ? ? 0 0 | 1 1 1 1 0 0 1 1 0 0 1 |
| ***Angolatitan*** | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? ? |
| ***Aragosaurus*** | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? 0 0 ? 0 | 0 0 1 0 ? ? ? ? 1 0 | 0 0 0 0 0 1 0 0 0 1 |
| ***Astrophocaudia*** | ? ? ? ? ? ? ? ? ? 1 | ? ? ? ? ? 0 0 0 0 ? 0 | 0 1 0 1 0 1 0 1 1 0 | 1 1 1 1 0 1 1 0 0 1 |
| ***Atlasaurus*** | 0 ? ? 0 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |

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APPENDIX 2 *Continued*

| | C161–170 | C171–180 | C181–190 | C191–200 |
|---|---|---|---|---|
| ***Australodocus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Baotianmansaurus*** | ? 1 0 1 1 1 1 1 1 1 | 1 ? 0 ? ? ? 0 0 ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Brachiosaurus*** | 0 1 1 0 1 1 0 ? ? 1 | 1 ? 1 0 ? 0 0 0 ? ? | 0 0 ? ? ? ? 0 1 1 0 | ? ? ? 0 0 0 0 0 ? ? |
| ***Brontomerus*** | ? ? ? ? ? ? ? ? ? 1 | ? ? ? ? ? ? ? ? ? ? | ? ? ? 1 0 ? ? ? ? ? | ? 1 1 ? ? ? ? ? ? 1 |
| ***Cedarosaurus*** | 0 ? ? ? ? ? ? ? ? ? | 1 ? ? ? 0 0 0 1 0 0 | 0 0 0 0 ? ? 0 1 ? 0 | ? 1 0 0 1 1 0 0 0 1 |
| ***Chubutisaurus*** | ? ? ? ? 0 ? 1 1 1 1 | 1 ? ? ? ? 0 0 0 ? ? | 0 0 0 0 ? ? ? ? 1 ? | ? 1 1 ? ? ? ? ? 0 1 |
| **Cloverly titanosauriform** | 0 0 0 0 1 1 1 1 1 ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Daxiatitan*** | 1 1 ? 0 ? ? ? ? ? 1 | 1 ? ? ? ? ? ? 0 ? ? | 1 ? ? ? ? ? ? ? 1 ? | ? ? ? ? ? 1 1 0 ? ? |
| ***Diamantinasaurus*** | ? ? ? ? ? ? ? ? ? 1 | 1 1 ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Dongbeititan*** | 0 ? 0 0 0 1 ? ? ? 1 | 1 ? ? ? ? ? ? 0 ? 1 | 0 0 ? ? ? ? ? ? 1 0 | ? ? ? 0 0 1 ? 0 ? ? |
| ***Dongyangosaurus*** | 1 ? 0 0 ? 1 ? ? ? 1 | ? ? ? 1 ? ? 0 0 ? ? | ? ? ? ? ? ? 1 ? 1 1 | ? ? ? 1 0 1 ? 0 ? ? |
| ***Erketu*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Euhelopus*** | 0 1 0 0 0 1 1 0 0 1 | 1 1 1 0 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Europasaurus*** | 0 1 1 0 1 ? 1 0 0 ? | ? ? 1 ? ? 0 0 0 ? 0 | 0 0 0 0 ? 0 ? ? ? 0 | ? 1 0 0 0 1 0 0 0 1 |
| **French *Bothriospondylus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? 0 ? ? ? | ? ? ? ? ? ? 0 ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Fukuititan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? 0 ? 1 ? ? ? ? | ? 1 ? ? ? ? ? ? ? ? |
| ***Fusuisaurus*** | ? ? ? ? ? ? ? ? ? 0 | ? ? ? ? ? ? 0 ? ? ? | ? ? ? ? ? ? 0 1 ? ? | ? ? ? 0 ? 1 0 0 ? ? |
| ***Galveosaurus*** | 0 1 ? 0 0 0 0 ? ? 0 | ? 0 0 ? ? 0 0 0 ? 0 | 0 0 1 0 ? ? ? ? ? ? | ? 1 0 ? ? ? ? ? ? ? |
| ***Giraffatitan*** | 0 1 1 0 1 1 0 ? ? 1 | 1 ? ? 0 0 0 0 1 0 1 | 0 0 0 1 0 0 0 0 1 0 | 0 1 0 0 0 1 1 0 0 1 |
| ***Gobititan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 0 ? ? ? ? 1 | 0 0 0 1 1 1 ? ? ? ? | 1 A 1 ? ? ? ? ? 0 1 |
| **HMN MB.R.2091.1-30** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 0 0 1 0 ? 1 | 0 0 1 0 ? ? 0 1 1 0 | 0 0 0 0 0 0 0 0 1 0 |
| ***Huanghetitan liujiaxiaensis*** | ? ? ? ? ? ? ? ? ? ? | ? ? 0 1 ? 0 0 0 ? ? | 1 0 ? ? ? ? ? ? ? 0 | ? 1 ? 0 0 1 0 ? ? ? |
| ***Huanghetitan ruyangensis*** | ? ? ? ? ? ? ? ? ? 0 | 1 ? 0 1 ? 0 0 0 ? 0 | 1 0 ? ? ? ? 1 ? 1 0 | ? ? ? 0 0 1 0 0 ? ? |
| ***Janenschia*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Jiangshanosaurus*** | 0 ? ? 0 ? ? ? ? ? 1 | ? ? ? ? ? ? ? 0 ? ? | ? ? 0 0 ? ? ? ? ? ? | ? 1 ? ? 0 1 1 0 ? ? |
| ***Lapparentosaurus*** | 0 0 0 0 0 1 0 ? ? 0 | ? 0 0 ? ? ? 0 0 ? 1 | 0 0 ? 0 ? 0 0 1 1 ? | ? 0 ? ? 1 1 0 0 ? ? |
| ***Ligabuesaurus*** | 0 0 0 0 ? ? 1 ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Liubangosaurus*** | 1 1 0 1 0 1 ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Lusotitan*** | 0 1 ? ? ? ? 0 ? ? ? | ? ? ? ? ? 0 0 0 ? 1 | 0 0 0 0 ? ? 0 1 ? 0 | ? 1 0 0 ? ? 0 0 ? ? |
| ***Malarguesaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? 0 0 ? ? | ? ? 0 1 0 ? 1 ? 0 0 | 1 1 1 0 1 1 0 0 ? 1 |
| ***Malawisaurus*** | 0 0 0 1 ? 1 1 0 0 1 | 1 ? ? 1 0 1 2 1 0 1 | 1 1 0 0 ? ? 0 1 1 1 | 1 1 1 1 1 1 0 0 0 1 |
| ***Mongolosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Opisthocoelicaudia*** | 1 1 0 1 1 ? 1 0 0 1 | 1 ? 0 1 1 ? 0 0 ? ? | 1 1 0 0 ? 1 0 ? 0 ? | 0 1 1 1 0 1 ? 0 0 1 |
| ***Paluxysaurus*** | 0 0 0 0 1 1 1 0 1 1 | 1 ? 1 ? 0 0 0 0 ? 0 | 0 ? 0 0 ? ? ? ? 0 0 | ? 1 1 0 0 1 0 0 0 1 |
| ***Pelorosaurus becklesii*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Phuwiangosaurus*** | 0 1 0 0 0 1 0 ? ? 1 | 1 ? 1 0 0 0 0 0 ? ? | 0 1 0 0 ? 1 0 ? 1 0 | ? 1 ? 0 1 1 1 0 ? ? |
| ***Qiaowanlong*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Rapetosaurus*** | 0 1 0 1 0 1 1 0 0 1 | ? 1 1 ? ? ? 2 0 ? ? | 1 ? 0 1 1 ? 1 ? 0 0 | 1 1 1 0 1 1 1 0 0 1 |
| ***Ruyangosaurus*** | ? ? ? 0 1 ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Saltasaurus*** | 0 1 0 1 0 1 1 0 0 ? | ? 1 0 ? ? 1 2 0 ? ? | 1 1 ? 1 1 1 0 1 0 ? | 0 1 1 1 0 0 1 0 0 1 |

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| | C161–170 | C171–180 | C181–190 | C191–200 |
|---|---|---|---|---|
| ***Sauroposeidon*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Sonorasaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? 0 0 ? ? | 0 0 ? ? ? ? ? ? ? ? | ? ? ? ? ? 1 ? ? ? ? |
| ***Tangvayosaurus*** | ? ? 0 0 1 1 ? ? ? ? | 1 ? ? ? 0 0 0 0 ? ? | 0 1 0 1 1 1 0 1 0 0 | 0 1 1 0 1 1 0 0 0 1 |
| ***Tastavinsaurus*** | 0 0 0 0 0 1 0 ? ? 1 | ? 1 1 1 0 0 1 0 ? ? | 0 0 0 1 0 ? 1 ? 1 0 | 1 1 1 0 1 1 0 0 0 1 |
| ***Tehuelchesaurus*** | 0 ? 0 0 0 1 ? ? ? 0 | 1 ? 1 ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Tendaguria*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Venenosaurus*** | ? ? ? ? ? ? ? ? ? 1 | ? ? ? ? ? 0 0 1 0 0 | 0 0 0 0 ? ? 0 1 1 0 | ? 1 0 0 1 1 0 0 0 1 |
| ***Wintonotitan*** | ? 1 ? ? ? ? 1 ? ? 1 | 1 1 0 ? ? 0 0 0 ? 0 | 0 0 1 0 ? 1 1 ? ? ? | ? 1 ? ? ? ? ? 0 ? ? |
| ***Xianshanosaurus*** | ? ? ? ? ? ? ? ? ? 1 | ? ? ? ? ? 1 2 1 1 1 | 1 1 ? ? ? ? 1 ? 1 1 | ? ? ? 0 0 0 0 0 ? ? |
| | **C201–210** | **C211–220** | **C221–230** | **C231–240** |
| ***Shunosaurus*** | 0 0 0 0 1 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 |
| ***Omeisaurus*** | 0 0 0 0 2 1 0 1 0 0 | 0 0 0 0 0 1 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 1 |
| ***Mamenchisaurus*** | 0 0 0 0 1 0 0 1 0 0 | 0 ? 0 1 0 1 ? ? 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 ? 0 0 1 |
| ***Camarasaurus*** | 0 0 0 0 1 0 0 0 0 0 | 0 1 0 0 0 0 1 0 0 1 | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 1 0 0 1 |
| ***Nigersaurus*** | 0 ? ? ? ? ? ? 0 ? ? | ? 0 0 1 0 0 1 ? ? ? | ? ? 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 ? ? 1 0 |
| ***Apatosaurus*** | 0 0 0 1 1 0 0 1 0 0 | 0 1 1 1 0 0 1 1 0 0 | 1 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 1 0 0 1 |
| ***Diplodocus*** | 0 0 0 1 1 0 ? 1 0 0 | 0 1 0 1 0 0 1 0 0 0 | 1 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 1 1 0 0 ? |
| ***Abydosaurus*** | ? 1 ? ? 2 1 ? ? ? ? | ? ? 0 ? ? ? ? ? ? ? | ? ? 0 ? ? ? ? ? 0 ? | ? ? ? ? ? ? ? ? 1 0 |
| ***Alamosaurus*** | 1 0 0 0 2 0 ? 0 0 1 | 1 0 1 0 1 1 0 1 1 0 | 2 1 A 1 1 1 1 1 1 1 | 0 ? 1 1 0 1 1 1 0 0 |
| ***Andesaurus*** | 0 1 0 0 2 1 1 0 0 0 | 0 ? ? ? ? ? ? ? ? ? | ? ? 1 ? 1 ? ? 1 ? ? | ? ? ? ? ? ? ? ? 1 0 |
| ***Angolatitan*** | ? ? ? ? ? ? ? ? ? ? | ? ? 1 0 1 0 ? ? ? ? | ? ? 1 1 1 0 1 1 0 0 | 0 0 0 1 0 0 ? ? 1 0 |
| ***Aragosaurus*** | ? ? ? ? 1 0 ? 0 0 1 | 0 1 0 0 0 0 1 ? ? ? | ? ? 0 ? ? 0 0 0 0 0 | 0 1 0 0 1 0 ? 0 1 ? |
| ***Astrophocaudia*** | 0 ? ? 0 2 1 ? 0 0 ? | ? ? ? ? ? ? 0 ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Atlasaurus*** | ? ? ? ? ? ? ? 0 ? ? | ? ? ? ? 0 0 ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? 1 0 0 ? |
| ***Australodocus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Baotianmansaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Brachiosaurus*** | ? ? ? 0 1 0 ? ? ? ? | ? ? ? ? ? ? ? 0 ? 0 | ? ? 0 0 0 0 ? 0 0 0 | ? ? ? ? ? ? ? ? ? ? |
| ***Brontomerus*** | ? ? ? ? ? ? ? ? ? ? | ? 0 ? ? 0 0 0 ? ? ? | 2 0 ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Cedarosaurus*** | 0 ? ? 0 2 1 ? 0 0 ? | ? ? 0 ? 1 0 1 1 ? ? | 2 0 0 1 1 0 0 0 0 0 | 0 1 0 0 0 ? ? ? 1 ? |
| ***Chubutisaurus*** | ? ? ? 0 2 1 ? 0 0 ? | ? ? 1 ? 1 0 0 ? ? ? | ? ? 1 1 1 0 1 0 0 0 | 0 0 ? ? ? 0 ? ? 1 0 |
| **Cloverly titanosauriform** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? 0 ? ? ? ? ? ? ? ? | ? ? 0 1 0 1 ? ? ? ? |
| ***Daxiatitan*** | ? ? ? ? 1 0 ? 1 ? ? | ? 0 ? 1 1 0 0 0 0 1 | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Diamantinasaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? 0 ? 1 0 1 ? ? ? | ? ? 1 0 0 0 0 1 0 0 | ? ? 1 1 0 0 ? ? 0 1 |
| ***Dongbeititan*** | ? ? ? 0 ? ? ? 1 0 ? | ? ? 1 0 ? 0 1 0 0 1 | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Dongyangosaurus*** | ? ? 1 0 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Erketu*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | 2 1 ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Euhelopus*** | ? ? ? ? ? ? ? ? ? ? | ? 0 1 1 0 1 0 1 0 1 | ? ? 1 0 0 0 0 0 0 0 | ? ? ? ? ? ? ? ? ? ? |
| ***Europasaurus*** | 0 ? ? 0 2 0 ? 0 ? 1 | 0 1 0 1 0 0 0 0 0 0 | 0 0 ? ? 0 0 ? 0 0 0 | ? ? 0 0 0 0 ? ? 1 ? |

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| | C201–210 | C211–220 | C221–230 | C231–240 |
|---|---|---|---|---|
| **French *Bothriospondylus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? 0 1 1 ? 0 ? 0 0 | 0 ? 0 0 0 ? ? 0 1 ? |
| ***Fukuititan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? 1 1 0 0 1 0 0 | 0 ? ? ? ? ? ? ? ? ? |
| ***Fusuisaurus*** | ? ? ? 0 2 1 ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Galveosaurus*** | ? ? ? 0 2 0 ? ? 0 ? | ? ? ? 0 0 0 1 ? ? ? | ? 0 0 1 0 0 0 0 0 0 | ? ? ? ? ? ? ? ? ? ? |
| ***Giraffatitan*** | 0 1 0 0 2 1 1 0 0 1 | 0 1 0 1 A 0 1 0 0 0 | 2 0 0 1 1 0 0 1 0 0 | 0 0 0 1 0 1 1 0 1 0 |
| ***Gobititan*** | ? ? ? ? ? ? ? 0 1 1 | 0 ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| **HMN MB.R.2091.1-30** | 0 ? ? 0 0 0 ? 1 0 ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Huanghetitan liujiaxiaensis*** | ? ? ? ? 2 0 ? 0 ? ? | ? 0 1 0 1 0 ? 0 0 1 | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Huanghetitan ruyangensis*** | 0 0 0 0 2 0 ? 0 1 ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Janenschia*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? 0 0 0 0 0 0 0 0 | 0 0 1 1 0 0 ? 0 ? ? |
| ***Jiangshanosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? 1 0 0 1 ? 1 1 ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Lapparentosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? 0 0 0 0 0 1 ? ? 0 | ? ? 0 1 0 0 0 0 0 0 | 0 0 0 0 0 0 ? ? 0 0 |
| ***Ligabuesaurus*** | ? ? ? ? ? ? ? ? ? ? | ? 0 1 1 1 0 1 0 ? 0 | ? ? 1 1 1 0 0 1 0 0 | ? ? ? ? ? ? ? ? 1 ? |
| ***Liubangosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Lusotitan*** | 0 ? ? 0 2 0 ? ? 0 ? | ? ? ? ? ? ? ? ? ? ? | ? ? 0 ? 0 0 ? ? ? ? | 0 0 0 0 1 ? ? ? ? ? |
| ***Malarguesaurus*** | ? ? ? 0 2 0 ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Malawisaurus*** | 0 ? ? 0 2 0 1 0 0 1 | 1 ? ? ? ? ? ? 0 ? 1 | 2 1 1 1 1 0 1 1 0 0 | 1 ? 1 1 0 1 ? ? ? 0 |
| ***Mongolosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Opisthocoelicaudia*** | 1 ? ? 0 2 0 ? 0 ? 1 | 1 0 1 1 ? ? 1 1 1 1 | 2 1 1 0 1 1 1 1 1 1 | ? 1 1 1 0 0 1 1 1 0 |
| ***Paluxysaurus*** | 0 ? ? 0 2 0 ? 0 0 ? | ? ? 1 0 1 1 0 0 0 0 | 2 0 1 ? 0 0 0 1 0 0 | 0 1 0 ? 0 1 ? ? 1 ? |
| ***Pelorosaurus becklesii*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? 1 0 0 0 0 1 0 0 | 0 0 0 1 0 0 ? ? ? ? |
| ***Phuwiangosaurus*** | ? 1 1 0 2 0 ? 0 ? 1 | 1 1 1 1 0 1 1 ? ? ? | 2 0 1 0 0 0 0 ? 0 0 | ? 0 0 0 0 ? ? ? 1 ? |
| ***Qiaowanlong*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Rapetosaurus*** | 0 ? ? 0 ? ? ? 0 0 1 | 1 1 1 1 0 0 0 0 0 0 | 2 1 1 0 0 0 1 1 1 0 | 1 1 0 0 0 1 ? ? 1 0 |
| ***Ruyangosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Saltasaurus*** | ? 0 0 0 2 0 ? 0 ? ? | 0 1 1 0 0 0 0 1 1 1 | 2 1 1 0 1 1 1 1 1 1 | ? 1 1 1 0 ? ? ? ? ? |
| ***Sauroposeidon*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Sonorasaurus*** | ? ? ? ? 2 1 ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 1 0 |
| ***Tangvayosaurus*** | 0 ? ? 0 2 1 ? 0 ? 1 | 0 ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? 1 0 0 0 | ? ? ? ? ? ? ? ? 1 ? |
| ***Tastavinsaurus*** | 0 1 0 0 2 1 1 0 0 0 | 0 ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | 0 1 ? ? ? ? ? ? ? ? |
| ***Tehuelchesaurus*** | ? ? ? ? ? ? ? ? ? ? | ? 0 0 1 0 0 1 1 0 1 | ? ? 1 1 0 0 0 0 0 0 | 0 0 0 0 1 0 ? ? ? ? |
| ***Tendaguria*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Venenosaurus*** | ? 1 ? 0 2 0 ? 0 0 ? | ? 1 1 0 0 0 1 ? ? ? | ? ? ? ? ? ? ? ? ? ? | 0 0 0 1 0 0 ? ? 1 ? |
| ***Wintonotitan*** | ? ? ? 0 2 0 ? 0 0 ? | ? 0 ? 0 1 0 0 ? ? ? | ? ? ? 0 ? 0 ? 0 ? ? | 0 1 0 ? ? 1 ? ? 1 ? |
| ***Xianshanosaurus*** | 0 ? ? 0 0 0 ? 1 ? ? | ? ? ? ? ? ? ? 0 ? 1 | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Qiaowanlong*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |

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| | C241–250 | C251–260 | C261–270 | C271–279 |
|---|---|---|---|---|
| ***Shunosaurus*** | 0 0 0 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | ? 0 0 0 0 0 0 0 ? 0 | 0 0 0 0 0 0 0 0 0 0 |
| ***Omeisaurus*** | 0 0 1 0 0 0 0 0 0 1 | 0 0 0 0 0 0 0 ? 0 0 | 0 0 0 1 0 0 0 0 ? ? | ? 1 0 0 0 0 0 0 0 |
| ***Mamenchisaurus*** | 0 0 ? 0 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 0 ? 0 0 0 0 0 0 ? | ? 1 0 0 ? ? 0 0 0 |
| ***Camarasaurus*** | 0 0 1 1 0 0 0 0 0 0 | 0 0 0 0 0 0 0 1 1 0 | 0 0 0 0 1 1 1 0 1 0 | 0 0 1 0 0 0 1 0 0 |
| ***Nigersaurus*** | ? ? ? 1 ? 0 ? 0 0 ? | 0 ? ? 0 0 1 0 0 1 1 | 1 0 0 0 1 1 0 1 ? ? | ? ? ? ? ? ? ? ? 0 |
| ***Apatosaurus*** | 0 0 1 1 0 0 0 0 0 0 | 0 1 0 0 0 0 0 1 1 0 | 1 0 0 0 1 1 1 0 0 1 | ? 1 0 0 0 0 1 0 0 |
| ***Diplodocus*** | 0 0 ? 1 0 0 0 0 0 0 | 0 0 0 0 0 0 0 0 0 0 | 0 1 0 0 1 1 0 0 ? 0 | 0 1 1 0 ? ? 1 0 0 |
| ***Abydosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? 0 ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? 1 ? ? 0 |
| ***Alamosaurus*** | 0 1 ? 1 ? 1 1 1 1 1 | 1 1 1 0 0 ? 1 0 2 ? | ? 1 ? 1 ? ? ? ? ? ? | ? 1 1 1 1 0 ? ? 0 |
| ***Andesaurus*** | ? ? ? ? ? ? ? ? ? 1 | ? 1 1 0 ? ? ? 1 ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 |
| ***Angolatitan*** | 0 ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? |
| ***Aragosaurus*** | ? ? ? ? ? ? ? ? ? ? | 0 0 0 0 1 1 0 0 1 ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? 0 0 |
| ***Astrophocaudia*** | ? ? ? ? ? ? ? ? 0 ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 |
| ***Atlasaurus*** | 0 0 ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 |
| ***Australodocus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? |
| ***Baotianmansaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? |
| ***Brachiosaurus*** | ? ? ? 1 0 1 ? 1 ? ? | ? ? ? ? 1 0 0 1 1 ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 |
| ***Brontomerus*** | ? ? ? 1 0 1 ? 1 0 ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? |
| ***Cedarosaurus*** | 1 0 ? ? ? ? ? ? ? 1 | 1 ? ? 0 ? ? 0 1 0 0 | ? ? ? ? 1 ? ? ? ? ? | ? 1 0 0 1 ? ? 1 0 |
| ***Chubutisaurus*** | 1 ? ? ? ? ? ? ? ? ? | ? ? 0 0 1 0 0 0 1 0 | 1 ? ? ? ? ? ? ? ? ? | ? ? ? ? 1 0 ? ? 0 |
| **Cloverly titanosauriform** | ? ? ? ? ? ? ? ? ? ? | 0 ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 0 |
| ***Daxiatitan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? 0 ? ? 0 ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 0 |
| ***Diamantinasaurus*** | 0 0 ? 1 1 1 0 1 1 1 | 1 1 1 0 1 1 ? 0 2 0 | 1 1 1 ? 1 1 0 1 1 ? | ? ? ? ? ? ? ? ? 0 |
| ***Dongbeititan*** | ? ? ? ? ? ? ? ? ? ? | ? 0 0 0 1 0 0 0 2 0 | 1 0 0 0 1 1 0 0 0 0 | 0 0 1 0 ? ? ? ? 0 |
| ***Dongyangosaurus*** | ? ? ? 1 1 1 ? ? ? 1 | 0 ? ? 0 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 0 |
| ***Erketu*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 0 | ? 1 1 1 1 1 0 1 1 0 | 0 ? ? ? ? ? ? ? 0 |
| ***Euhelopus*** | ? ? ? ? ? ? 0 ? 1 1 | 0 0 0 0 1 0 0 0 0 0 | 1 1 0 1 1 1 1 1 1 0 | 0 0 1 1 0 0 ? 1 0 |
| ***Europasaurus*** | ? 0 ? 1 0 1 0 1 ? ? | ? 0 0 0 1 0 0 1 1 0 | ? 0 0 0 1 ? ? ? ? ? | ? ? ? ? ? ? ? 0 0 |
| **French *Bothriospondylus*** | 1 0 ? ? ? ? ? ? ? ? | ? 0 ? 0 1 0 0 ? 0 0 | ? ? ? ? 1 1 1 0 1 ? | ? 0 ? ? ? ? ? ? 0 |
| ***Fukuititan*** | ? ? ? ? ? ? ? ? ? ? | ? ? 0 ? ? ? ? ? ? ? | ? 0 ? 1 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? |
| ***Fusuisaurus*** | ? ? ? 1 0 1 0 1 ? 1 | ? ? ? ? ? ? ? ? 0 ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? |
| ***Galveosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? 0 0 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 |
| ***Giraffatitan*** | 1 0 0 1 0 1 1 1 0 1 | 1 0 0 1 1 0 0 1 1 0 | 0 0 1 0 1 1 1 1 1 0 | 1 0 0 0 0 1 ? 0 0 |
| ***Gobititan*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? 0 ? 0 0 | 1 1 1 1 1 1 1 1 1 0 | 0 1 0 1 0 0 1 1 0 |
| **HMN MB.R.2091.1-30** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 |
| ***Huanghetitan liujiaxiaensis*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 |
| ***Huanghetitan ruyangensis*** | ? ? ? ? ? ? ? ? ? ? | ? ? 0 0 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 |
| ***Janenschia*** | ? 0 ? ? ? ? ? ? ? ? | 0 0 ? 0 1 0 0 0 1 0 | 0 0 0 0 1 1 1 0 0 ? | ? 0 1 0 0 0 1 0 0 |
| ***Jiangshanosaurus*** | ? ? ? ? ? ? ? ? ? ? | 1 ? ? 0 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 |
| ***Lapparentosaurus*** | 1 0 ? 1 0 0 0 0 0 1 | 0 1 0 1 1 0 0 0 1 1 | 0 0 ? ? 1 0 1 ? 0 0 | 1 1 0 0 ? ? ? ? 0 |

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| | C241–250 | C251–260 | C261–270 | C271–279 |
|---|---|---|---|---|
| ***Ligabuesaurus*** | ? 0 ? ? ? ? ? ? ? ? | ? ? ? ? ? 1 ? 0 0 1 1 | 0 0 1 0 1 1 1 ? 1 ? | ? 1 1 ? 1 0 ? ? 0 |
| ***Liubangosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 0 |
| ***Lusotitan*** | ? ? ? ? ? ? ? ? 0 1 | 0 0 0 0 ? ? ? ? ? 0 | 0 0 ? ? 1 1 1 1 0 ? | ? ? ? ? ? ? ? ? ? 0 |
| ***Malarguesaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? 0 1 ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 0 |
| ***Malawisaurus*** | ? ? ? ? ? ? ? ? ? ? | 0 1 1 0 1 1 0 0 ? 1 | ? 1 ? ? 1 ? ? ? ? ? | ? ? ? ? ? ? ? ? 1 1 |
| ***Mongolosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Opisthocoelicaudia*** | 0 1 ? 1 1 1 0 1 ? ? | 0 1 1 0 0 1 0 0 2 0 | ? 1 1 1 1 1 1 1 1 1 | ? 0 ? ? 0 ? 1 ? 0 |
| ***Paluxysaurus*** | 0 ? ? 1 0 ? 0 ? ? 1 | 0 0 0 0 1 1 0 1 0 0 | 1 1 1 1 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 0 |
| ***Pelorosaurus beckylesii*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Phuwiangosaurus*** | ? ? ? 1 0 1 1 0 ? ? | 1 ? ? 0 1 ? 0 1 0 1 | 0 1 0 1 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? 0 0 |
| ***Qiaowanlong*** | ? ? ? 1 0 1 0 0 ? 0 | 0 0 0 0 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 0 |
| ***Rapetosaurus*** | 1 1 ? 1 0 1 0 1 ? 1 | 0 0 1 0 0 1 0 0 2 0 | 0 1 1 1 ? ? ? ? ? ? | ? 1 1 0 0 0 ? 0 1 |
| ***Ruyangosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? 1 1 ? 1 1 | 1 ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 0 |
| ***Saltasaurus*** | ? ? ? 1 1 1 1 0 1 ? | 1 ? 1 0 0 1 1 0 2 1 | ? ? 1 1 ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 1 |
| ***Sauroposeidon*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Sonorasaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? 0 ? ? ? ? ? | ? 0 ? ? ? 1 1 ? ? ? |
| ***Tangvayosaurus*** | ? ? ? ? ? ? ? ? ? 1 | 1 0 0 0 0 1 0 0 1 1 0 | 0 1 ? 0 1 1 1 ? 0 ? | ? ? 0 ? ? ? ? 1 1 0 |
| ***Tastavinsaurus*** | ? ? ? 1 0 1 0 1 ? 1 | 1 0 0 0 0 0 1 0 0 0 1 | 0 1 1 1 1 1 1 1 1 0 | 1 0 0 0 0 1 0 1 1 0 |
| ***Tehuelchesaurus*** | ? ? ? ? ? ? ? ? ? 0 | 0 ? 0 0 0 1 0 0 1 1 ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 0 |
| ***Tendaguria*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |
| ***Venenosaurus*** | 1 ? ? ? ? ? ? ? ? 1 | 0 0 0 0 0 ? ? ? ? ? ? | ? ? ? ? ? 1 1 1 ? 1 | ? 0 1 0 1 1 ? ? 0 |
| ***Wintonotitan*** | 1 ? ? ? 1 0 ? ? 0 ? | ? 0 ? ? 0 ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? 0 |
| ***Xianshanosaurus*** | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? 0 1 0 0 0 ? | ? ? ? ? ? ? ? ? ? ? | ? ? ? ? ? ? ? ? ? ? |

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## APPENDIX 3

DATA MATRIX: CONTINUOUS DATA (CHARACTERS 1–74 ONLY)

| | C1 | C2 | C3 | C4 | C5 | C6 | C7 | C8 | C9 | C10 | C11 | C12 | C13 | C14 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Shunosaurus*** | 0.1 | 1.3 | ? | 1 | 1 | 1.2 | 0.4 | 1.4 | 2 | 2.3 | 2.3 | 21 | 25 | 13 |
| ***Omeisaurus*** | 0.1 | 0.8 | ? | 0.8 | ? | ? | ? | ? | ? | 1.4 | 1.9 | 17 | 23 | 17 |
| ***Mamenchisaurus*** | 0.2 | 1.1 | 1.1 | 0.7 | 1.2 | 1.6 | ? | 1.2 | 2.5 | 1.9 | 2.9 | 18 | 23 | 18 |
| ***Camarasaurus*** | 0.1 | 1.1 | 1.3 | 1.7 | 1.5 | 1.4 | 0.5 | 1.6 | 2.1 | 2.4 | 2 | 10 | 13 | 12 |
| ***Nigersaurus*** | 0 | 1.1 | ? | ? | ? | ? | 0.6 | 1.5 | 4 | 1.2 | 5 | 25 | 34 | 13 |
| ***Apatosaurus*** | 0 | 0.8 | 0.9 | ? | ? | 1.6 | 0.6 | 1.4 | ? | ? | 4.6 | 13 | ? | 15 |
| ***Diplodocus*** | 0 | 0.7 | ? | 1.8 | 4.2 | 1.1 | 0.7 | 1.3 | 4 | 1.3 | 5.2 | 11 | 14 | 15 |
| ***Abydosaurus*** | 0.3 | 0.8 | ? | ? | 1.4 | ? | ? | ? | ? | 1.4 | 2.8 | 14 | 14 | ? |
| ***Alamosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Andesaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Angolatitan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Aragosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2.5 | ? | ? | ? |
| ***Astrophocaudia*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2.7 | ? | ? | ? |
| ***Atlasaurus*** | ? | ? | 1.2 | 0.8 | ? | 1.3 | 0.7 | 1.3 | 3.9 | ? | 2.5 | 15 | 14 | ? |
| ***Australodocus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Baotianmansaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Brachiosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Brontomerus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Cedarosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Chubutisaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| **Cloverly titanosauriform** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Daxiatitan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Diamantinasaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Dongbeititan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 17 |
| ***Dongyangosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Erketu*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Euhelopus*** | 0.3 | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2.1 | 10 | 13 | 17 |
| ***Europasaurus*** | 0.2 | ? | 0.9 | 0.9 | 1.4 | 1.2 | 0.7 | 1.3 | 3.5 | 2.4 | 2.7 | ? | 13 | ? |
| **French *Bothriospondylus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2.5 | ? | ? | ? |
| ***Fukuititan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 3 | ? | ? | ? |
| ***Fusuisaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Galveosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Giraffatitan*** | 0.4 | 1.2 | 1.1 | 0.5 | 1.6 | 1.5 | 0.8 | 1.2 | 3.3 | 4.1 | 2.3 | 11 | 13 | ? |
| ***Gobititan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| **HMN MB.R.2091.1-30** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Huanghetitan liujiaxiaensis*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Huanghetitan ruyangensis*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Janenschia*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Jiangshanosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Lapparentosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Ligabuesaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2.7 | ? | ? | ? |
| ***Liubangosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Lusotitan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Malarguesaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Malawisaurus*** | 0.1 | ? | ? | 1.4 | ? | 0.8 | 0.5 | 1.8 | 4.5 | ? | 4 | ? | 15 | ? |
| ***Mongolosaurus*** | ? | ? | ? | ? | ? | ? | 0.7 | 1.8 | ? | ? | 4 | ? | ? | ? |
| ***Opisthocoelicaudia*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Paluxysaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2.7 | ? | ? | ? |
| ***Pelorosaurus becklesii*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Phuwiangosaurus*** | ? | ? | ? | ? | ? | 1 | 0.6 | 1.4 | 3.4 | ? | 4.4 | ? | ? | ? |
| ***Qiaowanlong*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Rapetosaurus*** | 0 | ? | 0.6 | 1.4 | ? | 0.9 | 0.5 | 1.4 | 3.3 | 3.2 | 4.2 | ? | 11 | 17 |
| ***Ruyangosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |

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APPENDIX 3 *Continued*

| | C1 | C2 | C3 | C4 | C5 | C6 | C7 | C8 | C9 | C10 | C11 | C12 | C13 | C14 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Saltasaurus*** | ? | ? | ? | ? | ? | 1.7 | 0.5 | 1.6 | ? | ? | ? | ? | ? | ? |
| ***Sauroposeidon*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Sonorasaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Tangvayosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Tastavinsaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Tehuelchesaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Tendaguria*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Venenosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Wintonotitan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Xianshanosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |

| | C15 | C16 | C17 | C18 | C19 | C20 | C21 | C22 | C23 | C24 | C25 | C26 | C27 | C28 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Shunosaurus*** | 1.8 | ? | 0.9 | 0.7 | 1.7 | 13 | 1 | 1 | 2.2 | 4 | 0.8 | 0.5 | 0 | 0.9 |
| ***Omeisaurus*** | 4 | 1.1 | 1.6 | 0.5 | 1.2 | 12 | 1.2 | 0.8 | 1.3 | 5 | 0.8 | 0.6 | 0 | 0.8 |
| ***Mamenchisaurus*** | 3.2 | ? | 0.8 | 0.6 | 0.8 | 12 | 1.2 | 0.8 | 1.1 | 5 | 0.8 | 0.8 | 0.8 | 0.9 |
| ***Camarasaurus*** | 2.5 | 0.9 | 0.6 | 0.6 | 1.3 | 12 | 1.2 | 1.2 | 0.9 | 5 | 1.2 | 0.4 | 0 | 0.8 |
| ***Nigersaurus*** | 2.8 | 1 | 1.6 | 1.1 | 1.3 | 12 | 1 | 0.9 | ? | ? | ? | ? | ? | 0.7 |
| ***Apatosaurus*** | 3.4 | 1 | 0.8 | 0.7 | 1.7 | 10 | 1.4 | 1 | 2.4 | 5 | 1 | 0.6 | 0.3 | 1.1 |
| ***Diplodocus*** | 3.3 | 0.9 | 0.9 | 0.6 | 1.2 | 10 | 1.1 | 1.1 | 1.8 | 5 | 1.1 | 0.6 | 0.3 | 1 |
| ***Abydosaurus*** | 3.5 | 0.6 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0 | ? |
| ***Alamosaurus*** | 2.5 | ? | 0.5 | ? | ? | ? | ? | ? | ? | 6 | 0.9 | 0.9 | 1 | 0.9 |
| ***Andesaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | 2.1 | ? | 0.6 | 0.9 | 0.3 | 0.6 |
| ***Angolatitan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Aragosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 0.5 | 0 | 1 |
| ***Astrophocaudia*** | 2.5 | ? | 0.8 | ? | ? | ? | ? | ? | ? | ? | 1.6 | 0.7 | 0 | 1 |
| ***Atlasaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | 1.8 | 5 | ? | ? | ? | ? |
| ***Australodocus*** | 3.8 | ? | 0.9 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Baotianmansaurus*** | ? | ? | ? | ? | ? | ? | 1.1 | ? | 1.3 | ? | 0.8 | 0.5 | 0 | ? |
| ***Brachiosaurus*** | ? | ? | ? | ? | ? | ? | ? | 1.1 | 1.4 | 5 | 1.1 | 0.6 | 0 | ? |
| ***Brontomerus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Cedarosaurus*** | ? | ? | ? | ? | ? | ? | ? | 1 | ? | ? | 1 | 0.8 | 0 | 1.3 |
| ***Chubutisaurus*** | ? | ? | ? | ? | ? | ? | 1.2 | 1.3 | ? | ? | 1.2 | 0.5 | 0 | 1 |
| **Cloverly titanosauriform** | ? | ? | ? | ? | ? | ? | 1.5 | 0.9 | 1.8 | ? | ? | ? | ? | ? |
| ***Daxiatitan*** | 3.3 | ? | 1.1 | ? | 0.7 | ? | ? | ? | ? | ? | ? | ? | 1.1 | ? |
| ***Diamantinasaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Dongbeititan*** | ? | ? | ? | ? | ? | ? | 1.3 | ? | 1.2 | ? | 0.9 | 0.5 | 0.8 | ? |
| ***Dongyangosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | 6 | ? | 0.6 | 0 | ? |
| ***Erketu*** | 5.6 | 1.3 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Euhelopus*** | 5.5 | 1.4 | 1.2 | ? | 0.8 | 13 | 0.9 | 0.9 | 0.9 | 6 | ? | ? | ? | ? |
| ***Europasaurus*** | 2.8 | 0.7 | 0.8 | 0.6 | ? | ? | 1.1 | 1 | 1.7 | 5 | 1.3 | 0.9 | 0 | 1 |
| **French *Bothriospondylus*** | ? | ? | 1.3 | ? | ? | ? | ? | ? | ? | ? | 1 | ? | 0 | ? |
| ***Fukuititan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Fusuisaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1.1 | ? | 0 | ? |
| ***Galveosaurus*** | 3.7 | ? | ? | ? | ? | ? | 0.9 | 1.4 | 2 | 5 | 1.2 | 0.8 | 0 | 1.1 |
| ***Giraffatitan*** | 3.7 | 0.8 | 0.9 | 0.6 | ? | ? | 1.1 | 1.8 | 1.6 | 5 | 1 | 0.6 | 0 | 1.3 |
| ***Gobititan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1.1 |
| **HMN MB.R.2091.1-30** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 0.8 | 0.6 | 1 |
| ***Huanghetitan liujiaxiaensis*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | 5 | 1.1 | 0.8 | 0 | ? |
| ***Huanghetitan ruyangensis*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | 6 | 1.1 | 0.7 | 0 | ? |
| ***Janenschia*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Jiangshanosaurus*** | ? | ? | ? | ? | ? | ? | ? | 0.8 | 1.1 | ? | 1 | 0.5 | ? | 0.9 |
| ***Lapparentosaurus*** | ? | 1 | ? | ? | ? | ? | ? | 1.1 | ? | ? | 0.9 | 0.7 | 0 | 1 |
| ***Ligabuesaurus*** | ? | ? | ? | 0.3 | 2 | ? | 2.2 | 1.4 | ? | ? | ? | ? | ? | ? |

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APPENDIX 3 *Continued*

| | C15 | C16 | C17 | C18 | C19 | C20 | C21 | C22 | C23 | C24 | C25 | C26 | C27 | C28 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Liubangosaurus*** | ? | ? | ? | ? | ? | ? | ? | 0.7 | 0.9 | ? | ? | ? | ? | ? |
| ***Lusotitan*** | ? | ? | ? | ? | ? | ? | ? | 1.3 | ? | ? | 1.1 | 0.6 | 0 | 1.2 |
| ***Malarguesaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1.2 | 0.8 | 0 | 1.1 |
| ***Malawisaurus*** | 5.2 | 0.9 | 0.7 | 0.5 | 0.9 | ? | 1.5 | 1 | 1.3 | 6 | 1.1 | 0.6 | 0.8 | 0.9 |
| ***Mongolosaurus*** | ? | 0.7 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Opisthocoelicaudia*** | ? | ? | ? | ? | 1.4 | ? | 1.5 | 1.7 | 0.9 | 6 | 1.3 | 0.5 | 0 | 1.2 |
| ***Paluxysaurus*** | 5.5 | 0.8 | ? | ? | ? | ? | 1.2 | 1.2 | 1.9 | 5 | 1.1 | 0.5 | 0 | 1.1 |
| ***Pelorosaurus becklesii*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Phuwiangosaurus*** | 3.1 | 0.7 | 0.7 | ? | 0.6 | ? | 1.3 | 1 | 1 | 6 | 1.1 | 0.6 | 0 | 1 |
| ***Qiaowanlong*** | 3.1 | ? | 0.8 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Rapetosaurus*** | 4 | 0.8 | 0.8 | 0.4 | 0.6 | 10 | 1.5 | 1.3 | 1.4 | 6 | 1.1 | 0.7 | 0.7 | 1 |
| ***Ruyangosaurus*** | ? | ? | ? | ? | ? | ? | ? | 1.3 | ? | ? | ? | ? | ? | ? |
| ***Saltasaurus*** | 2.1 | 0.8 | 0.7 | ? | ? | ? | ? | 1 | 1.3 | 6 | 1.3 | 0.7 | 0.8 | 1.3 |
| ***Sauroposeidon*** | 5.9 | ? | 0.9 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Sonorasaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1.2 | ? | 0 | ? |
| ***Tangvayosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | 1 | ? | 1 | 0.4 | 0 | ? |
| ***Tastavinsaurus*** | ? | ? | ? | ? | ? | ? | ? | 1.1 | 1.2 | 5 | 0.9 | 0.6 | 0.1 | 1 |
| ***Tehuelchesaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Tendaguria*** | ? | ? | 0.8 | 0.4 | 0.7 | ? | 1.5 | ? | ? | ? | ? | ? | ? | ? |
| ***Venenosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1.2 | 0.6 | 0 | 1.1 |
| ***Wintonotitan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1.1 | 0.7 | 0 | ? |
| ***Xianshanosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1.4 | 0.6 | 0.7 | ? |

| | C29 | C30 | C31 | C32 | C33 | C34 | C35 | C36 | C37 | C38 | C39 | C40 | C41 | C42 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Shunosaurus*** | 1.3 | 1.2 | 1.6 | 1.9 | 0.9 | 1 | 0.2 | 2.4 | 2 | 1.2 | 0.3 | 0.7 | 0.4 | 0.2 |
| ***Omeisaurus*** | 1.2 | 0.8 | 1.7 | 1.2 | 0.9 | 1.9 | 0.3 | 3 | 1.8 | 0.9 | 0.4 | 0.8 | 0.4 | 0.2 |
| ***Mamenchisaurus*** | 1.3 | 1 | 1.6 | 1.5 | 0.8 | 1.4 | 0.2 | 3.5 | 2.2 | 1.1 | 0.3 | 0.7 | 0.4 | 0.1 |
| ***Camarasaurus*** | 0.9 | 1.1 | 1.3 | 1.2 | 1.4 | 3 | 0.4 | 3.3 | 2.2 | 1.3 | 0.6 | 0.7 | 0.4 | 0.2 |
| ***Nigersaurus*** | 1.3 | 1.2 | 2.4 | 1.7 | 1 | 1.6 | 0.3 | 2.3 | 2.5 | ? | ? | ? | 0.4 | 0.1 |
| ***Apatosaurus*** | 1.2 | 1 | 2.3 | 1.6 | 1.1 | 1.8 | 0.3 | 3.8 | 1.9 | 1.1 | 0.5 | 0.7 | 0.5 | 0.2 |
| ***Diplodocus*** | 1.9 | ? | 2.5 | 1.8 | 1.7 | 2.4 | ? | 3.3 | 1.9 | ? | ? | 0.7 | 0.3 | 0.2 |
| ***Abydosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Alamosaurus*** | 1.4 | 1.4 | 1.8 | 0.9 | 0.7 | 1.4 | 0.5 | 3.2 | 1.7 | 1.2 | 0.8 | ? | ? | 0.2 |
| ***Andesaurus*** | 1.6 | 0.8 | 1.9 | ? | 0.2 | 1.3 | 0.5 | ? | ? | ? | ? | ? | ? | ? |
| ***Angolatitan*** | ? | ? | ? | ? | ? | ? | ? | 3.6 | ? | ? | ? | ? | 0.3 | 0.2 |
| ***Aragosaurus*** | 1.1 | 1.1 | 1.6 | 1 | 1 | 2.2 | 0.4 | 3.4 | ? | ? | ? | ? | ? | 0.1 |
| ***Astrophocaudia*** | 1.3 | 1.1 | 1.8 | ? | 0.9 | 1.7 | 0.4 | ? | ? | ? | ? | ? | ? | ? |
| ***Atlasaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | ? | ? |
| ***Australodocus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Baotianmansaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Brachiosaurus*** | ? | ? | ? | 0.9 | 0.9 | 2.8 | ? | ? | ? | 1 | ? | 1 | 0.3 | 0.1 |
| ***Brontomerus*** | ? | 1.1 | 1.7 | ? | ? | ? | ? | ? | 1.9 | ? | ? | ? | ? | ? |
| ***Cedarosaurus*** | 1.2 | ? | ? | 0.8 | 0.4 | 1.4 | 0.6 | 3.5 | ? | 1.1 | 0.5 | 1 | 0.3 | 0.1 |
| ***Chubutisaurus*** | 1.3 | 1.2 | 1.5 | ? | ? | ? | ? | ? | ? | ? | ? | 0.9 | 0.3 | 0.2 |
| **Cloverly titanosauriform** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Daxiatitan*** | ? | ? | ? | ? | ? | ? | 0.2 | 3.5 | 2.1 | 1 | ? | ? | ? | ? |
| ***Diamantinasaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0.8 | 0.5 | 0.2 |
| ***Dongbeititan*** | ? | ? | ? | ? | ? | ? | 0.3 | ? | ? | 1.1 | ? | ? | ? | ? |
| ***Dongyangosaurus*** | ? | ? | ? | 0.8 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Erketu*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Euhelopus*** | ? | ? | ? | ? | ? | ? | ? | 4.6 | 2.3 | 1.2 | ? | ? | 0.4 | 0.1 |
| ***Europasaurus*** | 1.4 | 1.1 | 1.9 | 0.8 | 0.3 | 1.3 | 0.4 | 2.9 | ? | 1.3 | ? | ? | ? | 0.2 |
| **French *Bothriospondylus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0.9 | 0.3 | 0.1 |

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| | C29 | C30 | C31 | C32 | C33 | C34 | C35 | C36 | C37 | C38 | C39 | C40 | C41 | C42 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Fukuititan*** | ? | 1.1 | 1.8 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Fusuisaurus*** | ? | ? | ? | 0.6 | 0.9 | 1.3 | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Galveosaurus*** | 1.3 | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0.4 | ? | 0.3 | 0.2 |
| ***Giraffatitan*** | 1.1 | 1.2 | 1.4 | 0.8 | 0.3 | 1.2 | 0.5 | 3.5 | 2.2 | 1.4 | 0.5 | 1 | 0.3 | 0.1 |
| ***Gobititan*** | 1.1 | 1.2 | 1.4 | ? | ? | ? | 0.4 | ? | ? | ? | ? | ? | ? | ? |
| **HMN MB.R.2091.1-30** | 1.4 | 0.9 | 2 | 1.4 | 1 | 2 | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Huanghetitan liujiaxiaensis*** | ? | ? | ? | ? | 0.8 | 1.4 | ? | 4.1 | 2.1 | 1.4 | ? | ? | ? | ? |
| ***Huanghetitan ruyangensis*** | ? | ? | ? | 0.8 | 0.9 | 1.3 | 0.4 | ? | ? | ? | ? | ? | ? | ? |
| ***Janenschia*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0.5 | 0.2 |
| ***Jiangshanosaurus*** | 1 | ? | ? | 1.1 | 0.7 | 1.3 | ? | 3.6 | 1.2 | 1.2 | ? | ? | ? | ? |
| ***Lapparentosaurus*** | 1.3 | ? | ? | ? | 0.3 | 1.3 | ? | ? | 2.1 | 1 | ? | ? | 0.3 | 0.1 |
| ***Ligabuesaurus*** | ? | ? | ? | ? | ? | ? | ? | 4 | 1.7 | 1 | ? | ? | 0.3 | 0.1 |
| ***Liubangosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Lusotitan*** | 1.2 | ? | ? | ? | 0.4 | ? | 0.5 | ? | ? | ? | ? | ? | ? | ? |
| ***Malarguesaurus*** | 1.2 | 1 | 1.7 | 1.1 | 0.4 | 1.5 | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Malawisaurus*** | 1.6 | 1.2 | 2.1 | 0.9 | 1 | 1.5 | 0.6 | ? | ? | 1.2 | 0.7 | ? | 0.4 | 0.1 |
| ***Mongolosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Opisthocoelicaudia*** | 0.9 | 1.3 | 1.6 | ? | 1.5 | 1.3 | 0.5 | 2.9 | 1.4 | 1.2 | 0.8 | 0.7 | 0.5 | 0.2 |
| ***Paluxysaurus*** | 1.3 | 0.9 | 1.7 | 0.8 | 1 | 1.6 | 0.3 | 3.5 | 1.8 | ? | ? | ? | 0.3 | 0.1 |
| ***Pelorosaurus becklesii*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 0.5 | 0.2 |
| ***Phuwiangosaurus*** | 1.3 | ? | ? | 0.9 | 0.6 | 2 | 0.5 | 3.4 | ? | ? | ? | 0.8 | ? | 0.1 |
| ***Qiaowanlong*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Rapetosaurus*** | 1.6 | ? | ? | 1 | 0.9 | 1.5 | 0.4 | 2.8 | 1.2 | 1.5 | 0.7 | 0.8 | 0.4 | 0.2 |
| ***Ruyangosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Saltasaurus*** | 1.4 | 1.7 | 1.8 | 1.3 | 1.6 | ? | 0.3 | 2.4 | 1.6 | ? | ? | ? | 0.5 | 0.2 |
| ***Sauroposeidon*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Sonorasaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Tangvayosaurus*** | ? | 1.3 | 1.8 | 0.8 | 2.1 | 1.3 | 0.4 | ? | ? | ? | ? | ? | ? | ? |
| ***Tastavinsaurus*** | 1.3 | 0.9 | 1.6 | 1 | 1.3 | 2.1 | 0.5 | ? | ? | ? | ? | ? | ? | ? |
| ***Tehuelchesaurus*** | ? | ? | ? | ? | ? | ? | ? | 3.9 | 1.6 | 1.1 | ? | 0.7 | 0.4 | 0.2 |
| ***Tendaguria*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Venenosaurus*** | 1 | 1.2 | 1.9 | 1.1 | 0.9 | 1.4 | 0.4 | 2.5 | ? | ? | ? | ? | ? | ? |
| ***Wintonotitan*** | ? | 1.1 | 1.7 | ? | ? | ? | 0.2 | ? | ? | ? | ? | ? | ? | ? |
| ***Xianshanosaurus*** | ? | ? | ? | 1 | ? | 1.3 | 0.3 | ? | ? | 1.4 | ? | ? | ? | ? |

| | C43 | C44 | C45 | C46 | C47 | C48 | C49 | C50 | C51 | C52 | C53 | C54 | C55 | C56 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Shunosaurus*** | ? | 0.7 | 0.3 | 1.3 | 1.7 | ? | 0 | 0.3 | ? | 0.3 | 1.6 | 0.7 | 0.7 | 2 |
| ***Omeisaurus*** | 1.6 | 0.7 | 0.2 | 1.2 | 2 | 1.5 | ? | 0.2 | 1.3 | 0.3 | 1.2 | 0.8 | 0.8 | 1.1 |
| ***Mamenchisaurus*** | ? | 0.7 | 0.2 | 1 | 1.8 | ? | 0 | 0.3 | 1 | 0.4 | ? | 0.8 | 0.8 | ? |
| ***Camarasaurus*** | 1.3 | 0.7 | 0.3 | 1.1 | 2.3 | 1.4 | 10 | 0.4 | 1.3 | 0.5 | 1.5 | 0.9 | 1 | 0.7 |
| ***Nigersaurus*** | 1.3 | 0.7 | 0.2 | 1.2 | 1.7 | 1.1 | 0 | 0.3 | 1.2 | ? | 1.9 | ? | ? | ? |
| ***Apatosaurus*** | 1.3 | 0.7 | 0.3 | 1.1 | 2.2 | 1.3 | 20 | 0.4 | 1 | 0.4 | 1.7 | 0.9 | 1.1 | 0.8 |
| ***Diplodocus*** | 1.4 | 0.7 | 0.2 | 1 | 1.7 | 1.4 | 15 | 0.3 | 1.1 | 0.4 | 1.9 | 0.8 | 0.9 | 0.7 |
| ***Abydosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Alamosaurus*** | ? | 0.6 | 0.3 | 0.9 | 2.6 | 2.9 | 35 | 0.4 | 1.3 | 0.5 | 1.7 | 1 | 1.1 | 0 |
| ***Andesaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1.9 | ? | ? | ? |
| ***Angolatitan*** | 2.8 | 0.6 | 0.2 | 0.8 | 1.8 | 1.8 | 20 | 0.3 | 1.1 | 0.5 | 1.5 | 1 | 1.1 | ? |
| ***Aragosaurus*** | 1.7 | 0.7 | 0.2 | 1 | 2 | 1.3 | 17 | 0.4 | 1.1 | ? | ? | ? | ? | ? |
| ***Astrophocaudia*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Atlasaurus*** | ? | 0.6 | ? | ? | ? | ? | ? | ? | ? | 0.4 | ? | 0.9 | 0.9 | ? |
| ***Australodocus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Baotianmansaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Brachiosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |

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| | C43 | C44 | C45 | C46 | C47 | C48 | C49 | C50 | C51 | C52 | C53 | C54 | C55 | C56 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Brontomerus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Cedarosaurus*** | ? | 0.6 | 0.2 | 1.4 | 1.7 | 1.1 | 10 | ? | 2.9 | 0.5 | ? | ? | ? | ? |
| ***Chubutisaurus*** | 1.9 | 0.6 | 0.3 | 1 | 1.9 | 1.5 | 16 | ? | ? | 0.5 | 2 | 1 | 1.1 | ? |
| **Cloverly titanosauriform** | ? | ? | ? | ? | ? | 1.2 | ? | 0.4 | 2.2 | ? | ? | ? | ? | ? |
| ***Daxiatitan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Diamantinasaurus*** | 1.5 | ? | ? | ? | ? | ? | ? | 0.4 | 1 | ? | 1.4 | 1 | 1.1 | 0.5 |
| ***Dongbeititan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Dongyangosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Erketu*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Euhelopus*** | 1.8 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Europasaurus*** | 1.2 | ? | ? | ? | ? | ? | ? | 0.3 | 1.1 | ? | ? | ? | ? | ? |
| **French *Bothriospondylus*** | ? | 0.7 | 0.2 | 1.4 | 1.7 | ? | 10 | 0.3 | ? | 0.4 | ? | ? | ? | ? |
| ***Fukuititan*** | 1.6 | ? | 0.3 | 1 | 1.7 | ? | ? | ? | ? | 0.5 | ? | ? | ? | ? |
| ***Fusuisaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Galveosaurus*** | 2.1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Giraffatitan*** | 1.4 | 0.6 | 0.2 | 1.1 | 2 | 1.5 | 16 | 0.3 | 1.4 | 0.5 | 1.7 | 1 | 1 | 0.2 |
| ***Gobititan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| **HMN MB.R.2091.1-30** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Huanghetitan liujiaxiaensis*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Huanghetitan ruyangensis*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Janenschia*** | 1.5 | 0.7 | 0.3 | 0.9 | 2.1 | 1.6 | 21 | 0.5 | ? | ? | ? | ? | ? | ? |
| ***Jiangshanosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Lapparentosaurus*** | 1.1 | ? | 0.2 | 1.2 | 1.7 | 1.3 | 23 | 0.3 | 1.1 | ? | 1.4 | ? | ? | ? |
| ***Ligabuesaurus*** | 1.2 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Liubangosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Lusotitan*** | 1.7 | ? | 0.2 | 1.1 | 1.8 | 1.7 | 19 | ? | ? | ? | ? | ? | ? | ? |
| ***Malarguesaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Malawisaurus*** | ? | ? | 0.3 | 1 | 2.3 | 1.4 | 27 | 0.4 | 1.1 | ? | 1.2 | 1.2 | 1.7 | ? |
| ***Mongolosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Opisthocoelicaudia*** | 1.6 | 0.6 | 0.4 | 1.1 | 2.1 | 1.5 | 25 | 0.5 | 0.9 | 0.5 | 1.4 | 1 | 1.2 | 0 |
| ***Paluxysaurus*** | 1.4 | ? | 0.2 | 1.1 | 2.1 | 1.9 | 10 | 0.3 | 1.5 | ? | ? | 0.9 | ? | ? |
| ***Pelorosaurus becklesii*** | 1.5 | 0.7 | 0.2 | 1 | 1.7 | 1.4 | 21 | 0.4 | 1.2 | ? | ? | ? | ? | ? |
| ***Phuwiangosaurus*** | ? | ? | 0.3 | 1.3 | 2 | 1.4 | 22 | ? | ? | ? | ? | ? | ? | ? |
| ***Qiaowanlong*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Rapetosaurus*** | 1.5 | 0.7 | 0.2 | 0.9 | 1.9 | 2 | 20 | 0.3 | 1.1 | 0.5 | 2.4 | 1 | 1 | 0 |
| ***Ruyangosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Saltasaurus*** | 1.7 | ? | 0.3 | 1.3 | 1.7 | 1.9 | 31 | 0.4 | ? | ? | ? | ? | ? | ? |
| ***Sauroposeidon*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Sonorasaurus*** | ? | ? | 0.2 | 1 | ? | ? | ? | ? | ? | 0.6 | ? | ? | ? | ? |
| ***Tangvayosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Tastavinsaurus*** | ? | ? | 0.2 | 1.1 | 1.8 | 2.4 | 14 | ? | ? | ? | ? | ? | ? | ? |
| ***Tehuelchesaurus*** | 1.3 | 0.7 | 0.3 | 1 | 2.1 | 1.8 | 20 | 0.4 | 1.3 | ? | ? | ? | ? | ? |
| ***Tendaguria*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Venenosaurus*** | ? | ? | 0.2 | 1.1 | 1.7 | 1.2 | 16 | 0.3 | 2 | 0.5 | 2.2 | ? | ? | ? |
| ***Wintonotitan*** | ? | ? | 0.3 | 0.8 | 2.1 | 2 | 26 | 0.4 | ? | 0.5 | 1.4 | ? | ? | ? |
| ***Xianshanosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |

| | C57 | C58 | C59 | C60 | C61 | C62 | C63 | C64 | C65 | C66 | C67 | C68 | C69 | C70 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Shunosaurus*** | ? | ? | 0.4 | 0.9 | 0.4 | 0.6 | 0.3 | 2.3 | ? | ? | 2.2 | ? | 2.2 | 2 |
| ***Omeisaurus*** | ? | 0.7 | 0.4 | 1.3 | 0.3 | 0.5 | 0.2 | 1.7 | 1.4 | 1.2 | 1.7 | ? | ? | 2 |
| ***Mamenchisaurus*** | ? | ? | 0.4 | 1 | 0.3 | 0.6 | 0.2 | 1.7 | ? | 1.2 | 1.7 | 2.6 | ? | 1.9 |
| ***Camarasaurus*** | 0.7 | 1.2 | 0.5 | 1.2 | 0.3 | 0.4 | 0.1 | 1.5 | 1.6 | 1.1 | 2.1 | 1.5 | 1.9 | 2 |
| ***Nigersaurus*** | ? | ? | ? | ? | ? | 0.3 | ? | ? | 1.3 | ? | 1.6 | 1.3 | 1.7 | 1.6 |

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| | C57 | C58 | C59 | C60 | C61 | C62 | C63 | C64 | C65 | C66 | C67 | C68 | C69 | C70 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Apatosaurus*** | 0.5 | 0.9 | 0.3 | 1.2 | 0.4 | 0.4 | 0.3 | 2.7 | 1.4 | 1.1 | 2.1 | 1.2 | 1.6 | 1.8 |
| ***Diplodocus*** | 0.7 | ? | 0.3 | 1 | 0.3 | 0.5 | 0.2 | 2.7 | 1.4 | 1.1 | 1.5 | 1.2 | 1.9 | 2.1 |
| ***Abydosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Alamosaurus*** | ? | ? | 0.3 | ? | 0.4 | 0.7 | 0.3 | 1.2 | ? | ? | 2 | 1.9 | 2.1 | ? |
| ***Andesaurus*** | ? | 3.1 | ? | ? | 0.3 | 0.5 | 0.2 | 1.2 | ? | ? | ? | ? | ? | ? |
| ***Angolatitan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Aragosaurus*** | ? | 0.8 | 0.4 | 1 | 0.3 | 0.6 | 0.2 | 1.8 | 2 | ? | ? | ? | ? | ? |
| ***Astrophocaudia*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Atlasaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Australodocus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Baotianmansaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Brachiosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | 2.1 | 1.1 | ? | ? | ? | ? |
| ***Brontomerus*** | 0.4 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Cedarosaurus*** | ? | ? | ? | ? | ? | 0.7 | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Chubutisaurus*** | ? | ? | ? | ? | ? | ? | 0.2 | 1.3 | 1.8 | ? | 1.6 | 1.4 | ? | ? |
| **Cloverly titanosauriform** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Daxiatitan*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1.2 | ? | ? | ? | ? |
| ***Diamantinasaurus*** | 0.5 | 1.9 | 0.5 | 0.7 | 0.3 | 0.5 | 0.5 | 2 | 2.2 | 1.2 | 2.1 | 1.3 | 2.6 | 1.6 |
| ***Dongbeititan*** | ? | ? | ? | 1.1 | ? | 0.5 | 0.2 | 1.7 | ? | ? | 1.3 | ? | ? | 2.5 |
| ***Dongyangosaurus*** | ? | ? | 0.4 | 1.1 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Erketu*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 2 | ? | 2 | 1.3 |
| ***Euhelopus*** | ? | ? | 0.3 | 1.1 | 0.3 | 0.5 | 0.3 | 1.6 | 1.6 | 1.3 | 1.9 | 1.5 | 1.6 | 1.6 |
| ***Europasaurus*** | ? | ? | ? | ? | 0.3 | 0.7 | 0.2 | ? | ? | 1 | 1.8 | 1.3 | ? | ? |
| **French *Bothriospondylus*** | ? | ? | ? | ? | 0.3 | 0.7 | 0.1 | 1.6 | ? | ? | 1.9 | ? | ? | ? |
| ***Fukuititan*** | ? | ? | ? | ? | ? | ? | ? | ? | 1.9 | ? | ? | ? | ? | ? |
| ***Fusuisaurus*** | ? | ? | 0.4 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Galveosaurus*** | ? | ? | ? | ? | 0.3 | 0.6 | 0.2 | 1 | ? | ? | ? | ? | ? | ? |
| ***Giraffatitan*** | ? | 2.3 | 0.4 | 1 | 0.2 | 1 | 0.2 | 1.1 | 2.2 | 1.1 | 1.7 | 1.2 | 2.3 | 1.6 |
| ***Gobititan*** | ? | ? | ? | ? | ? | ? | ? | ? | 1.3 | 1.2 | 1.9 | 1.4 | 1.6 | 1.9 |
| **HMN MB.R.2091.1-30** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Huanghetitan liujiaxiaensis*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Huanghetitan ruyangensis*** | ? | ? | ? | ? | ? | 0.4 | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Janenschia*** | ? | ? | 0.4 | ? | 0.3 | 0.5 | 0.3 | 1.4 | 1.7 | 1.1 | 1.9 | 1.3 | 1.7 | 2.1 |
| ***Jiangshanosaurus*** | ? | ? | ? | ? | ? | ? | ? | 1.3 | ? | ? | ? | ? | ? | ? |
| ***Lapparentosaurus*** | 0.5 | 1.8 | 0.4 | ? | 0.3 | 0.5 | 0.2 | 1.2 | 1.5 | 1 | 1.7 | 1.4 | ? | 2.3 |
| ***Ligabuesaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | 2.4 | ? | 1.8 | 1.6 | ? | ? |
| ***Liubangosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Lusotitan*** | ? | ? | ? | ? | ? | 0.8 | ? | ? | ? | ? | 2.4 | 1.7 | ? | 1.9 |
| ***Malarguesaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Malawisaurus*** | ? | ? | ? | ? | 0.3 | 0.6 | 0.3 | ? | ? | ? | 2.7 | 1.3 | ? | ? |
| ***Mongolosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Opisthocoelicaudia*** | ? | ? | 0.3 | 0.7 | 0.4 | 0.5 | 0.2 | 2 | 2.3 | 1.3 | 2.3 | 1.6 | 2 | 1.7 |
| ***Paluxysaurus*** | ? | ? | 0.4 | 0.8 | 0.3 | 0.5 | 0.1 | 1.6 | 1.9 | 0.9 | 1.6 | 1.1 | 1.4 | ? |
| ***Pelorosaurus becklesii*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Phuwiangosaurus*** | ? | 2.2 | 0.4 | 0.7 | 0.3 | 0.6 | 0.2 | 1.5 | 2.6 | 0.9 | ? | 1.5 | 2.3 | ? |
| ***Qiaowanlong*** | ? | ? | 0.4 | 0.7 | 0.3 | 0.7 | 0.3 | 1.6 | ? | ? | ? | ? | ? | ? |
| ***Rapetosaurus*** | ? | ? | 0.4 | 0.7 | 0.4 | 0.4 | 0.2 | 1 | 1.6 | 1.1 | ? | ? | 1.6 | ? |
| ***Ruyangosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1.3 | 1 | ? | ? |
| ***Saltasaurus*** | ? | ? | ? | ? | ? | 0.9 | ? | ? | 2 | ? | 2 | 1.5 | ? | ? |
| ***Sauroposeidon*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Sonorasaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | 1.8 | ? | ? | ? | ? | ? |
| ***Tangvayosaurus*** | ? | ? | 0.5 | 0.7 | 0.3 | 0.7 | 0.2 | 1.1 | ? | ? | 1.7 | ? | 1.6 | 3.1 |
| ***Tastavinsaurus*** | 0.4 | 1.1 | 0.4 | 0.7 | 0.3 | 0.6 | 0.3 | 1.4 | 1.7 | 1.4 | 1.9 | 1.6 | 2 | 1.6 |
| ***Tehuelchesaurus*** | ? | ? | 0.5 | 1.1 | 0.3 | 0.7 | 0.2 | 1.8 | 1.6 | 1.1 | ? | ? | ? | ? |

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APPENDIX 3 *Continued*

| | C57 | C58 | C59 | C60 | C61 | C62 | C63 | C64 | C65 | C66 | C67 | C68 | C69 | C70 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Tendaguria*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Venenosaurus*** | ? | ? | ? | 1 | 0.2 | 0.6 | 0.2 | 1.5 | ? | ? | ? | ? | ? | 1.8 |
| ***Wintonotitan*** | ? | ? | ? | ? | ? | 0.4 | ? | ? | ? | ? | ? | ? | ? | ? |
| ***Xianshanosaurus*** | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |

| | C71 | C72 | C73 | C74 |
|---|---|---|---|---|
| ***Shunosaurus*** | ? | 1 | 0.2 | 1.7 |
| ***Omeisaurus*** | 1.8 | 1 | 0.3 | 2.5 |
| ***Mamenchisaurus*** | 1.6 | ? | ? | 2.1 |
| ***Camarasaurus*** | 1.5 | 1.2 | 0.2 | 1.8 |
| ***Nigersaurus*** | ? | ? | ? | 1.7 |
| ***Apatosaurus*** | 1.6 | 0.8 | 0.2 | 1.9 |
| ***Diplodocus*** | 1.5 | 1.3 | 0.2 | 1.4 |
| ***Abydosaurus*** | ? | ? | ? | ? |
| ***Alamosaurus*** | ? | 0.7 | ? | 2.1 |
| ***Andesaurus*** | ? | ? | ? | ? |
| ***Angolatitan*** | ? | ? | ? | ? |
| ***Aragosaurus*** | ? | ? | ? | ? |
| ***Astrophocaudia*** | ? | ? | ? | ? |
| ***Atlasaurus*** | ? | ? | 0.3 | ? |
| ***Australodocus*** | ? | ? | ? | ? |
| ***Baotianmansaurus*** | ? | ? | ? | ? |
| ***Brachiosaurus*** | ? | ? | ? | ? |
| ***Brontomerus*** | ? | ? | ? | ? |
| ***Cedarosaurus*** | ? | 0.6 | ? | 1.4 |
| ***Chubutisaurus*** | ? | ? | ? | ? |
| **Cloverly titanosauriform** | ? | ? | ? | ? |
| ***Daxiatitan*** | ? | ? | ? | ? |
| ***Diamantinasaurus*** | 1.5 | ? | ? | ? |
| ***Dongbeititan*** | 1.6 | 1 | ? | 1.6 |
| ***Dongyangosaurus*** | ? | ? | ? | ? |
| ***Erketu*** | ? | ? | ? | ? |
| ***Euhelopus*** | 1.5 | ? | 0.2 | ? |
| ***Europasaurus*** | ? | ? | ? | ? |
| **French *Bothriospondylus*** | 1.7 | ? | 0.3 | ? |
| ***Fukuititan*** | ? | ? | ? | ? |
| ***Fusuisaurus*** | ? | ? | ? | ? |
| ***Galveosaurus*** | ? | ? | ? | ? |
| ***Giraffatitan*** | 1.5 | ? | ? | ? |
| ***Gobititan*** | 1.2 | 0.9 | 0.2 | 1.5 |
| **HMN MB.R.2091.1-30** | ? | ? | ? | ? |
| ***Huanghetitan liujiaxiaensis*** | ? | ? | ? | ? |
| ***Huanghetitan ruyangensis*** | ? | ? | ? | ? |
| ***Janenschia*** | 1.8 | 1.3 | 0.2 | 1.6 |
| ***Jiangshanosaurus*** | ? | ? | ? | ? |
| ***Lapparentosaurus*** | 1.8 | ? | ? | ? |
| ***Ligabuesaurus*** | ? | 0.8 | 0.2 | 1.8 |
| ***Liubangosaurus*** | ? | ? | ? | ? |
| ***Lusotitan*** | 1.8 | ? | ? | ? |
| ***Malarguesaurus*** | ? | ? | ? | ? |
| ***Malawisaurus*** | ? | ? | ? | 1.6 |
| ***Mongolosaurus*** | ? | ? | ? | ? |
| ***Opisthocoelicaudia*** | 1.2 | 1.1 | 0.3 | ? |

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APPENDIX 3 *Continued*

| | C71 | C72 | C73 | C74 |
|---|---|---|---|---|
| ***Paluxysaurus*** | ? | ? | ? | ? |
| ***Pelorosaurus becklesii*** | ? | ? | ? | ? |
| ***Phuwiangosaurus*** | ? | ? | ? | ? |
| ***Qiaowanlong*** | ? | ? | ? | ? |
| ***Rapetosaurus*** | ? | 1.1 | ? | 3.2 |
| ***Ruyangosaurus*** | ? | ? | ? | ? |
| ***Saltasaurus*** | ? | ? | ? | ? |
| ***Sauroposeidon*** | ? | ? | ? | ? |
| ***Sonorasaurus*** | ? | 0.8 | 0.3 | 2.2 |
| ***Tangvayosaurus*** | 1.5 | ? | ? | ? |
| ***Tastavinsaurus*** | 1.6 | 0.9 | 0.3 | 2.1 |
| ***Tehuelchesaurus*** | ? | ? | ? | ? |
| ***Tendaguria*** | ? | ? | ? | ? |
| ***Venenosaurus*** | 1.4 | ? | ? | ? |
| ***Wintonotitan*** | ? | ? | ? | ? |
| ***Xianshanosaurus*** | ? | ? | ? | ? |

## APPENDIX 4

### SYNAPOMORPHIES OF HIGHER TAXA BASED ON THE LSDM MATRIX

Ambiguous character support is indicated by an asterisk. Note that synapomorphies are based on using the LSDM agreement subtree.

*Macronaria*

1. Surangular, dorsoventral height to maximum dorsoventral height of angular ratio is 2.0 or greater (C10*).
2. Radius, distal end mediolateral width to midshaft mediolateral width ratio is 2.0 or greater (C47*).
3. Metacarpal I to metacarpal IV proximodistal length ratio is 1.0 or greater (C55*).
4. Posterior end of prefrontal broadly rounded or 'square' in dorsal view (C82*).
5. External mandibular fenestra absent (C102*).
6. Anterior half of ventral surfaces of postaxial cervical centra are flat or mildly convex mediolaterally (C118*).
7. Ventral midline keel absent in postaxial cervical centra (C120*).
8. Lateral pneumatic foramina have acute posterior margins in anterior dorsal centra (C146).
9. Anterior articular faces of middle-posterior dorsal centra are strongly convex, with degree of convexity approximately consistent along the dorsal sequence (C147*).
10. Cross-sectional shape of anterior thoracic ribs plank-like (C171*).
11. Infraglenoid lip present on ventral margin of coracoid (C220*).
12. Proximolateral margin of femur, above the lateral bulge, is medial to the lateral margin of the distal half of the shaft (C255*).
13. Metatarsal I lacks a prominent ventrolateral expansion along its distal half (C272*).
14. Lateral margin of metatarsal II is straight in proximal view (C273*).

*Titanosauriformes*

1. Manual ungual on digit I to metacarpal I proximodistal length ratio is less than 0.5 (C56*).
2. Anteroposterior to mediolateral width ratio of pubic peduncle of ilium is 0.5 or less (C57*).
3. Fossa/fossae on the posterior surface of the basal tubera (C98*).
4. Tooth crowns aligned along jaw axis, crowns do not overlap (C106*).
5. Anterior half of ventral surfaces of postaxial cervical centra are concave mediolaterally (C118).
6. Internal tissue texture of middle-posterior dorsal vertebrae is camellate (C141).
7. Posterior centroparapophyseal lamina (PCPL) present as two parallel laminae in middle-posterior dorsal neural arches (C148*).
8. Dorsal neural spines narrow dorsally to form a triangular shape in lateral view, with the base approximately twice the width of the dorsal tip (C159*).
9. Thoracic (dorsal) ribs are pneumatized (C170).
10. Small, shallow vascular foramina pierce the lateral and/or ventral surfaces of anterior–middle caudal centra (C180).

11. Middle caudal centra lack an anteroposteriorly elongate ridge situated at approximately two-thirds of the way up the lateral surface (C183).
12. Hyposphenal ridge is block-like in anterior caudal neural arches (C188*).
13. First caudal rib with prominent ventral bulge (C202*).
14. Anteroposteriorly flattened and V-shaped first chevron, with dorsoventrally reduced distal blade (C207*).
15. Sternal plate with an elliptical shape in dorsal view, with a mildly or strongly concave lateral margin (C221*).
16. Preacetabular process of ilium has a semicircular, or rounded outline, such that it does not continue to taper along its anterior-most portion (C246*).
17. Highest point on the dorsal margin of the ilium occurs anterior to the anterior margin of the base of the pubic process (C248*).
18. Pubic obturator foramen, in lateral view, is oval or elliptical, with long axis orientated in same plane as long axis of pubis (C250*).

*Brachiosauridae*

1. Humerus to femur proximodistal length ratio is greater than 0.9 (C40*).
2. Minimum mediolateral width divided by proximodistal length of humerus is less than 0.15 (C42*).
3. Ratio of anteroposterior length of ischial proximal plate to ischium proximodistal length is 0.25 or less (C61*).
4. Ratio of anteroposterior length of iliac peduncle of ischium to anteroposterior length of ischial proximal plate is 0.7 or greater (C62*).
5. Tooth serrations/denticles present (C113*).
6. Maxillary teeth are twisted axially through an arc of 30–45° (C114*).
7. Dorsal centra possess ventral keel (C142*).
8. Anterior–middle dorsal diapophyses are elongate and dorsoventrally narrow (C154*).
9. Anterior dorsal neural spines dorsoventrally taller than posterior dorsal neural spines (C158*).
10. Spinopostzygapophyseal lamina (SPOL) divided into medial and lateral branches in middle-posterior dorsal neural spines (C165).
11. Infraglenoid lip absent from ventral margin of coracoid (C220*).
12. Metacarpal IV has a prominent proximolateral projection that wraps around the dorsal (anterior) face of metacarpal V (C241*).
13. Femoral fourth trochanter visible in anterior view (C258*).

*Somphospondyli*

1. More than 15 cervical vertebrae (C14*).
2. Maximum mediolateral width to minimum mediolateral width ratio of anterior caudal neural spines is less than 2.0 (C34*).
3. Distal end of radius bevelled at least 20° to long axis of shaft (C49*).
4. Ratio of dorsoventral width across the ischial distal shaft to ischium proximodistal length is 0.2 or greater (C63).
5. Anteroposterior length ratio of tibial to fibular femoral distal condyles is 1.2 or greater (C66).
6. Mediolateral width to maximum anteroposterior length ratio of astragalus is less than 1.5 (C71).
7. Metatarsal I to metatarsal V proximodistal length ratio is less than 1.0 (C72*).
8. Medial plate-like projections of the maxillary ascending processes do not contact each other on the midline (C78*).
9. Medial convexity on frontal in dorsal view (C83*).
10. Foramen/foramina present between basal tubera and basipterygoid processes (C99*).
11. Lower tooth crowns smaller than upper tooth crowns (C107*).
12. Posterior centrodiapophyseal lamina (PCDL) expands and bifurcates towards its ventral tip in middle-posterior dorsal neural arches (C151*).
13. Middle-posterior dorsal neural spines with absent or weakly developed triangular aliform processes (C163).
14. Sacral vertebrae with camellate internal tissue structure (C172*).
15. Posterior articular surfaces of middle-posterior caudal centra convex (C184*).
16. Biconvex distal caudal centra (C186*).
17. Scapular glenoid surface deflected to face anteroventrally and medially (C213*).
18. Humeral proximolateral corner 'squared' (C223*).
19. Tibia lacks a 'second cnemial crest' (C261).
20. Tuberosity on ventral margin of pedal unguals (C278*).

*Euhelopodidae*

1. Posterior articular face mediolateral width to dorsoventral height ratio of middle-posterior dorsal centra is less than 1.0 (C22*).
2. Dorsoventral height of posterior dorsal neural spines divided by posterior centrum dorsoventral height is less than 1.0 (C23).
3. Six or more sacral vertebrae (C24*).
4. Epipophyses on cervical neural arches extend beyond the posterior margin of the postzygapophyses (C128*).
5. Intrapostzygapophyseal lamina projects beyond the posterior margin of the neural arch in middle-posterior cervical vertebrae (C131*).

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6. Postaxial cervical and anterior dorsal neural spines bifurcated (C132*).
7. Posterior-most cervical and anterior dorsal neural spines are 'trifid' (C138*).
8. Distal end of middle-posterior dorsal diapophyses is set off from the remaining dorsal surface by a lip, forming a distinct area (C156*).
9. Posterior margin of the dorsal part of the scapular acromial plate concave (C214*).
10. Subtriangular process at anteroventral corner of scapular blade (C216*).
11. Metatarsal II distal articular surface extends prominently up onto the dorsal surface (C274*).

*Titanosauria*

1. Average elongation index of middle caudal centra is 1.4 or higher (C29*).
2. Anteroposterior to mediolateral width ratio of the iliac articular surface of the pubis is 2.0 or greater (C58*).
3. Ratio of dorsoventral width of distal end of ischial shaft to minimum shaft dorsoventral width is less than 1.5 (C64*).
4. Lateral surfaces of postaxial cervical centra lack an excavation or have a shallow fossa (C122*).
5. Lateral pneumatic foramina in dorsal centra are shallow fossae or excavations that do not ramify throughout the centrum (C144*).
6. Lateral pneumatic foramina in dorsal centra are set within a lateral fossa (C145*).
7. Small, shallow vascular foramina pierce the lateral and/or ventral surfaces of anterior–middle caudal centra (C180).
8. Distinct ventrolateral ridges, extending the full length of the centrum, in anterior–middle caudal vertebrae (C182).
9. Prespinal and postspinal laminae form distinct mediolaterally narrow ridges or laminae in anterior caudal neural spines (C197).
10. Humeral deltopectoral crest extends medially across the anterior face of the humerus (C225*).
11. Acetabular margin of ischium is strongly concave in lateral view, such that the pubic articular surface forms an anterodorsal projection (C252*).
12. No emargination of ischium distal to pubic articulation (C253).

*Lithostrotia*

1. Mediolateral width of basal tubera to occipital condyle mediolateral width ratio is 1.5 or greater (C8*).
2. Slenderness index values of tooth crowns are 4.0 or greater (C11*).
3. Posterior cervical neural arch to centrum dorsoventral height ratio is less than 0.5 (C18*).
4. Mediolateral width to dorsoventral height ratio of posterior caudal centra is 1.2 or greater (C30*).
5. Maximum length of sternal plate to humerus proximodistal length ratio is 0.65 or greater (C39*).
6. Metacarpal I to metacarpal II or III proximodistal length ratio is 1.0 or greater (C54*).
7. Mediolateral width of distal end of tibia to long axis of a cross-section horizontally through the midshaft ratio is 2.0 or greater (C67*).
8. Paroccipital process with ventral non-articular process (C96*).
9. Teeth with high-angled planar facets (C105).
10. Cylindrical tooth crowns (C109*).
11. Tooth crowns with convex lingual surface (C110*).
12. Apicobasally orientated lingual ridge absent from tooth crowns (C111*).
13. Hyposphene–hypantrum system absent in middle-posterior dorsal neural arches (C149).
14. Distal end of middle-posterior dorsal diapophyses is set off from the remaining dorsal surface by a lip, forming a distinct area (C156*).
15. Middle-posterior dorsal neural spines project strongly posterodorsally, with summit approaching level of diapophyses (C164*).
16. Sharp-lipped spinodiapophyseal fossa in anterior-most caudal neural spines (C194).
17. Middle-posterior chevrons lack a posterior expansion of the distal blade (C211*).
18. Prominent posterolateral expansion of sternal plate produces a 'kidney'-shaped profile in dorsal view (C222*).
19. Anterior surface of distal lateral condyle of humerus is undivided (C227).
20. Prominent ulnar olecranon process, projecting well above proximal articulation (C233*).

## APPENDIX 5

### SYNAPOMORPHIES OF HIGHER TAXA BASED ON THE LCDM MATRIX

Ambiguous character support is indicated by an asterisk. Only synapomorphies based on qualitative characters (C75–279) are presented.

*Macronaria*

1. Posterior end of prefrontal broadly rounded or 'square' in dorsal view (C82*).
2. Deep excavation in the posterior surface of the quadrate (C91*).
3. External mandibular fenestra absent (C102*).
4. Tooth rows restricted anterior to orbit (C104*).
5. Ventral midline keel absent in postaxial cervical centra (C120).
6. Lateral pneumatic foramina have acute posterior margins in anterior dorsal centra (C146).

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7. Anterior articular faces of middle-posterior dorsal centra are strongly convex, with degree of convexity approximately consistent along the dorsal sequence (C147).
8. Middle-posterior dorsal neural spines flared distally with triangular aliform processes projecting laterally from the top (C162*).
9. Infraglenoid lip present on ventral margin of coracoid (C220*).
10. Metatarsal I lacks a prominent ventrolateral expansion along its distal half (C272*).
11. Lateral margin of metatarsal II is straight in proximal view (C273*).

*Titanosauriformes*

1. Posterior margin of jugal excluded from articulation with quadratojugal (C81*).
2. Palatobasal contact for basipterygoid articulation lacks a dorsomedially orientated 'hook'- or 'finger'-like projection (C93*).
3. Fossa/fossae on the posterior surface of the basal tubera (C98*).
4. Tooth crowns aligned along jaw axis, crowns do not overlap (C106*).
5. Posterior centroparapophyseal lamina (PCPL) present as a single lamina in middle-posterior dorsal neural arches (C148*).
6. Spinopostzygapophyseal lamina (SPOL) divided into medial and lateral branches in middle-posterior dorsal neural spines (C165*).
7. Lateral pneumatic foramina or very deep depressions present in sacral centra (C173*).
8. First caudal rib with prominent ventral bulge (C202*).
9. Anteroposteriorly flattened and V-shaped first chevron, with dorsoventrally reduced distal blade (C207*).
10. Anteromedial process of ulna slopes downwards at an angle less than 40° (C235).
11. Preacetabular process of ilium has a semicircular, or rounded outline, such that it does not continue to taper along its anterior-most portion (C246*).
12. Highest point on the dorsal margin of the ilium occurs anterior to the anterior margin of the base of the pubic process (C248*).
13. Posterior margin of astragalus lacks a tongue-like projection posteromedial to the ascending process (C269).
14. Medial surface of the proximal portion of metatarsal IV is concave, for reception of metatarsal III (C275*).

*Brachiosauridae*

1. Parietal lacks an elongate posterolateral process (C84*).
2. Anterior ramus of quadratojugal possesses a ventral triangular projection (C90*).
3. Degree of divergence of basal tubera extends into dorsal half of basal tubera (C97*).
4. Maxillary teeth are twisted axially through an arc of 30–45° (C114*).
5. Anterior–middle dorsal diapophyses are elongate and dorsoventrally narrow (C154*).
6. Anterior dorsal neural spines dorsoventrally taller than posterior dorsal neural spines (C158*).
7. Middle-posterior dorsal neural spines with strongly developed triangular aliform processes so that the lateral tips of these processes extend further laterally than the postzygapophyses (C163*).
8. Lateral pneumatic fossae or foramina present in anterior caudal centra (C178).
9. Lateral pneumatic fossae or foramina in anterior caudal centra lack sharply defined margins (C179*).
10. Small, shallow vascular foramina absent from lateral and/or ventral surfaces of anterior–middle caudal centra (C180).
11. Area situated posterior to the scapular acromial ridge forms a separate excavated area (C212*).
12. Infraglenoid lip absent from ventral margin of coracoid (C220*).
13. Metacarpal IV has a prominent proximolateral projection that wraps around the dorsal (anterior) face of metacarpal V (C241).
14. Distal end of metatarsal IV bevelled to face medially (C276).

*Somphospondyli / Titanosauria*

1. Prespinal lamina present in posterior-most cervical and anterior dorsal unbifurcated neural spines (C137*).
2. Lateral pneumatic foramina in dorsal centra are set within a lateral fossa (C145).
3. Middle-posterior dorsal diapophyses are directed strongly dorsolaterally at approximately 45° to the horizontal (C155*).
4. Prespinal and postspinal laminae in middle-posterior dorsal neural spines form distinct mediolaterally narrow ridges or laminae (C167*).
5. Sacral vertebrae with camellate internal tissue structure (C172*).
6. Biconvex distal caudal centra (C186).
7. Prezygapophyses switch from projecting anterodorsally, anteriorly, and back to anterodorsally along the sequence in anterior–middle caudal neural arches (C191).
8. Distance that prezygapophyses extend beyond the anterior margin of the centrum in middle-posterior caudal neural arches is 20% or greater of centrum length (excluding ball) (C193).

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9. Area situated posterior to the scapular acromial ridge is flat or convex (C212*).
10. Rectangular cross-sectional shape at base of scapular blade (C217).
11. Sternal plate with an elliptical shape in dorsal view, with a mildly or strongly concave lateral margin (C221*).
12. Humeral proximolateral corner 'squared' (C223).
13. Distal-most part of the posterior surface (supracondylar fossa) of humerus deeply concave between prominent lateral and medial vertical condylar ridges (C228*).
14. Tibia lacks a 'second cnemial crest' (C261*).
15. Proximal end of fibula forms an anteromedially directed crest (C262).
16. Shaft of fibula sigmoidal in lateral view (C264).
17. Tuberosity on ventral margin of pedal unguals (C278).

*Andesauroidea*

1. Spinodiapophyseal laminae divided into anterior and posterior branches in posterior-most cervical and anterior dorsal neural arches (C136).
2. Dorsal neural spines narrow dorsally to form a triangular shape in lateral view, with the base approximately twice the width of the dorsal tip (C159).
3. Postspinal lamina absent along proximal (lower) half of neural spine in middle-posterior dorsal vertebrae (C169).
4. Dorsal portions of at least sacral neural spines 1–4 fused, forming a dorsal 'platform' (C174).
5. Hyposphenal ridge absent in anterior caudal neural arches (C187).
6. Subtriangular process at posteroventral corner of scapular acromial plate (C215).
7. Articular surface of anteromedial process of ulna concave (C234).

*'Titanosauroidea'*

1. Medial convexity on frontal in dorsal view (C83*).
2. Lower tooth crowns smaller than upper tooth crowns (C107*).
3. Distinct mesial and distal carinae along the full tooth crown length (C112).
4. Postaxial cervical and anterior dorsal neural spines bifurcated (C132*).
5. Distal end of middle-posterior dorsal diapophyses is set off from the remaining dorsal surface by a lip, forming a distinct area (C156*).
6. Anterior dorsal neural spines project posterodorsally (C160*).
7. Distinct ventrolateral ridges, extending the full length of the centrum, in anterior–middle caudal vertebrae (C182).
8. Posterior articular surfaces of middle-posterior caudal centra convex (C184).
9. Anterior caudal neural spines project dorsally (C195).
10. Posterior margin of the dorsal part of the scapular acromial plate concave (C214*).
11. Metatarsal II distal articular surface extends prominently up onto the dorsal surface (C274*).
12. Medial surface of the proximal portion of metatarsal IV straight or convex (C275*).

*Euhelopodidae*

1. Parapophyses unexcavated in postaxial cervical centra (C121).
2. Dorsal surfaces of middle-posterior cervical centra parapophyses deflected to face strongly dorsolaterally, such that the cervical ribs are displaced ventrally at least the same height as the centrum (C124).
3. Lateral pneumatic foramina in dorsal centra are shallow fossae or excavations that do not ramify throughout the centrum (C144*).

*Lithostrotia*

1. Ventral midline keel absent in postaxial cervical centra (C120*).
2. Postaxial cervical and anterior dorsal neural spines unbifurcated (C132*).
3. Spinodiapophyseal laminae divided into anterior and posterior branches in posterior-most cervical and anterior dorsal neural arches (C136*).
4. Lateral pneumatic foramina in dorsal centra are shallow fossae or excavations that do not ramify throughout the centrum (C144*).
5. Hyposphenal ridge present in anterior caudal neural arches (C187).
6. Sharp-lipped spinodiapophyseal fossa in anteriormost caudal neural spines (C194).
7. Humeral deltopectoral crest extends medially across the anterior face of the humerus (C225).

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Appendices S1–S3.** MESQUITE files.

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